Rice Science: Innovations and Impact for Livelihood

Edited by T.W. Mew,
D.S. Brar, S. Peng,
D. Dawe, and B. Hardy

IRRI
CAE

Rice Science: Innovations and Impact for Livelihood

Edited by T.W. Mew,
D.S. Brar, S. Peng,
D. Dawe, and B. Hardy

2003
IRRI

The International Rice Research Institute (IRRI) was established in 1960 by the Ford and Rockefeller Foundations with the help and approval of the Government of the Philippines. Today IRRI is one of 16 nonprofit international research centers supported by the Consultative Group on International Agricultural Research (CGIAR – www.cgiar.org).

IRRI receives support from several CGIAR members, including the World Bank, European Union, Asian Development Bank, International Fund for Agricultural Development, Rockefeller Foundation, and agencies of the following governments: Australia, Belgium, Canada, People's Republic of China, Denmark, France, Germany, India, Islamic Republic of Iran, Japan, Republic of Korea, The Netherlands, Norway, Philippines, Portugal, Sweden, Switzerland, Thailand, United Kingdom, United States, and Vietnam.

The responsibility for this publication rests with the International Rice Research Institute.

Mailing address: DAPO Box 7777, Metro Manila, Philippines
Phone: +63 (2) 580-5600,845-0563,844-335 1 to 53
Fax: +63 (2) 580-5699, 891-1292, 845-0606
Email: irri@cgiar.org
Home page: www.irri.org
Riceweb: www.riceweb.org
Riceworld www.riceworld.org
Courier address: Suite 1009, Pacific Bank Building
6776 Ayala Avenue, Makati City, Philippines
Tel. (63-2) 891-1236, 891-1174, 891-1258, 891-1303

Suggested citation:
Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Cover design: Juan Lazaro IV
Print production coordinator: George R. Reyes
Page makeup and composition: Arthur V. Africa
Figures and Illustrations: Graphoteknik Enterprises
Cover photos: Gene Hettel and Ariel Javellana

ISBN 971-22-01848

We dedicate this book to Gurdev S. Khush,
whose work, with many collaborators,
has provided more rice for millions.

Contents

Genomics

Molecular markers

Biology of developmental and physiological traits

Enhancing nutritional quality

Integrated crop management

Climate change and photosynthesis

Mechanization and nonfood use of rice

Poverty alleviation

Natural resource management

Trade liberalization

Foreword

Rice helps feed almost half of the world's population on a daily basis, employs tens of millions in jobs they cannot live without, and has an enormous impact on our environment. Rice production has been described as the world's single most important economic activity—more than two billion of our poorest people depend on it for their daily food requirement. But, for those who live in Asia, rice means even more. For many, it has helped form the basis of their culture, has influenced traditions and customs, and is a source of great national pride. Most important of all, rice is the one thing that ties Asia together. The world's most populous region shares no common religion, no common political system, no common set of cultural values, and no common physical appearance. The one thing that Asia does share is rice.

In recognition of rice's crucial importance to the world's poor and hungry, IRRI has organized the International Rice Research Conference (IRRC) every two years for almost four decades as part of its efforts to ensure that rice farmers and consumers have access to the new technologies and options that can help improve their lives. However, the world's rice industry has changed enormously since the first IRRC was held in 1968. Now, many more stakeholders in rice production are from countries that are far more developed—all of them with better knowledge, greater interest, and many more demands. No longer does a simple scientific conference seem enough to fairly represent the interests of rice producers and consumers who, while they still come from poor, deprived communities, live in a completely different world.

Because of this, IRRI worked with a range of partners to expand the IRRC into the world's first major event for all those involved in the rice industry. The First International Rice Congress was held in Beijing (16-20 September 2002) and was organized by the International Rice Research Institute (IRRI), the Chinese Academy of Engineering (CAE), the Chinese Academy of Agricultural Sciences (CAAS), and the State Development Planning Commission of China, with strong support from China's Ministry of Agriculture. The Congress, billed as the "first comprehensive event for the world's most important crop," had simultaneous conferences and exhibitions based on the challenging themes of "innovation, impact, and livelihood." The International Rice Congress's simple aim was to make sure that rice production continued to get the recognition it deserves both in Asia and internationally. But we also wanted to make sure that we paid more attention to the world's millions of poor rice farmers and consumers. We believe that we achieved this objective through the various events, including the inauguration speech delivered by Chinese President Jiang Zemin and the roundtable meeting of 13 ministerial representatives from all of the world's major rice producers, that occurred during the Congress, together with the scientific program in which many of the world's most renowned scientists participated.

This publication is the proceedings of the 24th International Rice Research Conference, the scientific program of the first International Rice Congress. It contains the selected papers presented during the 24th IRRC, along with President Jiang Zemin's opening address and some keynote speeches. The selected papers are the latest in cutting-edge rice research represented by some of the world's most distinguished agricultural scientists.

We dedicate this book to the world's thousands of rice researchers from the developing and developed world. Without their dedicated efforts in research and development, it would be impossible to maintain rice production at its current level despite the continuing population growth.

RONALD P. CANTRELL
Director General
IRRI

SHEN GUOFANG
Vice President
Chinese Academy of Engineering

ZHAI HUQU
President
Chinese Academy of Agricultural Sciences

LIUJIANG
Vice Minister
State Development Planning Commission, China

Acknowledgments

The success of the International Rice Congress in general and the 24th IRRC in particular would not have been possible without the devoted efforts and assistance of so many people. It is almost impossible to acknowledge some individuals without missing others; therefore, we are not mentioning specific persons. Nonetheless, we especially wish to acknowledge the assistance of our colleagues from the International Rice Research Institute (IRRI), the Chinese Academy of Engineering (CAE), and the Chinese Academy of Agricultural Sciences (CAAS). Without their help in all aspects of the development and preparation of the Rice Congress and IRRC, we would not have had a successful and smooth operation of these events. Specifically, we want to thank the members of the Secretariat of the Congress and the staff of the IRRI-China Office, the Department of International Cooperation of CAAS, the Department of International Cooperation of CAE, the Division of Agriculture, Light Industry, Textiles, and Environmental Engineering of CAE, and the International Professional Exchange of China's International Conference Center for Science and Technology for their work throughout. For preparation of the proceedings, we wish to thank the personnel in IRRI's Communication and Publications Services and researchers who helped review some papers. And, to the authors of all the papers, we thank you for your kind cooperation.

Welcoming address

Honorable Jiang Zemin
President, People's Republic of China

The inaugural International Rice Congress opens ceremoniously in Beijing today. First of all, I would like to extend, on behalf of the Chinese Government and in my own name, a cordial welcome to our guests from various circles and warm congratulations to the Congress.

Rice is a main staple food for most people in the world and the crop with the longest history of cultivation. More than 90% of the world's rice is produced in Asia, and 2.5 billion people depend on it for their food. Rice occupies an important position in the agricultural development, history, and civilization of Asian nations. It is of important significance that scientists, entrepreneurs, government officials, and representatives of international agencies from all over the world gather here to discuss rice-related topics and its research and development, promotion, production, trading, management, and international cooperation.

The fast scientific and technological progress over the past century has forcefully promoted the development of productive forces and the improvement of people's living conditions. The advances in material science, life science, information science, space science, ocean science, environmental science, and in other realms have enabled human beings to unveil the mystery of nature continuously and have provided new knowledge, new concepts, new theories, and new methods. The scientific and technological revolution in agriculture, brought about by new scientific and technological developments, has greatly boosted agricultural production globally, particularly grain production, and strengthened the capacity of developing countries for grain production. This has laid an important foundation for economic growth and social stability for all countries, the developing countries in particular. It has also created favorable conditions for improving the patterns of food supply and demand in the world and easing the pressure of population growth on the environment and natural resources.

However, we must be aware of the new challenges facing world agriculture. The problem of global food security remains unsolved. The increase in population means a growing demand for food in the world, whereas the essential factors in food production such as cultivated land and freshwater are decreasing continuously. For many countries and regions, food is still a problem that cries out for a fundamental solution. About 800 million people still suffer from malnutrition across the world. These problems and challenges call for closer cooperation among governments and visionaries from all walks of life to seek a solution together.

A review of world agriculture shows that it is imperative to find a scientific and rational way to develop it, a way that can not only steadily increase output but also ensure the long-term sustainable use of resources in the process of promoting agricultural development. This way can both help meet people's daily needs and give more economic returns to farmers. Agriculture can thus make a greater contribution to economic and social development globally in the 21st century.

To this end, it is important to strengthen international cooperation and exchanges in agriculture so that people worldwide can share the results of scientific and technological advances and achieve common development. This is the very purpose of this Congress in the first place.

Since the late 20th century, a new revolution in agro-science and technology has been developing. This will bring profound changes to agriculture in concept, structure, function, and system, thus effectively pushing agriculture toward becoming a modernized industry. Now, a major breakthrough has been made in international joint research on plant genomics as represented by rice-related research. In this grand international cooperation, Chinese scientists independently completed and took the lead in publicizing the rice genome working draft and the draft sequence of the indica rice genome. These achievements and the findings of emerging functional genomics are common assets of humanity and should serve all people. Above all, the developing countries should be ensured of equal opportunities to use the results and technologies of research in this regard.

The international community should cherish the development opportunity brought about by scientific and technological advances. Developing countries should seize the opportunity and actively participate in the process to promote national economic and social development. Developed countries should be keenly aware of the effects of the widening North-South wealth gap on world stability and sustainable development and they should provide more assistance to the developing countries in technology, funds, human resources, and information.

China has a long history of agricultural civilization. Archaeological studies indicate that, more than 7,000 years ago, our ancestors of the Chinese nation had already created the brilliant Yangshao culture and Hemudu culture, thus ushering in the dawn of the agricultural civilization we know of. Since the founding of the People's Republic of China, Chinese scientists have, mainly by depending on their own strength, conducted research on breeding dwarf rice varieties in parallel with the international Green Revolution. Breakthroughs have been made, resulting in plenty of high-yielding rice varieties. Since the early 1970s, Chinese scientists have creatively developed the theory of cultivating improved seeds in rice cross-breeding and have invented and improved the technology of selecting and cultivating seeds for cross-breeding, which has been extensively applied. Scientific and technological progress have played an important role in enhancing agricultural production and overall productivity. This is evidenced by the increase in annual grain yield from 200 million tons in the early 1960s to 500 million tons now. China has managed to feed 22% of the world's population with less than 10% of the world's arable land. Now, the 1.2 billion and more Chinese people have sufficient food and clothing and by and large lead a well-to-do life. China has made its contribution to world grain production and food security.

Despite the remarkable achievements in agriculture, China remains a large agricultural country with a big population, scarce land and water, and insufficient per capita resources. These are our basic national conditions. The major problems that call for our redoubled efforts to tackle remain how to effectively upgrade the quality and efficiency of agricultural production and press ahead with the structural readjustment needed to achieve agricultural modernization.

So that all countries can enjoy the benefits of scientific and technical advances and achieve common development, it is essential that all governments and people, scientists in particular, work together and make joint efforts. China's fruitful exchanges and cooperation with the world rice science community over the decades prove that it is in the interest of the development of all participants and the world to conduct scientific and technological exchanges and cooperation among countries with different cultural traditions, economic modes, and development levels. We stand for active international cooperation based on the principles of equality and mutual benefit, sharing of achievements, and respect for intellectual property rights. We encourage closer research and development cooperation between Chinese scientists and their foreign counterparts, with a view to contributing to common development and universal prosperity for all countries.

It is the common aspiration of people of all countries to lead a happy life. To promote the lofty cause of peace and development of mankind and to help all poverty-stricken people deliver themselves from their predicament as soon as possible, world agricultural production must reach a new high and agricultural science and technology must make new breakthroughs. This calls for unremitting efforts by all agricultural scientists and technicians as well as extensive support from all countries. We hope that this Congress will instill new vitality in the development of world agricultural science and technology.

I wish the Congress complete success and our guests an enjoyable stay in China.

Thank you.

Sustaining food security

Jian Song

I would like to begin by expressing, on behalf of the scientific community of China and the sponsoring institutions, my heart-felt thanks to you, President Jiang Zemin, for being with us today. I would also like to extend our warmest welcome to the scientists and guests coming here from all over the world.

It is a glorious task and sacred mission of the scientific community, especially the agricultural scientific community, to secure our food supply and to improve human nutrition. Rice is one of the primary staple foods that sustain human life, accounting for 23% of the world's total crop area and 29% of the world's total grain output. The number of people living on rice is expected to reach 3.5 billion in 2025, according to projected population growth. It is therefore a crucial task in the 21st century for the scientific community to enhance rice research and the development of related technologies.

China is an ancient agrarian country. Since the People's Republic was founded in 1949, China has given top priority to agriculture and rural development. As a result, China has succeeded in sustaining 22% of the world population with only 9% of the world farmland. In the past 20 years, China's population has increased by 270 million, but the per capita grain supply has increased from 300 to 400 kilograms. The Chinese agricultural science community has won respect and praise from its whole populace for this and for its historic contribution to the food security of 1.27 billion people.

China has a long history of rice cultivation. Archaeological findings prove that cultivation of rice began as early as 7,000 years ago. Because of the ceaseless efforts of agricultural scientists and agronomists, China has witnessed a continuous upgrading of rice varieties and a fast advancement in farming practices. Total output and yield per hectare have both continued to increase.

China has now become the world's biggest rice producer and consumer, accounting for 20% of the world's total rice area and 31% of the world's total production. Yield per hectare in China is 1.6 times that of the world average. In 2000, China's total rice yield amounted to 190 million tons, 46.4% of the country's total crop yield. The successful development of hybrid rice, a major breakthrough in

China's rice production, has opened a new way to markedly increase rice yield, and this made China the first country to popularize hybrid rice nationwide. In recent years, hybrid rice has accounted for more than half of the rice land and 60% of the total rice output in China. Chinese scientists and agronomists made this significant contribution to the Chinese people.

Now, up to 800 million people in the world are still hunger-stricken because of insufficient food supply. As many as 14 million children under age 4 die of hunger every year. The world population is expected to reach 9 billion in the mid-21st century from the 6 billion now. The Chinese population will stabilize at a peak of 1.6 billion in 30 years' time. The scientific community, especially the agronomic community, is duty-bound to secure the world's food supply.

Our Congress today is a comprehensive event, composed of sessions on scientific research, technology exchange and exhibition, and trade activities. It will provide the Chinese scientific community with an excellent opportunity for technological exchange and international cooperation. I am convinced that, with our joint efforts, the Congress will yield rich fruits in various fields and play a major role in promoting world rice agriculture and related technologies for the 21 st century.

May our Congress be a complete success!

Notes

Author: Jian Song is vice chairman of the Chinese People's Political Consultative Conference.

Supporting rice research in Asia

Angeline Kamba

Rice supplies about half of the calories and protein consumed every day in Madagascar, not far from my home in Zimbabwe. At the other end of the continent, in West Africa, along the coast from Mauritania and Senegal down to Côte d'Ivoire, rice supplies from 20% to 40% of people's calories and protein.

Asians and Africans share a common feature: rice. Ninety-two percent of the world's rice is grown and consumed in Asia. The poor in Asia typically depend on rice for at least two-thirds of their calories and some 60% of their protein. So, anything that helps make rice farming more productive and profitable improves nutrition and public health and alleviates poverty, both in the countryside and in the cities.

The last four decades have seen remarkable progress. Rice production in Asia has grown an impressive 170% since 1961—somewhat faster than population growth—without taking up much more land. And the real, inflation-adjusted price of rice has dropped by 40%.

Still, 70% of the world's 1.3 billion poor people live in Asia. Malnutrition continues to plague the continent. This is especially so in South Asia, where malnutrition appears to affect a substantially larger share of the population than in sub-Saharan Africa.

Much remains to be done and much can be done. Advances in molecular biology and genomics—in particular the sequencing of the genome, or genetic makeup, of rice—are putting powerful tools into the hands of agricultural scientists. These tools can leverage past successes to root out the ancient scourges of hunger, malnutrition, and poverty.

But here is the irony: at this pivotal moment, many donors' long-standing commitment to publicly funded agricultural research appears to be faltering. Why? Bountiful harvests and low food prices—the legacy of the Green Revolution since the 1960s—have sown complacency toward publicly funded agricultural research and assistance. Funding cuts have been dramatic.

- The United Nations' Food and Agriculture Organization calculated in 1996 that international assistance to agriculture in developing countries stood at less than US$10 billion per year in 1994, little more than half of the nearly $19 billion in assistance offered in 1986.

- Funding directed by the United States Agency for International Development toward agricultural research in less-developed countries declined by 75% from the mid-1980s to 1996. In that period, Asia suffered the steepest losses, as its share of USAID annual funding plunged from around $57 million to a mere $1.4 million.
- The CGIAR (Consultative Group on International Agricultural Research), a global association of 16 research centers and their donor governments, agencies, and foundations, in 2000 spent $305 million, 10% less than the $338 million it spent in 1990.
- Total funding for IRRI has been on a downward trend since 1993, when funding peaked at $44.5 million. This trend accelerated in 2000. Funding will plunge from $33.8 million in that year to $19.7 million in 2004, when the full force of a recent halving of a major donor's support for the CGIAR takes effect. That's a drop of 42% in four years.

How do we cope? One attractive option for cash-strapped publicly funded rice researchers is cooperation with the private sector. Private-sector investments in agricultural research have risen rapidly over the past several decades. By the mid-1990s, about one-third of the $33 billion total annual investment in agricultural research worldwide was private.

However potentially fruitful public- and private-sector collaboration may be, putting it into practice is a delicate balancing act. The problem hinges on what can rightfully be made private, and what must remain public. Where do we draw the line between protecting intellectual property and protecting public goods from restrictive patents?

This is a thorny question when applied to crops. The idea of patents on rice, in particular, draws unrelenting fire from those who abhor all so-called "patents on life." They fear that commercializing rice will subvert the right of farmers to grow the myriad traditional varieties their ancestors developed over millennia. And that poor farmers will lose access to the improved varieties that publicly funded research institutions have bred and distributed as public goods over the past few decades.

They roundly condemn private research on rice and public-private research partnerships. But they are silent on the question of how cash-strapped public research can move forward without private-sector participation.

The critics have a point. Whereas publicly funded research results are usually made freely available to poor farmers, the results of private research are deployed to maximize profits for the company that paid for them.

Another factor is where the research takes place. Thirteen of the 16 research centers of the CGIAR are located in developing countries, as are their national partners. Almost all private-sector research, in contrast, is conducted in developed countries.

But agricultural researchers must do more than provide finished products. They must train the national scientists that developing countries need to solve their own problems in agriculture, food security, poverty, and environmental protection. Conducting research in developing countries is the most practical, cost-effective way to include local agricultural scholars and scientists in the research process. It also taps the insights of people with firsthand knowledge of the needs of poor farmers in their countries.

We welcome the expertise and bountiful research budgets that the private sector can bring to bear in rice research. One of the goals of this Congress is to foster a spirit of cooperation between the public and private sectors. And IRRI is an attractive partner, given its 42 years of experience in rice research and its extensive contacts with other advanced research institutes and national partners.

These assets place IRRI in an excellent position to serve as the honest broker, or central clearinghouse, for collaborative rice research. So does its stewardship of the International Rice Genebank, the world's largest and most comprehensive storehouse of rice biodiversity.

But make no mistake. Privately funded research and public-private partnerships are no substitute, in the near term, for filling the yawning gap that has recently opened in public support for rice research.

Four decades ago, the threat of widespread famine galvanized the international community to fund the broad-based agricultural research initiative that became the Green Revolution. Throughout the second half of the 20th century, harvests kept pace with population growth, and global famine was averted. By some analysts' reckoning, it is now more remote a threat than it has been in modern times. But much work remains to be done to ensure long-term world food security, improve nutrition for the poor, boost rural incomes, and make agriculture cleaner and greener.

Today, the consequences of inaction appear to be less dire and immediate than in the 1960s. But complacency obscures the truly compelling reason for the international community to renew its commitment to agricultural research. Last time around, it was to forestall impending catastrophe. This time around, it is to seize unprecedented opportunity.

Thank you.

Notes

Author: The author is chairperson of the Board of Trustees of the International Rice Research Institute, Los Baños, Philippines.

Promoting Chinese rice production through innovative science and technology

Xu Kuangdi and Shen Guofang

The first-ever International Rice Congress has opened today in Beijing. On behalf of the organizing committee, we would like to extend our warm welcome to the experts, officials, and representatives from international organizations and various places all over the world.

Rice is a major grain crop. In recent years, its global planting area has been approximately 23% of the total of that of grain crops. The total rice output is approximately 29% of the total output of grain crops worldwide. Rice is planted in 122 countries around the world, most of which are developing countries. Rice produced in developing countries accounts for 95% of the world's total. About 90% of the planted area and total output is in Asia. Globally, approximately 50% of the people eat rice as their staple food. Of all the rice produced commercially, 90% is directly consumed as food by people. Therefore, this International Rice Congress has great significance for the sustainable development of world rice production and food security.

Rice is the most important grain crop in China. China is a large rice producer. From 1996 to 2000, the planting area of rice was 31.13 million ha on average, accounting for 20% of the world's total, second only to India. China's annual average rice output is 196.19 million tons, accounting for 35.26% of the world's total and ranking first in the world. China has a long history of rice cultivation. China is one of the centers of origin for rice. The ancestral species of *Oryza sativa, O. rufipogon,* has a very large distribution in China, from Sanya in Hainan Province in the south to Dongxiang in Jiangxi Province in the north, from Yingjiang in Yunnan in the west to Taoyuan in Taiwan in the east. There are more than 70 ancient sites of the New Stone Age where grains of rice, husked rice seeds, rice stalks, etc., have been unearthed. The earliest one was discovered in Luojiajiao of Tongxiang, Zhejiang Province (7050 ± 150 BC), and Hemudu of Yuyao, Zhejiang Province (6960 ± 130 BC). There are especially rich records of rice in ancient books. China has abundant rice resources. The distribution of rice in China spreads across five climatic zones: the tropical, subtropical, warm temperate, medium temperate, and cool temperate zones. The northernmost point for rice cultivation in the world is in China (i.e., Mohe in

Helongjiang Province, at 53°27’N). China has quite diverse ecological environments and especially abundant rice germplasm resources. By the end of 2000, 75,597 accessions of domestic rice resources had been put on China’s National List of Rice Resources, including 52,320 accessions of ancient local strains.

Ever since the founding of the People’s Republic of China, the Chinese government has given great importance to the production of grain and rice. With policy as the first measure, science and technology as the second, and inputs as the third, China has made a great achievement of producing 25% of the world’s total grain and feeding 22% of the world’s total population with only 7% of the world’s arable land. The total grain output has risen from 113.18 million tons in 1949 to 508.39 million tons in 1999, an increase of 4.5 times in half a century. The total output of rice has risen from 48.64 million tons in 1949 to 198.49 million tons in 1999, an increase of 4 times in half a century (the total rice output reached as high as 200.74 million tons in 1997). In the past two years, because of a structural adjustment in agriculture, the planted area of rice, especially that of early maturity species of indica (*hsien* rice), has decreased to a certain extent. But the total output has stabilized at more than 180 million tons, rice quality has improved, and the economy of the rice-producing areas has been booming.

Looking back on the development of food and rice production in China, the continuous increase in food and rice per unit area of yield is the major driving force for the overall constant increase in total output. Besides the adoption of a series of correct policies to fully promote farmers’ activity and increase inputs to capital construction on farmland to improve production conditions, the increase in yield mainly relies on research and extension of improved varieties and serial technologies for increasing yield, as well as progress and innovation in science and technologies for rice cultivation.

Science and technology lead to more productivity. Scientific and technological advances and innovation in agriculture brought about the first Green Revolution in the world, including in China, which helped China achieve the second breakthrough in rice breeding and prepare for the third, and have contributed to the continuous increase in China’s rice output, improvement of quality, and comprehensive development of the economy in rice-producing areas. This will promote a new scientific and technological revolution in agriculture.

Constant innovation in breeding technologies is the main route for developing science and technology in China’s rice cultivation

As early as the 1950s, the implementation of land reforms and a series of policies concerning rural areas greatly promoted farmers’ activity in developing agriculture and planting rice. Development of capital construction on farmland such as irrigation and water conservancy, the application of chemical fertilizers and pesticides, and improvements in farming systems and planting technologies provided advantageous production conditions for the development of rice. In the mid- and late 1950s, by using resources from both China and abroad as well as many new breeding methods, scientists all over China developed a large batch of high-yielding semidwarf varieties suitable for various regions, ecological and production conditions, and maturation periods, which were popularized in the mid-1970s. The yield of these semidwarf varieties increased by approximately 30% compared with that of the original high-stalk varieties. This brought about the first leap in rice yield in China.

In the 1970s, Chinese agricultural scientists went beyond the old belief that "rice is a self-pollinated crop and outcrossing does not generally demonstrate hybrid vigor." Guided by the theory of hybrid vigor, with exploitation of sterile cytoplasm as a breakthrough, and by using the backcross method to select sterile lines with nucleocytoplasmic interaction, indica (*hsien*) hybrid rice was developed successfully for the first time in China. In 1970, wild abortive cytoplasm was discovered. In 1973, the combination of three lines-cytoplasmic male-sterile lines, maintainer lines, and restorer lines—was realized. In 1974, the first indica hybrid rice with strong combinations was developed. In 1975, a set of technologies for hybrid seed production was developed. Since 1976, hybrid rice has been cultivated in large areas. China has become the first country in planting hybrid rice for commercial production. With joint coordination among research, production, and extension departments, hybrid rice combinations kept being upgraded and planting area kept expanding. In recent years, planting area has reached approximately 15 million hectares, with yield increasing by 15% to 20% compared with that of regular rice. This was the second leap in yield. During this period, conventional rice breeding also achieved some progress and a batch of high-yielding varieties with good quality and multiresistance was developed, forming a pattern of mutual promotion and advancement in research on hybrid rice and conventional rice, thus accelerating the development of China's rice breeding.

Since the 1980s, it has been recognized that, although improvements have been made in new hybrid combinations and conventional rice varieties in maturation, quality, and multiresistance, new breakthroughs have not been available in output potential. To ensure the sustainable development of food production and to provide technological reserves for development in the future, in the mid-1990s, China's "Super Rice" research program came into being. Chinese scientists promoted the technical method of using heterosis between indica and japonica (*keng*) subspecies to combine in the building of ideotype plants. By using two-way and three-way crosses to develop hybrid rice and homozygous rice, and by using conventional technologies with biological technologies in breeding programs, a set of new super high-yielding varieties such as Liangyoupeijiu, Xieyou 9308, Shennong 265, etc., has been developed and demonstrated in production. Output per hectare reached as high as 11 to 12 t. Now, work is under way to develop super rice varieties that can yield 15 t ha^{-1}. The third great leap in rice productivity is in progress.

Mutual promotion of improved varieties for the development of rice cultivation technologies in China

The breakthrough in rice breeding technologies and the success in developing excellent varieties have provided an internal foundation for advancing rice cultivation in China. The continuous improvement of the external environment, especially progress in planting technologies, has provided a guarantee for China's great leap in rice production. The combination of excellent land, systems, seeds, and methods is the summary of China's great leaps in grain production. The development of China's rice cultivation is a full demonstration of this successful experience. The breakthrough in rice breeding technologies facilitated the development of soil amelioration and fertilization, plant protection, irrigation and water conservancy, farming systems, and cultivation technologies as well as overall rice technologies, forming a set of accompanying technology with improved varieties as the center, thus enabling rice cultivation science and rice production to keep developing. Before the 1960s, China was still in an era of rice cultivation with high-stalk landraces. In cultivation technologies, methods summarized from mass experience were used in production. Some high-productivity experience developed by Chen Yongkang in the south and Cui Zhusong in the north was discovered, that is, "using good seeds and vigorous seedlings, planting few seedlings per hill with high density, rational fertilization, and frequent irrigation with shallow water." In the 1960s and 1970s, dwarf rice varieties were developed successfully and applied widely. They formed a technical mode of "vigorous seedlings, enough fertilizer, early germination, close planting, multiple panicles, and high productivity." After that, significant breakthroughs in hybrid rice breeding produced the radical revolution in cultivation and thus the model of "thin seeding but with vigorous seedlings, few seedlings but with big panicles" came into being as the core. In the 1980s, with the fast development in cultivation technologies, a series of new theories and new technologies emerged such as "wide spacing, few seedlings, and flat farmland" for producing 15 t ha^{-1} of grain, along with dry seeding, broadcasting, advances in the treatment of red and yellow soils, land improvement, wide application of fertilizer technologies, and the perfection and maturation of integrated pest management. All these acted as an important driving force for super rice breeding and its demonstration later, while facilitating the development of rice production, which made theoretical and technological preparations for the third great leap in rice production. In recent years, the comprehensive implementation of advanced cultivation techniques for high-quality rice and pollution-free production technologies has undoubtedly played a positive role in improving rice quality in China, thus providing technical support and guarantees for making Chinese rice accessible to international markets.

Only the establishment and perfection of an accompanying system for the conversion from technical innovations and results into practical productivity can propel productivity and the social economy. China has made it possible to build a powerful agricultural system for technical extension. Since the 1950s, seed stations, agricultural technology stations, soil and fertilizer stations, plant protection stations, veterinarian stations, and farm machine stations as the main body have been established at national, provincial, prefectural and county levels. Together with the local agricultural technical stations spread over all counties in the country, they have formed an extension network for agricultural technology and have played an important role in the extension of agricultural technology and the development of agriculture and grain production.

Thanks to the comprehensive development and continuous advancement of rice cultivation, rice yield and production have been increasing. Yield rose from 2 t ha^{-1} in 1961 to 3 t ha^{-1} in 1967, 4.0 t ha^{-1} in 1978, 5 t ha^{-1} in 1983, and 6.0 t ha^{-1} in 1995. Production rose from 53.642 million t in 1961 to 109.55 million t in 1970, 161.2 million t in 1982, and 200.73 million t in 1997.

Satisfying demand from production and markets is the essential target for developing rice cultivation technologies in China

China's rice cultivation technologies are closely connected with demand from rice production and markets. Before the mid-1980s, rice production in China focused on providing enough food to the people and on increasing the quantity of rice. Research on rice cultivation concentrated on the primary goal of how to increase total rice output. On the one hand, research on paddy-field farming system reforms was done to increase multiple cropping indices and, on the other hand, to satisfy society's demand for rice with research on the application of good seeds and methods to increase rice output.

Since the late 1980s till today, with the development of the national economy and elevation of people's living conditions, rice quality has received more and more attention. Rice production is gradually shifting from high yield to a combination of high yield with good quality, with emphasis on promoting the economic benefit of rice fields. Rice cultivation technologies in this period concentrate on research for adjusting varietal structure and optimizing plant structure. First is to select new varieties with high quality and for various purposes. According to statistics among high-quality rice varieties selected in recent years, approximately 10% have reached the Level 1 national standards for "quality rice" or the Level 1 standards for edible quality rice enacted by the Ministry of Agriculture. Some high-quality rice products after processing are comparable to the world-famous high-quality long-grain rice and high-quality japonica rice. Additionally, as some high-quality sterile lines have been selected, the technical barriers in high-quality breeding for hybrid rice have been preliminarily broken through, At the same time, some high-quality varieties have been developed especially for feed, the food industry, and wine making. Focusing on the promotion of high-quality rice varieties, research on good quality, high yield, and pollution-free planting technologies has been done in various places. The purpose is to further increase the quality of rice and food security. Second, research and development focus on simple planting technologies such as broadcasting and direct seeding for saving labor and costs. This will further promote labor productivity and lower labor intensity. Third, new rice-planting methods have been summarized in various areas, such as the rotation of rice with cash crops, fields being used to plant vegetables and herbal fruits in winter and spring and to plant rice in summer and autumn with fish-raising, and combining rice culture with poultry raising to further increase the benefit of the rice fields and promote the economic development of the rice-producing areas. After 20 years of opening and reforms as well as fast development, agriculture and the rural economy in China have entered a new stage. Comprehensive agricultural production capacity has grown by a large extent and the shortage of produce has basically ceased. Generally, people's lives have changed from having adequate food and clothing to having a comfortable life. In the new stage for agricultural development, the central task for agriculture and the rural economy is to raise farmers' income. Implementing a strategic adjustment for the agricultural structure is the essential way to increase farmers' income. Promoting the process of agricultural adjustment and improving the quality and benefits of agricultural and rural economic operations mainly depend on advances and innovations in agricultural science and technology.

Promoting the new revolution in agricultural science and technology to develop rice science and technology in China

China's strategic target of modernization is to catch up with the world's middle class in developed countries by the middle of the 21st century. China is a developing country and agriculture is the foundation of the national economy as well as the basic guarantee for people's health, economic prosperity, social stability, and national independence. Although China's agriculture has made achievements that have attracted the world's attention, it confronts new challenges. After the problem of product quantity has been basically solved, the problems of low-quality products, irrational agricultural structure, and low agricultural benefit have not been solved. The township enterprises have entered a key stage of structural adjustment and mechanism innovation. To increase farmers' income and to reduce employment pressure in rural areas have become an urgent task. The shortage of water resources, reduction in arable land, soil erosion, land desertification and environmental pollution, the relative surplus of farm products, and the problem of double constraints by resources and the market are becoming more severe. The problems of high cost, low comparative benefit, and weak competitiveness in the world still exist in agriculture, especially in grain production. Facing a population growth peak that will appear in the 21st century, a decline in per capita resource endowment, and the increase in people's requirements for life, if there is no strong development in agricultural science and technology, the problems concerning agriculture, rural areas, and farmers cannot be solved in China. Therefore, the essential path for the sustainable development of agriculture in the new stage is a new revolution in agricultural science and technology.

Developments in rice cultivation technology not only safeguard food security to a large extent but also lead to advances in agricultural science and technology. Rice is a cereal crop. The boost in research on hi-tech technologies in recent years has consolidated the foundation for the new agricultural scientific and technological revolution. In the field of biotechnology, a batch of new rice varieties have been developed through anther culture, somatic tissue culture, and the combination of tissue culture with radiation mutations. These varieties have spread over large areas. Through wide cross and anther culture, improved germplasm resources have been obtained by introducing positive genes of wild rice into cultivated rice. Significant progress has been made in research on gene mapping with important agronomic characters of rice, especially on the aspects of fertile genes, resistance genes, yield characters, and other quantitative genes. By using molecular markers as a supporting tool in breeding, some new varieties have been developed, tested, and demonstrated in production. By using transgenic technology, transgenic hybrid rice varieties with resistance to herbicide and *Bt* resistance to rice stem borer have been developed and released for environmental evaluation. Especially, the achievement of constructing the rice gene map and mapping of the indica rice genome will greatly facilitate research on rice and other crops at the molecular biological level. In information technology, computer networks develop fast and serve farmers. Expert agricultural systems for rice field management, fertilization, pest control, irrigation, and water conservancy have been established as well as databases for information on production and market trade. Additionally, remote sensing for rice yield estimation models and technologies for forecasting major rice diseases and pests have been tested.

For future innovations in rice science and technology, we shall focus on several aspects. First, we will combine regular technologies with biotechnology and radiation mutation technologies to enhance innovations in breeding materials and to breed new super rice varieties as well as new varieties for food, feed, and industry. Second, we will fully use the research results of rice gene sequence to study rice genomics, to exploit excellent resources, and to clone functional genes with China's own intellectual property rights. Third, we will conduct hi-tech research on mechanical intensification for rice cultivation, focusing on the technological integration of super rice and high-quality rice planting technologies, and to establish a standardized mode. Fourth, we will conduct detailed research on rice hulls, use new technologies to rebuild traditional industries, and increase the added-value and international competitiveness of rice and its products. Fifth, we will do research on precision rice cultivation to improve the ecological environment in rice fields by managing farming practices and applying fertilizer and pesticides. We will also conduct research on saving water in rice to facilitate the sustainable development of agriculture.

Of course, when we do research on scientific and technological innovations, we should establish a new system for agricultural innovations, a system for technical extension, and a system for social service to accelerate the conversion of research findings and to facilitate the development of rice production and cultivation science to higher levels.

The 21st century is an era for the development of our intellectual economy. To initiate a new revolution in agricultural science and technology and enhance the innovations in agriculture and rice cultivation will for sure move China's realization of agricultural modernization ahead of schedule and promote the development of agriculture and rice production in developing countries. The prospects are bright. Let's take advantage of this occasion to discuss and communicate with each other and to welcome mankind's beautiful future together.

Notes

Authors: Xu Kuangdi and Shen Guofang are President and Vice President of the Chinese Academy of Engineering, respectively.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Technological advances and social mobilization: walking on two legs to alleviate poverty

Fazle Hasan Abed

I feel honored to address the first International Rice Congress held in China, a great country that is showing the world the way to economic progress and poverty reduction under extreme population pressure on limited natural resources. It gives me great pleasure to share with you my thoughts on the challenges to alleviating hunger and poverty, the unfinished agenda of the 20th century.

The 20th century saw profound changes in many areas of human welfare. The production of staple food increased faster than population growth, defying Malthusian predictions to the contrary. Developments in transportation, communication, and information technology have turned the world into a global village, making it possible to communicate instantaneously with people on the other side of the globe. This has facilitated an intensive dialogue between North and South and between East and West to resolve differences emanating from variations in stages of development and cultural perceptions.

Politically, we have seen the end of colonialism and the increasing prevalence of democratic governance enshrining human rights and people's participation in activities that affect their livelihood. Advances in medicine and a greater understanding of diseases have led to longer life expectancy and enhanced quality of life for many.

The remaining challenges, however, are many. We have come to see the environment as an increasingly important and fragile partner in our lives. The threat of nuclear conflict endures and the use of biological weapons has become an increasingly frightening threat. Numerous armed conflicts and struggles for freedom continue as we speak, depriving people of their livelihood and sense of safety in their own homes and countries.

Numerous exercises sought to nominate the greatest thinker or most influential person of the 20th century. While these celebrations of humanity's achievements are not misplaced, we must also reflect on and come to terms with what we have failed to do. We must acknowledge these failures and posit them as the most pressing challenges for the future, placing them at the top of our agenda.

The most profound challenge of the 2 I st century, and our greatest failure of the 20th century, I believe, is our inability to alleviate poverty. It is a shame for all of us that, at the dawn of the 21st century, when we are able to produce enough food to feed the entire population of the world, 800 million people go to bed hungry and suffer from malnutrition, and one-fifth of humanity, about 1.2 billion people, lives on earnings of less than a dollar per day. Two-thirds of these people live in Asia, which has seen robust economic growth over the past 40 years. The advances in technology, communication, and medicine are rather irrelevant to these people, who struggle every day in an effort to make sure that their families can eat. They are denied opportunities for education and basic health care, which condemns another generation to struggle against all odds just to survive.

Those of us who have tried to grapple with the dilemma of poverty know that poverty is not an accident. It is not our lack of ability that has left this problem unsolved. Pervasive poverty is the outgrowth of a certain pattern of development and it reflects certain values and priorities. Poverty is the result of a complex interlinking of political, economic, and cultural systems that have a long history and are deeply entrenched. The poor are oppressed by a profound lack of opportunity to obtain the basic necessities of life.

Let me elaborate on the achievements, limitations, and challenges of two major efforts at alleviating poverty with which I have been associated. The first is the development and dissemination of improved agricultural technologies for the increased production of food, for which I am concerned as a member of the Board of Trustees of the International Rice Research Institute (IRRI). The second is the mobilization of disadvantaged groups of people to produce employment and income, and raise awareness of people's rights, roles, and responsibility in society. I have devoted my entire career to the second pursuit as the founder-president of the Bangladesh Rural Advancement Committee (BRAC). I consider these equally important means for reducing hunger and poverty.

I shall fail in my duty if I do not recognize the contribution made by scientists in the national agricultural research and extension systems as well as in the international research centers such as IRRI, many of whom are attending this Congress, in meeting the most basic human need, food. Despite the closing down of the land frontier, particularly in the densely settled countries in the most populous continent, Asia, the world did remarkably well in meeting the food needs of its fast-growing population during the last half of the 20th century. The phenomenal increase in agricultural productivity, made possible by the adoption of genetically improved varieties, has enabled many countries to increase food supplies faster than demand and to nullify the dire predictions of food insecurity and famine in land-scarce countries.

Technological progress has contributed to a decline in the unit cost of production, which enabled farmers to share the benefits of improved technologies with consumers by offering food to them at affordable prices. The long-run decline in the real prices of food was the major factor contributing to the moderate progress in poverty reduction over the past few decades. The scientists who developed these technologies and the extension workers who took them to the doorsteps of farmers should be proud of this achievement.

But we must not be complacent about that achievement. Although enough food is being produced today globally, the unequal access to food because of differences in land endowment in relation to population between the North and the South and the lack of buying power of low-income people in the poorest countries continue to be major problems for achieving food security. In addition, we should be mindful of the need to further increase food supplies to meet the growing demand.

The developed countries may not need more food, particularly staple grains, as they already have a stable population and will experience an absolute decline in population in the near future. Many of them have abundant land resources and unused capacity for producing more food. These countries now face the problem of disposal of surplus food and the downward pressure on prices in the world market that dampens farmers' incentives to produce more food.

But the situation in low-income countries is completely the opposite. For people living there, the race between the increase in population and food production is not yet over. The world population has more than doubled over the last 50 years from 2.5 to 6.1 billion, and may not stabilize before 2100, when another three billion people will be added to our planet, most of them in the low-income countries where poverty and hunger are still widespread. Meeting the food needs of this additional population in an environment-friendly way will not be an easy task. Already, prime agricultural land is being diverted to nonagricultural uses to meet the growing demand from housing, urbanization, and industrialization. A water crisis is looming in countries inhabited by half of the world's population. The heavy use of agrochemicals in our pursuit to increase yield has already strained soil fertility and has had harmful effects on human health and the environment. The challenge to countries that are poorly endowed with natural resources is therefore how to produce more food grains with less land, less water, and fewer harmful agrochemicals.

I am aware of the argument made by the supporters of trade liberalization that the solution to the mismatch of the demand-supply balances between the developed and developing countries lies in the movement of surplus grains through free trade in the international market. The pressure on natural resources in the food-deficit countries would be less if the developed countries exploited their unused capacity to produce surplus food to meet the deficit in countries with limited natural resources. But the problem is not that simple to solve. A large part of the future demand for food will originate in countries in sub-Saharan Africa and South Asia that do not have enough foreign exchange earnings to pay for commercial food transactions. The countries with extensive poverty must meet their demand for food with additional production within their national borders. They must also create productive employment for the growing labor force to augment buying power to acquire food. As the production of staple food is the most important economic activity in the low-income countries, importing food means importing unemployment and reduced capacity to obtain food.

I am confident, however, that feeding the world is not an impossible task. With recent advances in science in molecular biology and biotechnology, scientists can develop appropriate technologies for regions with unfavorable environments that have had limited benefits from past innovations. But there must be political will, commitment, and determination to make this happen. We are concerned about under-investment in agricultural research in developing countries and the declining support from developed-country donors for the international agricultural research centers that support and complement the work of the national agricultural research and extension systems. Political leaders of the high- and middle-income countries must demonstrate that they are willing to support the agricultural research that produces technologies to be made freely available to poor farmers in low-income countries. The governments in low-income countries must allocate adequate resources to support their own public-sector institutions.

I would now like to mention the equally important subject of creating productive employment to alleviate poverty. Most studies on the poor suggest that poverty harms those who lack access to natural resources and have poor nutrition and little education. They have no choice but to make their living by selling their manual labor or converting their labor into commodities through self-employment because the market cannot produce enough employment for them. Recently, nongovernment organizations (NGOs) have come forward to organize resource-poor households through social mobilization to help create productive self-employment and by providing access to credit and development of skills.

In my own country, Bangladesh, the NGOs have already mobilized more than six million rural landless families and assisted them in various ways to develop skills and facilitate the creation of productive self-employment. This social mobilization has also contributed to raising awareness of the need for education, health care, sanitation, and family planning, which has helped reduce population growth and the demand for food. Such NGOs are working in many poverty-stricken countries in Asia and Africa. While the agricultural research and extension community has contributed to keeping food prices within affordable limits, social mobilization by NGOs has helped create more employment and increase labor productivity and income of landless households that do not directly benefit from the technological advances that aim to increase land productivity.

I must stress, however, that poverty and hunger cannot be alleviated simply by providing food and jobs. The system that perpetuates inhuman living conditions for a large section of humanity must be undone. What is needed is a “cultural revolution” that attempts to overcome the root causes of poverty and not only its symptoms. This is perhaps the most challenging task facing us in the 21st century.

BRAC has been working to bring about this cultural transformation in Bangladesh for the past 28 years. We have come to understand many of the factors involved in the perpetuation of poverty in our country, the most profound of which, I believe, is the role of women. Nothing can match women’s experience with poverty. They are the ones who seek to maintain their family with no resources or access to services that we consider to be basic. They do much of the work to provide the minimum subsistence needs of their families, but have to go without food when there is not enough. They are also the victims of discrimination, violence, and abandonment. Poverty is largely a problem for women. If we are to successfully overturn the culture of poverty, we must first attempt to change the culture of subjugation that restricts women's mobility, educational and economic opportunities, choice over their reproductive behavior, and, most of all, their ability to exercise their basic human rights. If one subject stands out above all others as the unfinished agenda of the 20th century, it is gender equity. And it will be the transformation of the culture of subjugation in many low-income countries that will have the most profound effect on poverty in the years to come.

Allow me to describe our experience at BRAC so that you will understand the events and history that shape my current thinking.

BRAC is a development organization with more than 27,000 full-time staff members working in more than 60,000 villages of Bangladesh. Empowerment of the poor and poverty alleviation are the two facets of BRAC's primary goal. Social mobilization is the sine qua non for empowering the poor. It is also the most cost-effective way to reach large numbers of households. We look at poverty from a holistic viewpoint. In the words of Amartya Sen, the Nobel-laureate economist, "The point is not the irrelevance of economic variables such as personal incomes, but their severe inadequacy in capturing many of the causal influences on the quality of life and the survival chances of people." Along with income and the creation of jobs, BRAC helps in forming organizations of the poor, building awareness, training for gender equity, and developing human resources. The logic of these programs is the creation of an enabling environment in which the poor can participate in their own development. But increasing awareness alone cannot bring about change. Economic empowerment is at the heart of other forms of empowerment.

When BRAC began in 1972, it was essentially a relief and reconstruction effort to help the victims of the civil war in one of the remotest parts of the country. But we soon realized that the needs were much greater. Poverty was so prevalent that we could not walk away from the people. Even so, we thought we would take a limited number of initiatives and in two or three years develop replicable models of the kind of work that needed to be done to alleviate rural poverty. The rest would be up to the national government and the people. But, as time passed, we realized that we were too optimistic.

Now, nearly three million poor women, representing as many families, are directly involved in BRAC's development activities. We have extensive programs in many aspects of food and cash crop production, as well as in other income-producing activities. We run 34,000 nonformal primary schools for children who have been deprived of education because of poverty and bias against females. More than 1.2 million children are currently enrolled; 70% of these children are girls who are taught by female teachers. BRAC emphasizes educating girls to empower the future generation of women.

BRAC covers a population of 31 million with the help of more than 99,000 village health workers in preventive, curative, and reproductive health. With the technical input of the International Centre for Diarrhoeal Disease Research, Bangladesh (ICDDRB), financial support from the international community, and the cooperation of the government, BRAC has successfully empowered every household in the country to deal with the age-old scourge of death from cholera and acute diarrhea by mobilizing and educating women to administer a simple homemade treatment. We have also pioneered the "Directly Observed Therapy Short Course" (DOTS) for treating tuberculosis, which has been described as a breakthrough by the World Health Organization. Human resource development and institutional capacity building have been important areas for nearly as long as BRAC has been in existence.

Our income-producing programs and other activities in economics have brought BRAC into the world of the free-market economy. Until quite recently, the conventional wisdom was that NGOs are inherently incapable of entering the rough-and-tumble world of business. Although we have had our fair share of failures, we have also proved our ability to create economic institutional value without sacrificing our values.

Providing credit to the poor is an important component of our Rural Development Program (RDP). An equivalent of US$1.64 billion has been given as loans to poor rural women without collateral. The repayment rate is 99% and the members have accumulated savings of more than $80 million. Awareness, peer group dynamics, and BRAC staff supervision are important factors for the success of the credit program.

Realizing the fullest potential of micro-credit to improve the lives of the poor on a sustainable basis has been held back by the virtual absence of modern production technology in rural Bangladesh. Much of the micro-credit has been used for traditional activities, and not enough has been done to include new technology. The profit made from traditional activities is modest, not enough to produce an investible surplus. In the case of BRAC, 70% of its loan portfolio is in traditional activities. The need to infuse more productive technology is being gradually recognized, and BRAC has made a significant commitment toward this. BRAC provides training, improved raw materials, and marketing support in certain sectors. Examples are high-yielding varieties of birds, vaccination, hatcheries, and chick-rearing units in poultry; artificial insemination in livestock; fish hatchery development; seed multiplication, tissue culture, and the use of hybrid seeds in crop production; improved varieties of mulberry trees; the high-quality production of cocoons; and modern reeling facilities. About 30% of the existing loan portfolio is devoted to technology-oriented/intensive activities. These activities increase the profit margin of the participants through increased productivity.

Wherever possible, BRAC seeks vertical and horizontal integration in its income-producing projects. For example, in the case of its poultry program, activities cover the whole process from eggs to chicken to eggs. BRAC-financed hatcheries sell day-old chicks to women who rear them as broilers or layers. The eggs and birds are then sold to consumers as well as BRAC hatcheries. BRAC is also involved in ancillary activities such as training, veterinary care, and feed. BRAC pioneered poultry raising in Bangladesh. Today, this is a thriving industry and eggs and chickens are no longer the food of the fortunate few. Similar backward and forward linkages have also been successfully established in other programs. Before starting a new experiment, we do consider whether it would be financially and operationally feasible nationally.

Reaching the poorest of the poor, those who have nothing at all, households headed by women with small children and no ostensible means of income, or households in which the head of the household is chronically sick is a daunting challenge. These extremely poor people are unable to take advantage of the traditional development programs of the government or even the more grass-roots programs of the NGOs. BRAC has responded to the needs of these people by initiating a program called Income Generation for the Vulnerable Group Development (IGVGD). BRAC has been working with the government since 1988 to provide training on poultry raising to these women for the period in which they receive free wheat as a ration from the government's relief program. With the help of the government, BRAC has provided easy loans to them to purchase and rear poultry. The idea is that, when the ration is withdrawn after 18 months, the women can continue to earn an income from the poultry equivalent at least to the value of the food ration. BRAC has also linked these women with the government livestock department to receive vaccines for their poultry. Currently, more than 300,000 women participate in this program.

In 1986, BRAC started experimenting with a nonformal primary education program for children from poorer families. We knew from our years of experience in rural areas that there was much demand for education among the poorer families. Accordingly, we developed the Non-Formal Primary Education Program (NFPE) that best suited the realities of rural Bangladesh. We are humbled by the overwhelming response of the parents and children, and proud of our ability to open and operate more than 34,000 one-room schools where more than a million children—70% girls—are receiving an education they would have never received otherwise. We expect to bring the joy of learning to several million children in years to come.

In short, BRAC has been promoting a new culture in the development field, with women at the forefront of all its activities. Most of the recipients of credit are women, 70% of the students and 80% of the teachers of BRAC schools are women, and the health and poultry workers are all women. Women entrepreneurs are running rural restaurants, vaccinating poultry, treating patients, doing carpentry, and managing people. All of these activities were traditionally done by males.

Despite our focus on the economic and social empowerment of women within our programs, we have discovered that no organization can remain immune from the values and norms of the society in which it is situated. The negative attitude toward women's abilities, effectiveness, and status as decision makers that we were fighting in our programs was found within our organization itself. We were having difficulty attracting and retaining female staff to work in the field, not because of the rigors of the work, but because of the subtle harassment and lack of respect within and outside of the organization. But we are optimistic that our dual-track approach—of raising gender awareness in our organization and continuing to focus on women's empowerment in all aspects of our programming—will move us toward creating a productive, enabling environment for all women and men that come into contact with our organization.

Let me now conclude. All over the world, the work of women in the home and the workplace is undervalued. Women are subject to harassment, be it subtle or overt. And even their homes can be a place where they endure physical violence. The 20th century witnessed the Universal Declaration of Human Rights, the Civil Rights Movement, and the end of colonial domination. But we have yet to achieve the transformation to a culture in which women are valued, empowered, and free to pursue their own life choices.

Empowering women can help reduce population growth, which continues to be the single most important factor behind the increase in demand for food and pressure on Earth's limited natural resources. Poverty will never be alleviated if women are not seen as partners in their families, participants in the economy, and directors of their own lives. In my mind, this is the unfinished agenda of the 20th century. We all must make gender equity the primary goal of the 21st century. Through social mobilization, let us work toward the transformation to a culture that respects, values, and listens to both men and women and uses all of their skills, experience, and knowledge to arrive at a time when we can rightly claim that all of humanity is truly free from poverty and discrimination.

If we can achieve this goal, only then can we truly say that we have had impact.

Notes

The author is founder and executive director, Bangladesh Rural Advancement Committee (BRAC).

Sustainable rice production, food security, and enhanced livelihoods

P. Kenmore

Rice has been gathered, consumed, conserved, and cultivated by women and men for more than 10,000 years, longer than any other crop. In 2000, more than half of the world's population depended on rice as its major daily source of calories and protein. Each of these people consumes from 100 to 240 kg of rice per year. More than two billion people in Asia alone derive 80% of their calorie intake from rice, and thus the importance of this crop, for food security and socioeconomic stability, is self-evident. Throughout the history of Asia, the ability to produce a surplus of rice contributed significantly to the development of communities, whereas the failure of a rice crop led to widespread famine, death, and political instability.

Rice is becoming increasingly popular in Africa, the Americas, and elsewhere. In high-income countries in the Near East, Europe, and North America, rice is considered to be a healthy and tasty food and its consumption is growing. The importance of this crop is progressively recognized for its nutritional value and because it is an integral part of religious and social ceremonies.

Rice is a key source of food energy and rice-based production and processing are major employers and sources of income for the poor. Rice production activities provide employment for several hundred million people who work either directly in rice production or in related support services. With the harvest of the rice crop, activities shift to postproduction operations: threshing, drying, milling, storage, product processing, and trading of rice, which together provide employment for millions more people.

In all major rice-growing countries, the rice-land farming systems—involving crops, livestock, and fish—produced, and continue to sustain, agricultural infrastructure and many associated value-adding rural enterprises and services. Indeed, agriculture—including rice-based agriculture—provides much of the raw material needed by the manufacturing industry. Thus, poor harvests have an adverse effect on many nations' economies.

FAO fully realizes that rural families derive much of their gainful employment and income from nonfarm and off-farm activities and this nonfarm component is particularly important for rural women and those in nonirrigated rice systems.

Sustainable increases in the efficiency of rice-based production systems are a key to Improving the livelihood of both small-scale rice farmers in developing and rice-producing countries and poor families in urban centers who depend on low-cost rice in many countries worldwide. Meeting the challenge of sustainable increases in rice production and production efficiency is vital not only for food security but also for the alleviation of poverty of several hundred million poor families in low-income and developing countries.

Environmental concerns in rice-land management relate particularly to water and to agrochemicals. The uncontrolled extraction of groundwater for irrigation depletes the aquifers. The excessive use of pesticides results in operator morbidity and in damage to nontarget, often beneficial, organisms. Globally, agriculture is a source of nitrate in groundwater and in surface water, and of phosphate-associated pollution of waterways. Agriculture also contributes to atmospheric ammonia, methane, and nitrous oxide. Therefore, FAO is working hard to assist its member governments in reducing agriculture-based pollution and in harnessing the potential of good agricultural practices to be part of the solution for sustainable development, including improvement in the quality of life of the rural poor.

Why are many rice farmers so poor?

The continuing decline in the world's rice prices since the Green Revolution has affected rice growers' livelihoods. The prevailing decline caused by bumper crops during the last few years has greatly aggravated the poverty of millions of rice producers. The global depression in rice prices is also a concern in Latin America, where several governments have instituted trade barriers to protect national production from low-cost imports. At the same time, the declining price of this vital commodity has to a large extent helped to mitigate the effects of poverty and alleviate hunger in many cities of the world.

Historically, most governments in the major rice-producing and rice-consuming countries have developed policies that maintain stable paddy prices for consumers in urban centers and provide subsidies to rice farmers. These policies led to a continuous expansion in rice production and held market prices within the purchasing power of low-income consumers. While the goal of stable prices for urban consumers remains, new policy thinking reflects liberalized global trade and domestic adjustments that reduce subsidies. In countries that are major rice exporters, policies favored the export market, again often at the expense of producers. The current world prices are the lowest in several decades. Exports from Thailand, the world's biggest exporter, reached a record in 2001 -02, even though premium-quality white rice sold for only US\$178 t^{-1} vis-à-vis \$350 t^{-1} in 1995-96.

Many poor rice farmers live in remote areas, including the upland- and deepwater-rice ecozones. Such areas often have less-productive soils, erratic rainfall, and poor rural infrastructure; they consequently host a greater proportion of poor farmers than the irrigated rice ecozones. Economic returns are less and risk is higher.

Developing countries provide rice farmers with lower subsidies than developed countries. In the United States, Western Europe, and Japan, rice is one of the most highly subsidized commodities, resulting in huge government expenditures to support rice growers.

Rice farmers' livelihoods depend on their capacities and assets—natural, physical, financial, social, and human—applied through activities required for their means of living, including off-farm employment. Below I discuss various intervention points that could enhance the livelihoods of households in rice-based economies.

Strategies and opportunities for better rice-based livelihood-support systems

In FAO's view, sustainable livelihood strategies should help households cope with and recover from stresses and shocks, maintain or enhance capacities and assets, and provide net benefits to other livelihoods locally and more widely, both now and in the future, while not undermining the natural resource base. The sustainable livelihoods approach examines three key questions: What institutional arrangements can enable some poor people to achieve sustainable, secure livelihoods when others fail? What policies and strategies can support the poor? Which good practices can optimize economic returns in a sustainable way?

Policy, strategy, and institutional environment

The majority of rice farmers in developing countries are poor and caught in a cycle of endless poverty. National policies often favor the consumer and the export market, not the farmer. After all the efforts spent in seeding, weeding, irrigating, harvesting, and threshing, rice yields still do not provide farmers with a high income.

Governments should strengthen policies to support equitable and efficient access to natural resources (particularly land and water). Policies must also stimulate investments, institutions, including private and nongovernmental ones, micro-finance, and agricultural trade.

Improvement of rice farmers' livelihoods requires functional institutions. There is a current need, and indeed opportunity, to strengthen those national institutional capacities that enable government, civil society, and community-based organizations and cooperatives to participate collectively in the formulation and implementation of rural-development policies and programs. Such strengthening is expressly needed to enable the poor to secure and to retain usage/ownership entitlements to land and water resources.

National and local government policies need to be not only appropriate but also operational. For many rice-growing countries, a priority is to strengthen the institutional capacity to define and implement policies and procedures to enhance production, value-adding enterprises, and the necessary rural infrastructure.

FAO, through its mandate, undertakes studies and provides policy advice and program support for member countries to explore and identify alternative routes to sustainable livelihoods. It helps countries to analyze the core elements in fostering sustainable livelihoods: the dynamics of the natural resource base, strategies for poverty reduction and promotion of well-being, the reduction of risk, and the promotion of positive adaptation to change.

Strategically, decisions on priority areas for improvement of the various rice agroecological systems can substantially improve farmers' livelihoods. In many countries, irrigated rice systems will contribute most of the increased food production that will ensure urban and rural food security. However, many governments now accord high priority to the nonirrigated rice lands, perhaps to avoid the problems associated with the development, maintenance, and operation of irrigation systems.

A highly successful crop sequence in rainfed deepwater areas (notably in Vietnam, Bangladesh, and eastern India) has been the adoption of rice cultivars that use the slow-receding postmonsoon water to achieve high yield. In these lands, river water and shallow groundwater can be accessed for late-season supplementary watering using intermediate-technology low-lift water pumps. For premonsoon operations in flash-flood-prone areas, mixed or intercropped rice cultivation systems can minimize risks.

For the uplands, rice is one crop among many choices and FAO's program of "Alternative crops for new opportunities" may provide niche-specific options to produce other crops such as spices, feed, fiber, fuel, and nutraceutics.

Technological approaches to increase the productivity and efficiency of rice-based production systems

Farmers can benefit from technologies that boost production and/or increase their income and employment. Increases in rice production and farmers' income depend strongly on improved productivity and efficiency of the rice production system. Fortunately, the outlook for such increases is, in general, encouraging. However, for very poor farming households, and those in marginal areas, the priority is not so much yield, but, rather, the lessening of risk.

For genetic improvement, ecozone-specific cultivars with a broad genetic base are essential. Many cultivar-development programs are ongoing and vigorous. They examine yield potential and biotic and abiotic constraints. Chinese scientists applied heterosis—better known as hybrid rice—to increasing rice production in 1976. The area under hybrid rice production in China increased to about 15 million ha in 1990. Thanks to hybrid rice, Chinese farmers can now maintain sustainable rice production for food security, while saving several million hectares of rice land for other production activities to increase farmers' income. The first generation of hybrid rice was 3-line hybrids, which have 15% to 20% more yield than the high-yielding varieties. In the last few years, Chinese scientists have released 2-line hybrids, which have about 5% to 10% more yield than 3-line hybrids. During the last decade, FAO has assisted Asian countries in the development and use of hybrid rice. In 2001, it was estimated that about 800,000 ha of hybrid rice were planted in Asian countries outside of China, such as Vietnam, India, the Philippines, and Bangladesh. Various countries have nitrogen-efficient rice cultivars to facilitate economy in fertilizer use; specific cultivars will use direct seeding, thus permitting water economy in water-scarce areas. For human micronutrition, there are new rice cultivars that variously contain increased levels of vitamin A, iodine, iron, or zinc.

In all ecozones, rice seed quality is crucial: the use of poor-quality seed lowers yields on average by 9% to 15%. But only one-fifth of farmers' rice land is sown to high-quality seed. Seed management is often the preserve of the female members of the farm family so that special training and micro-finance support for them can be a highly cost-effective intervention, targeting and benefiting women directly.

Biotechnology holds potential for increasing yield and reducing some inputs. For instance, biotechnology could, in the future, create drought-tolerant varieties or eventually genotypes that are able to fix nitrogen from the atmosphere, thus reducing fertilizer inputs. The Rockefeller Foundation, in partnership with IRRI, national systems, and advanced research institutions, has led the global campaign in rice biotechnology and produced outputs such as Golden Rice, which, enriched with high levels of pro-vitamin A, holds promise for improving micronutrients in rice. The most important achievement in rice biotechnology is the sequencing and mapping of the rice genome that has been carried out by the International Rice Genome Sequencing Project (IRGSP) and other public and private institutions. Knowledge on rice genomics could effectively assist the breeding of new rice varieties, including the transfer of genes from other crops/organisms to rice. FAO believes that caution is required in the use of this technology. A careful case-by-case assessment of genetically modified organisms (GMOs) is essential. The first concern is human and environmental safety.

The methodology of yield-gap and constraints analysis gives opportunities to maximize the benefits of improved cultivars and of the associated crop and livestock husbandry. It identifies the yield-constraining effects of biophysical and socioeconomic factors, including suboptimal crop and resource management. Yield gaps may result from farmers' lack of technical knowledge associated with extension gaps, and in many countries from insufficient institutional support. The methodology involves community participatory analysis of biophysical and socioeconomic features, and requires practical training and institutional support.

Increasing the efficiency of inputs is becoming more critical as national policies face the options of moving from producer subsidies to trade mechanisms for maintaining stable rice prices for urban consumers. For water resources and irrigation systems, there is a general appreciation of the need for national strategies and policies for the near, medium, and long terms. For irrigation, it is recognized that, for rice and nonrice crops, the technical efficiency of irrigation-water distribution can be increased, with substantial water savings and opportunities to expand the land area serviced by irrigation facilities. Initial requirements are to regularize the rights and obligations of irrigation users and to reform irrigation agencies.

For plant nutrient management, environmental considerations as well as improvement of farmer income dictate that there must be an increase in fertilizer-use efficiency and a decrease in nutrient losses. The required procedures are well known: there are emergent methodologies and associated diagnostic and decision-support systems, notably for irrigated-rice systems. Fertilizer-use efficiency can be quantified in agronomic and in economic terms: well-founded recommendations for on-farm practices and government policies exist. Similarly, there are established procedures of integrated plant nutrition management, in which manufactured fertilizers are used in combination with animal or plant manures, and with existing soil nutrients, and making allowance for crop-sequence interactions.

The widespread use of semidwarf varieties of rice and nitrogen fertilizers and the increased use of insecticides have changed the status of pests from low to high economic importance in rice production. Integrated pest management (IPM) is the most effective method for controlling pests while improving productivity and caring for the environment. FAO has worked with national programs starting in Asia and then Africa and the Near East to develop *farmer schools* that emphasize participatory experiential learning, starting with IPM practices and concepts. These have evolved to include integrated plant nutrient management, participatory plant breeding, and community-based irrigation management, in what is now known as integrated production and pest management. More than two million rice farmers, including more than 100,000 in China, have set up and maintain farmer field schools, and they take the principles into diversified livelihood systems.

For the irrigated and favorable rainfed lowlands, the *Ricecheck* technology transfer program has been highly successful in increasing national yields by bridging the yield gap. This program is a decision-support tool in which a series of limitations to production are identified and corrective measures are integrated into a production program. Farmers are encouraged to follow the best management practices based upon “critical checks” that are known to have major effects on yield. In addition to the development of the “critical checks” concept, the approach to technology transfer is unique and is based upon establishing farmer groups that not only accelerate technology transfer but also serve as a feedback mechanism for researchers and extension workers. FAO is currently working with several national programs to adopt the *Ricecheck* concept that evolved in Australia.

Postharvest value-adding activities, at the household level within rice-growing communities, also provide opportunities for creation and expansion of employment and for income augmentation. For rice and its by-products of bran and broken rice, there are established and emerging options for the manufacture of food products, including cakes, baby foods, soups, starches, noodles, flours, and convenience foods. Brown rice and rice bran will become increasingly marketable as people become more health-conscious. Other ways to increase the income of farmers is to promote the full use of the biomass of the rice plant. For example, the use of rice husks for cooking energy, rice straw for the culture of mushrooms, rice bran for oil production, etc., under the FAO-developed concept of “thriving with rice,” could produce additional income for farmers.

In optimizing the production and income from smallholder agriculture, crop-livestock synergies can be particularly beneficial. Such smallholder crop-livestock integration also provides opportunities to intensify production, to accumulate assets, and to diversify risk. Rice-system livestock—poultry, cattle, and pigs—also provide value-adding and employment-creation opportunities, particularly for women. Among poultry, whether for meat or for eggs, native chicken and hybrid duck provide worthwhile income-producing options. Rice-system by-products and slaughterhouse wastes can be processed into low-cost poultry-feed ingredients.

Results of FAO field projects during the 1990s have demonstrated the potential contribution of the diversification of rice production systems as a means of increasing farmers' income. Multiple-cropping of rice, for instance, with tomatoes or cabbage can further increase income. However, basic food security for their families remains a primary concern of farmers and farmers are often willing to undertake diversification only when rice production can provide adequate food for their families. Increasing rice productivity is therefore an essential requirement for the successful promotion of crop diversification for many producers.

FAO has put these results into action in its "Special Program on Food Security," which now operates in more than 70 member countries. Rice has been a major focus of SPFS efforts, which examine the priorities of diversification, sustainable intensification, farm-level water control, and constraints analysis. China is a leading participant in this global program, and is its largest South-South cooperation partner.

Investment in vocational training will be highly worthwhile in preparing current and future farmers and farm women for the transformed rice-system agriculture in the future. Training of adult rural women in the basics of financial management would provide vital strengthening to farm-household economics and to family and community well-being. Similarly, for farm-family nutrition, interventions can assist rice-system women in availing of the proven systems to maximize benefits from home gardens and from programs to make maximal nutritional use of available food.

To combat poverty in remote rural areas, interventions to improve infrastructure and services, including financial services, are prerequisites. With such infrastructure and services, farmers in remote areas can increase food-crop and niche-crop production and feed supplies and develop enterprises.

Partnership promotion

Rice-household livelihoods depend not on food supply alone, but on complex interactions of social, economic, and natural-resource endowments. Wide-ranging partnerships are thus needed to supply the support that can lessen poverty among rice-system families and also lessen food insecurity in both rural and urban areas.

Improving the productivity and efficiency of rice-based production systems is too large a task for any single country, institution, or organization to handle individually. The global research and development community needs to focus attention on the role that rice can play in providing food security and alleviating poverty aiming at improving the livelihood of the population. In some cases, diversification out of rice may be part of the solution, especially in ecologies where rice adaptation is marginal.

FAO, with its experience in sustainable development and policy advice, is committed to working in the spirit of partnerships. Additionally, through its mandate to promote agricultural growth to alleviate hunger and rural poverty and enhance food security while conserving natural resources, FAO will help catalyze the contributions of many partners and stakeholders to improve farmers' livelihoods.

In this sense, during the recent 20th Session of the International Rice Commission, held in Bangkok, Thailand, 23 to 26 July 2002, the delegates recommended that FAO assist in increasing capacity-building in biotechnology relevant to rice improvement in developing countries, and provide assistance in preparing biosafety regulations. FAO, in concert with national programs and relevant international agricultural research centers, should facilitate the assessment of plant breeding capacities in support of the Treaty and Global Plan of Action on Plant Genetic Resources. FAO should promote integrated crop management and yield-gap-bridging through farmer participatory methodologies, such as the *Ricecheck* system and farmer field schools for integrated production and pest management, as well as emphasizing sustainable and diversification systems in rice production, especially in Asia.

In conclusion, there are many constraints and challenges to the lessening of rural hunger and poverty within rice-based livelihood-support systems. Fortunately, there are many technological, social, economic, institutional, and infrastructural opportunities to help overcome those constraints and meet the challenges. Encouragingly, recent forecasts permit optimism that there will be increased national resources to combat rice-system hunger and poverty.

Moreover, and as confirmed in the March 2002 Monterrey Consensus, the World Food Summit, and World Summit on Sustainable Development, there is a growing international willingness and political and social commitment to provide external resources to augment national resources. FAO is well positioned to help initiate and support the required multistakeholder rural-livelihood interventions. It can contribute technical, social, economic, and institutional expertise and experience to multiagency endeavors.

Strengthening awareness of the essential features and importance of these vital rice systems, particularly of the economic, social, and environmental significance of rice lands and of the more than 3 billion people who depend upon them for an often-substantial part of their daily food, is crucial.

With a view to raising further awareness among all stakeholders, I am pleased to inform you that, in November 2001, the FAO Conference adopted the Resolution of the International Year of Rice proposed by the delegation of the Philippines. The resolution requested the Director General of FAO to transmit this resolution to the Secretary-General of the United Nations with a view to having the UN declare 2004 as the International Year of Rice. 1 am sure you will share our hope that the United Nations will approve this resolution and declare 2004 the International Year of Rice.

I wish you a successful Congress.

Notes

The author belongs to the Food and Agriculture Organization of the United Nations.

Overview

Agriculture and poverty

C.P. Timmer

How does growth in the agricultural economy help reduce poverty? In a global economy with open commodity markets, the answer is different from that of a generation ago. Then, large Asian economies needed to produce their own food. Higher agricultural productivity impacted the poor directly through lower food prices. Their food intake increased significantly. The availability of cheaper food also stimulated investments in labor-intensive industries, speeding economic growth and raising real wages. Both contributed to reductions in poverty.

Globalization changes the story in important ways, but does not alter the importance of gains in agricultural productivity to reductions in poverty. The linkages are less direct, however. Stimulating them requires a far more subtle role for government. Attention is more on the rural economy broadly than on food crop production per se. Rural-urban linkages, including migration and remittances, are a major part of the story. Prices for staple grains in world markets are low, and emphasis has turned to diversification and access to supply chains that provide middle class (and foreign) consumers with fruits, vegetables, processed foods, and livestock products. Connecting the poor to growth in agricultural productivity is more complicated than during the first decades of the Green Revolution.

Most of the world's poor live in rural areas, or migrated from them in search of better opportunities. Many of these poor are farmers. It seems obvious that improving agricultural productivity should raise farmers' incomes and reduce the incidence of poverty. Further, more food means fewer poor people because poverty lines are usually defined with reference to the adequacy of food intake. Growth in agricultural productivity should be the surest way to end poverty.

Of course, the world is not so simple. In many circumstances, the poor do not have access to the returns from higher agricultural productivity. In many other environments, higher agricultural productivity leads to lower food prices. Consumers benefit, particularly poor consumers who spend a large share of their budget on food. But farmers can end up worse off. So, using agricultural technology to solve problems of rural poverty is complicated at best.

In an era of global markets and open economies, the connections between agricultural growth and reductions in poverty are even more tenuous. But, in the right policy environment, the connections remain powerful. Indeed, in most circumstances, there is still no alternative to "getting agriculture moving" if poverty is to be reduced significantly. The task of agricultural development was much easier under the impetus of the first Green Revolution, when the need for greater cereal output was met by new seed-fertilizer technologies. Now, with staple cereal prices at all-time lows in world markets, a dynamic agriculture will depend on diversification into crops and livestock with better demand prospects, such as fruits, vegetables, and a variety of livestock products.

Connecting the poor to this more diversified agricultural growth will be more difficult than during the first Green Revolution. But it remains important because, in many countries, the poor are more numerous than ever. Even in countries with sharply reduced numbers of poor, such as China and Indonesia, poverty remains as an urgent problem, especially in rural areas. If the first-generation Green Revolution did not solve these problems of poverty, hope must now fall on the far more complex mechanisms that will link the poor to the productivity gains of the next generation of agricultural innovations.

These mechanisms fall into three basic categories. First are the basic linkages that connect faster agricultural growth to faster growth in the overall economy. First articulated to a general economics audience by Johnston and Mellor (1961), these linkages have long been part of the core of modern development theory and practice (Timmer 2002b). Recent research has established that economic growth usually has a direct effect on poverty (Deininger and Squire 1996, Ravallion 2001). So, any contribution that agriculture makes to speeding up overall economic growth will, in most circumstances, also be a direct contribution to reducing poverty.

The second mechanism enables agriculture to make economic growth even more "pro-poor'' than it would be if the source of growth came from the industrial or service sectors. Growing evidence indicates that the "elasticity of connection" between the poor and overall economic growth depends in important ways on the sector of growth, along with initial conditions in the economy, especially the distribution of assets and income (Timmer 1997, Ravallion and Datt 1996,2002). New agricultural technologies that improve farm productivity seem to play an important role in improving this elasticity of connection.

The third mechanism linking agricultural growth to poverty reduction is both more direct and more subtle. In a wide variety of circumstances, the array and diversity of foods available in local markets have a direct effect on the quality of diets consumed by rural households. In rural markets, most of these foods come from local farms. Dietary quality is reflected in several ways, including the starchy staple ratio, the amount and quality of protein, and the availability of such critical micronutrients as iron, vitamin A, and iodine. Micronutrient deficiencies in particular, often called "hidden hunger" because availability of micronutrients in foods is not apparent without specific training and knowledge, can be reduced sharply by the consumption of appropriate vegetables and livestock products. Having these products available in local markets, and cheap enough for the poor to have reliable access, can make a significant contribution to lowering the welfare consequences of poverty (Block 2002).

This paper addresses each of these three mechanisms, focusing especially on the latter two as representing newer, and more controversial, roles for agriculture in reducing poverty. The next section reviews the literature on the causes and consequences of poverty to establish the validity of instruments to reduce it. After that, the specific role of agriculture is addressed. Some brief comments on policy implications and the role of government conclude the paper.

Reducing poverty

Defining poverty, establishing its causes, and finding mechanisms to reduce its incidence are major conceptual and empirical undertakings, the results of which can only be highlighted here. Fortunately, the literature is vast and easily accessible. This literature is not, however, easily summarized because the messages are contentious and overlaid with ideology and political rhetoric. Still, several robust themes can be noted here.

First, how poverty is defined matters to such elemental subjects as whether the numbers of poor are increasing or decreasing, in absolute terms or relative to population. When life expectancy and literacy, for example, are included with income in defining poverty, then unambiguous progress at a global level has been made in the past several decades in reducing the numbers of the population defined as poor (Fox 2002). By contrast, if poverty lines are established in U.S. dollars at market exchange rates, even the share of the population defined as poor seems to have risen in recent years (Wade 2001).

The confusion resulting from such disparate measures and results is important because the mechanisms by which poverty can be reduced are obscured. Is income growth everything? It is, if it is all that counts. Or can initiatives to direct health and education programs to the poor substitute effectively for the more difficult task of getting economic growth going? This debate easily leads to paralysis of action. Another form of paralysis stems from the rather sterile debate over global trends in poverty and income distribution. The important action is at the country level, or within, because that is where national policies can be effective. There are few global policy instruments for reducing poverty, "Globalization" is not a strategy for poverty reduction.

Still, the very complexity of country-specific determinants of poverty can mask the powerful but indirect effect of macroeconomic forces, trends in commodity prices, or evolving demands for skill in labor markets. These factors are the ultimate mechanisms for an escape from poverty.

In nearly all circumstances, low economic productivity of poor households is the proximate cause of poverty. Behind this low productivity can lie supply factors, such as limited availability of land, skills, or appropriate technology. Demand factors, such as prices for commodities grown and sold, availability of productive jobs, and access to urban markets for handicrafts can also sharply influence the incidence of poverty in any given setting. Key to both supply and demand factors is the importance of local markets to provide a low-cost and convenient arena of exchange for the goods and services produced by the poor. It is virtually impossible to escape from poverty except through market exchanges.

The importance of market exchanges illuminates the role of governance in causing and reducing poverty. Bad governance means poorly defined property rights, high transaction costs, large economic risks, and outright theft. Markets disappear in such environments and with them the hopes of the poor for an escape route from poverty. With lost hope often comes despair and fatalism. Sometimes this leads to migration to better opportunities, whether legal or not. On occasion, it breeds violence (Collier 2001).

One of the most visible determinants of poverty is hunger and malnutrition. The development profession continues to argue over which causes which, but hunger as a measure of poverty is widely established. Most poverty lines have an explicit or implicit food component. Preventing famines, children from becoming acutely malnourished, and mothers from delivering underweight babies has motivated much of the humanitarian assistance delivered around the world. With abundant food in rich countries, it seems a tragic waste not to feed the hungry in poor countries. With powerful political forces aligned behind this reasoning and much popular support for foreign assistance driven by television images of starving children, it would be foolish, even dangerous, to ignore the link between hunger and poverty.

And yet the link is more tenuous than supposed. The evidence for nutritional poverty traps, where workers are too malnourished to work hard enough to feed themselves and their families, has strong historical dimensions (Fogel 1991, 1994, Bliss and Stern 1978, Strauss 1986, Strauss and Thomas 1998). But simple energy shortages cannot account for very much of the chronic poverty observed over the past several decades because the cost of raw calories, in the form of staple foods, has fallen too sharply relative to wages for unskilled labor (Fox 2002). If inadequate food intake is the primary cause of poverty, the solution will be in sight. If, however, poverty is the main cause of inadequate food intake, hunger will be much harder to end.

How well do the poor connect to the growth process?

The publication by the World Bank of the Deininger-Squire (1996) data set on income distribution and levels of poverty allowed preliminary testing of many theoretical models that attempted to explain the links between economic growth and reduction in poverty. At one level, the new data have supported a very comforting story. There is no longer room to doubt that rapid economic growth reduces poverty. Even cursory analysis of the Deininger-Squire data set on changes in income distribution over time reveals only a small handful of examples where economic growth on average failed to increase per capita incomes in the bottom 20% or 40% of income distribution.

But additional insights are possible from more sophisticated examination of the empirical growth record, using the Deininger-Squire data set to understand the relationship between reductions in poverty and changes in income distribution and how to improve the connection between economic growth and poverty alleviation revealed by this record.

Income distribution matters because it affects how well the poor connect to the growth process. Society might care little about income distribution per se, but a great deal about those living in absolute poverty. Analyzing the prospects of these families requires data on their circumstances, such as from the Deininger-Squire data set, as well as an understanding of the economic and political mechanisms that connect the poor to economic growth. One of these connection mechanisms is mediated by income distribution, as the following analysis indicates.

Following on a burgeoning literature using the Deininger-Squire data set (reviewed in Gugerty and Timmer 1999), Timmer (1997) examined the question of how well the poor share in economic growth by directly estimating the "elasticity of connection," or the degree to which a percentage increase in overall per capita incomes translates into a percentage increase in the per capita income of the poorest quintile. In addition, this analysis addressed the question of whether the sectoral composition of growth matters for the incomes of the poor, thus moving beyond absolute connections to conditional ones.

The effect of income distribution on the "elasticity of connection"

The necessary technical details of this analysis are shown in Appendix 1. The conclusions, challenging as they are for the "growth-is-all-that-matters school," are easy to summarize. Both the sector in which growth originates and the initial distribution of income matter greatly to how well the poor connect to overall economic growth. Indeed, two fundamentally different growth processes seem to be at work for the roles of labor productivity in agriculture and nonagriculture, and how these affect incomes in each of the five quintiles of the income distribution. In countries where the gap between the incomes of the bottom quintile and the top quintile is less than twice as large as average per capita income—that is, where the income gap is relatively small, labor productivity in agriculture is slightly but consistently more important in producing income in each of the five quintiles than growth in labor productivity in the nonagricultural sector.

Furthermore, agricultural productivity has a noticeable "anti-Kuznets" effect in these countries, that is, economic growth actually improves income distribution rather than worsens it. A similar "anti-Kuznets" effect is seen from the nonagricultural sector and this effect is even more important to the poor in the long run because the nonagricultural sector makes up, on average, 75% of the overall economy. It also has the capacity to grow significantly faster than the agricultural economy over sustained periods of time. When the starting point for economic growth is a reasonably even distribution of income, the growth process itself reaches the poor in an effective manner. Agricultural growth is more effective than nonagricultural growth in such circumstances.

The contrast with countries where the relative income gap is large—more than twice the average per capita income—is striking. In the poorest quintile, workers are virtually disconnected from the national economy (see Figure 1 in Appendix 1). The effect of growth in either agriculture or nonagriculture is the same for the poor, a statistical disconnect. In economies with sharply unequal distributions of income, the poor do not participate significantly in economic growth. However, the elasticity of connection rises sharply by income class and exceeds one for the top quintile. There, agricultural productivity growth is especially favorable to the rich, no doubt because of unequal asset distribution, particularly of land. These results show the importance of understanding the effect of asset distributions on income prospects of the poor.

Asset distribution and poverty

It is virtually impossible to understand the effects of economic growth on income distribution and of income distribution on the rate and distribution of economic growth without incorporating the distribution of assets held by the society. Assets are important because they are a measure of the capital available to an individual, or society, for the production of goods and services. Assets are likely to be distributed even more unequally than income. In a world of perfect data, one would rather examine the distribution of assets than income, but, in reality, data on the distribution of assets are almost nonexistent, particularly for developing countries.

What empirical evidence there is, however, suggests important linkages between assets and incomes of the poor. Deininger and Squire (1998) find that initial income inequality and initial land inequality both have negative effects on the incomes of the poor, but not the rich. Using the initial distribution of land as a proxy for the distribution of assets, they find that asset inequality has a significant negative effect on subsequent growth and this effect is stronger in low-income countries than in high-income countries. In addition, initial land inequality has a negative effect on rates of schooling, suggesting that the link between inequality and growth for the poor is mediated through credit rationing; the poor are unable to borrow to make investments in human capital.

Birdsall and Londano (1997) also examine the effects of asset inequality on the income of the poor using the Deininger and Squire data. They find that inequality in the distribution of land and education negatively affect income growth of the poor. Datt and Ravallion (1997) examine the effects of inequality on the elasticity of poverty reduction in India using a model similar to Timmer (1 997). They conclude: “[c]ertain inequalities can severely impede the prospects for poverty reduction through nonfarm growth.. .. Initial intersectoral disparities in earnings . . . influence how much nonfarm economic growth reduces the incidence of poverty. In addition, the higher the initial poverty rate, the less effective is nonfarm economic growth in reducing poverty.” Nonfarm productivity is less effective in poverty alleviation in states with “poor” initial conditions.

Additional research extends this result. Ravallion and Datt (1996) have shown that the sectoral composition of growth matters to poverty reduction in India: poverty measures in India have responded far more to rural economic growth than urban economic growth. In addition, their work indicates that the connection of the poor to rural economic growth is quite robust over time, at least in India.

Both theoretical and empirical work, then, suggest that inequalities may persist over time, and that certain inequalities particularly penalize the poor. The next step in the research agenda is to better understand the underlying distribution of wealth in an economy and its implications for the economic and political sustainability of growth (Alesina and Perotti 1993, Anand and Kanbur 1993). Virtually no data are available on asset distribution in developing economies, but it is possible to use the Deininger and Squire data on income distribution to develop a simple, stylized model of asset distribution and its evolution over time. The details of this model are illustrated with an example in Appendix 2. The underlying framework and the key results are discussed here.

For the analysis here, capital assets are divided into four categories: physical labor, human capital, financial capital, and social capital. Some simple assumptions are made about the returns to these various forms of capital to produce several striking lessons.

1. *Physical labor* is what an individual can exert without using any other form of capital to raise productivity. Somewhat arbitrarily, this physical labor is valued at $365 per year in terms of purchasing power parity (PPP), which is simply one of the World Bank's poverty lines. If a worker's income depends entirely on competing with a horse, tractor, or bulldozer, by expending physical energy, the expected income is likely to be low indeed. Incomes below $365 per year reflect significant poverty and the likely depletion of human capital in the form of reduced health and nutritional status.

2. *Human capital* comes from education and on-the-job training (in addition to physiological contributions from health and nutrition). It is useful to consider three categories of human capital: (a) that arising from literacy and numeracy, both of which should result from a primary education; (b) more formal analytical and reasoning skills that result from a high school education; and (c) advanced professional skills and research training that come from college and postgraduate education.

Again, somewhat arbitrarily, primary education in a developing country is assumed to produce $1,000 per year (in $PPP) for the holder, whereas finishing high school results in an additional $5,000 per year in earnings. Thus, by assumption, a worker with a completed high school education, or the equivalent in on-the-job training, is expected to earn $6,365 per year ($365 for physical labor returns, $1,000 for primary school returns, and $5,000 for high school returns). This simple assumption about returns to human capital has powerful implications for the distribution of assets, including financial assets. Because earnings from college and postgraduate education vary so widely, and are often seen as a return on financial investment, they are included in the financial category.

3. *Financial capital* permits ownership of land, industrial plant and equipment, and other financial assets. This category, of course, is what most people think of as "assets," and determining their distribution has bedeviled both theorists and empiricists

for decades. As a simple example of an age-old controversy in economics, should capital assets be valued at what they cost, minus depreciation, or at market value as determined by the discounted flow of income? The market value approach has the obvious merit of putting all assets on a similar valuation basis, and of linking directly income flows with asset values. The disadvantage is the near tautology implied between incomes and asset values. The link can be altered only when the discount rate changes.

The empirical work reported in Appendix 2 does not break down financial capital into more workable components, especially land, industrial capital, and financial assets, because this whole category of capital does not become important to income production until well into the development process. Lack of access to land, or industrial jobs, will obviously reduce the earnings of the poor with no other capital at their disposal. But the surprising fact is that variations in human capital seem able to account for most of the differences in income distribution among poor countries, at least when income is disaggregated only to the quintile level. This fact opens important policy opportunities.

4. *Social capital* has taken the economic development profession by storm (Woolcock 1998, 1999). By various measures, it seems to account for order-of-magnitude differences in incomes among individuals in African villages (Narayan and Pritchett 1999), as well as similarly large differences in incomes among countries (Knack 1999). The social networks, institutional infrastructure, and level of trust among economic agents that might account for these differences in productivity are the subject of major research efforts, much of it in the field of economic history (North 1992). Without a consensus yet on how to define social capital or attribute productivity differences to it, this paper merely observes that there are likely to be at least two different levels at which social capital operates, with substantially different policy implications.

First, social capital seems to exist at the micro level, connecting individual villagers whose knowledge of each other can be turned into collateral for loans, for example. An entire microfinance industry is growing around this realization (Morduch 1999). At the other end of the spectrum, social capital in the form of deeply rooted institutions that support property rights and rule by law also seems to have macro-level implications for productivity and economic growth (Olson 2000). Indeed, North (1992) argues that these institutions fully account for the differences in welfare levels between rich and poor countries. Empirical analysis of the lasting effects of different types of institutional investments by colonial powers shows both the huge quantitative effect of institutions on income growth as well as their lasting footprints to the present (Acemoglu et al 2001, Easterly 2002). Consequently, it does not seem outlandish to suggest that societies with a full ‘‘portfolio’’ of social capital might have labor productivity that is twice as high as in a similar society with serious shortfalls in social capital, holding other forms of capital constant. Translating this reality into effective development policy is well beyond the scope of this paper, but the historical perspective it requires is an important lesson in itself.

The special role for agriculture in poverty reduction

The agricultural sector specifically and the rural economy more broadly are uniquely important to connecting the poor to the economic growth process because so many of them live in or come from rural areas. Further, growth in agricultural productivity has demonstrable economy-wide benefits, many of which receive no value in commodity markets where farmers sell their output. The case for developing an agricultural strategy as part of any poverty reduction strategy is clear. Still, such a strategy must be carefully constrained by market realities and institutional capabilities. This case, summarized here, is presented in detail in Timmer (2002b).

Agriculture and economic growth

Agricultural development has made important and direct contributions to the historical rate of economic growth in nearly all countries. As stressed by Lewis (1954) analytically and by Johnson (1997) empirically, lower food prices stimulated by rapid technological change in agriculture have contributed substantially to higher living standards directly, especially for the poor, who spend a large share of their budget on basic foodstuffs, and indirectly by keeping real wage costs low in the industrial sector, thus fostering investment and structural transformation. It is argued, however, that these benefits of low food prices are as easily obtained by trade as by investing in the domestic agricultural sector (Sachs 1997). What is the significance of other contributions from agricultural modernization that would be missed with a pure trade strategy?

Plausible candidates include the loss of backward and forward linkages that connect cities with the countryside. Without these linkages, societies risk greater vulnerability to fluctuations in world markets, inequities between rural and urban inhabitants, more underemployment in rural areas, and excess migration. The returns to good rural-urban linkages include a relatively smooth structural transformation, as seen in Taiwan Province of China, in contrast to the difficulties seen in Thailand (Tabor 2002, Timmer 1988).

Surprisingly, in view of the length of time the discussion has been going on, there are still no satisfactory tests of the effect of changes in agricultural productivity on the value of good rural-urban linkages. There is evidence produced by a large data-gathering project at the World Bank led by Don Larsen, Will Martin, and Yair Mundlak that total factor productivity in agriculture tends to grow faster than in manufacturing (Martin and Mitra 1996). This result alone argues that past investments in agriculture have had large economic returns (Mundlak 2001).

Still, the questions remain—How does agriculture affect economic growth and how much should governments invest to make it happen? First, there is the obvious national income accounting identity: the change in national income is equal to the growth rates in the agricultural and nonagricultural sectors, weighted by their respective shares in aggregate gross domestic product (GDP). It is worth noting that, where the agricultural share is large, the direct contribution of agriculture to total economic growth can also be substantial. This obvious but often forgotten fact is also an ingredient in the fast growth of city-states or city-regions such as Singapore and the Special Administrative Region Hong Kong of China, which never faced the drag of a large, slow-growing agricultural sector or the need to make large infrastructure investments to modernize that sector.

For countries where the share of agriculture is still significant, changes in agricultural productivity can also influence the growth process through a set of indirect and roundabout linkages. These linkages can be categorized by each of the variables in a standard production function used by neoclassical economists to describe quantitatively the relationship between inputs and output. These “input variables” include the location of the local technological frontier, the rate of physical capital deepening, the rate of human capital deepening, and any changes in the economic or institutional “environment” that influence how efficiently an economy operates relative to its local technological frontier (Timmer 2002b, Mundlak 2000, 2001).

Effect on the rate of shift in the local technological frontier. Increases in agricultural value added can produce exports (or substitute for imports) and earn foreign exchange that permits imports of foreign technology, where new technology, embodied in physical capital, determines the location of the local technological frontier. It should be noted that agricultural exports have a very high ratio of value added, unlike many manufactured exports that rely heavily on imported materials and components. On the other hand, there may be few knowledge spillover effects from exporting traditional agricultural products, thus forgoing one of the main growth stimulants from foreign trade specified in the endogenous growth literature (Romer 1990). Earning foreign exchange is one of the standard Johnston-Mellor linkages (Johnston and Mellor 1961). There is, however, evidence that very heavy dependence on primary exports is a significant factor influencing the probability of violent conflict within a country (Collier 2001).

Effect on the rate of physical capital deepening. Savings from the agricultural sector are a function of agricultural value added, and, in a semiclosed economy or one with imperfect capital markets, higher savings translate into faster physical capital deepening (Feldstein and Horioka 1980). The sector in which the investment takes place will depend on financial intermediaries (for private savings) or mechanisms of savings extraction (for example, taxation or pricing policy). This is a standard Lewis linkage (Lewis 1954). Even in a global economy with open financial markets, most investment in developing countries comes from their own domestic savings.

Savings may be less productive for growth if in government hands rather than private hands, after minimum government revenues are available to fund affairs of state. It should be recognized, however, that these public revenues can have very high productivity when invested in public goods and infrastructure that raise the profitability of private-sector investment in agriculture (Teranishi 1997). If agriculture is more easily taxed than nonagriculture in the early stages of development, perhaps by border taxes on exports, the agricultural sector may well provide revenue for this important initial stage of public-sector investment. No country has been able to develop successfully without making these public-sector investments.

Effect on the rate of human capital deepening. Rural education levels can be influenced by growth in agricultural productivity and rural incomes (Chai 1995, Birdsall et al 1995). Such education can raise farm productivity directly (Jamison and Lau 1982). It can also make the migration process much less painful and more economically rewarding for children who leave the farm (Johnson 1997, Larson and Mundlak 1997).

Improved nutritional intake can raise labor productivity through the processes examined in historical England and France by Fogel (1991, 1994). Although in principle staple foods are tradable, in fact there is a very high correlation between increases in food production and increases in food consumption within regions and countries. The "Fogel linkages" can thus be stimulated by growth in agricultural output, especially food output. Although the historical relevance of the Fogel linkages is usually discussed in terms of protein-energy availability, it is also possible that higher productivity in livestock operations may have contributed to micronutrient intake and improved nutritional status in that way.

Effect on the rate of change in "efficiency" variables. A wide range of variables might cause economies to produce at less than their technically efficient level. Lack of economic freedom, poor institutions, ineffective economic policies, and political instability all have been shown to slow down economic growth when controls are included for initial conditions and factor accumulation (Barro 1997). How changes in agricultural productivity might affect these "efficiency shifters" is a matter of considerable speculation and relatively little empirical evidence. Two mechanisms for which evidence is accumulating involve price stability, because investments are more efficient when signal extraction problems are reduced (Lucas 1973, Dawe 1996, Rock 2002), and political economy considerations, because restive rural populations can challenge political leaders if they are left behind during the process of rapid economic growth (Anderson and Hayami 1986, Gardner 2002).

Other linkages that Johnston and Mellor identified might also work through these "efficiency" variables. For example, producing raw materials for industrial processing suggests that capacity use in the industrial sector depends on agricultural productivity. Earning foreign exchange might have the same effect on imported intermediate goods, which are often crucial for producing manufactured exports.

With surpluses of agricultural commodities flooding world markets, investing in agricultural development as a way of speeding overall economic growth would seem to be a hopeless cause. A key lesson of postwar economic development has been the need for agricultural development to be led by market forces that provide incentives to farmers to increase their output. With market incentives so low, depressed especially by the farm subsidies in Organization for Economic Cooperation and Development (OECD) countries, What sense does it make to design strategies for further agricultural development in poor countries? Why invest in research designed to provide new, more productive technologies for their farmers? At least part of the answer lies in the realization that market prices do not always convey all the information needed to design appropriate government strategies (Timmer 1995). This is especially true when markets place no value on dimensions of a sector's output, such as reduced poverty, greater stability, or food security, that matter greatly to a country's policymakers. The next section examines the subject of nonmarket values of agricultural productivity.

Does rural growth mediate poverty reduction?

The work of Mellor, Ravallion, and Timmer shows the empirical role of rural growth in connecting the poor to economic growth, both within and outside the rural economy. Without firm theoretical underpinnings, however, these empirical observations provide only casual guidance to policymakers seeking to make the growth process more pro-poor. It would be better to understand the mechanisms at work as well as the facts (Sarris 2001).

Fortunately, much progress has been made in the past decade in identifying these mechanisms. Foremost in this effort is the recent model of agricultural growth, rural employment, and poverty reduction that emphasizes the role of nontradables in pulling underemployed workers out of agriculture into the nonagricultural rural economy (Mellor 2000). This model, drawing on Mellor's earlier work in India (Mellor 1976), shows the importance of rural incomes as the driver of demand for the goods and services produced in the nonagricultural rural economy and how this economy links to urban demand, especially when it is driven by rising incomes from workers in labor-intensive export industries. Having left their farms in search of better jobs, these workers often retain "rural" tastes in their consumption patterns.

The Mellor model is the first to explicitly recognize this connection among manufactured export performance, the role of the nontradable sector in the rural economy, and subsequent reductions in poverty. Thus, the model explains why countries with rapid growth from labor-intensive manufactured exports, that also have substantial agricultural sectors, had such good records of poverty reduction. But the nontradable sector is often ignored by policymakers and donors precisely because so much emphasis is placed on the role of exports and open-economy strategies for economic growth. Retargeting public expenditures in support of a more balanced strategy will not sacrifice overall growth performance but it will increase its effect on reducing poverty (Mellor 2000).

Two other components of the relationship between rural growth and poverty reduction should be noted. First, political commitments to rural growth imply a more balanced political economy, with less urban bias than has been seen in most developed countries historically (Lipton 1977, 1993, Timmer 1993). The developing world has already seen a notable reduction in the macroeconomic biases against agriculture, such as overvalued currencies, repression of financial systems, and exploitive terms of trade (Westphal and Robinson 2002). Further progress might be expected as democracy spreads and empowers the rural population in poor countries.

The second important component is the linkage between urban and rural labor markets, often in the form of seasonal migration and remittances. There is no hope of reducing rural poverty without rising real wages for rural workers. Rising wages have a demand and a supply dimension, and migration can affect both in ways that support higher living standards in both parts of the economy. Migration of workers from rural to urban areas raises other concerns, of course, but those concerns depend fundamentally on whether this migration is driven by the push of rural poverty or the pull of urban jobs. Either way, the food security dimensions of rural-urban migration are clear. Urban markets become relatively more important in supplying food needs for the population. Whether the country's own rural economy or the world market is the best source of this supply will be one of the prime problems facing economic policymakers (Naylor and Falcon 1995, Tabor 2002).

Agriculture and nutritional quality

The link between agricultural productivity and nutritional quality has often been weak, or even negative. The dramatic quantity effect of the seed-fertilizer revolution materialized as sharply higher cereal intake by the poor. But some anecdotal evidence suggests that legume production, and dietary intake, declined as the new technology was more profitable for farmers.

The new emphasis on micronutrients suggests that there are other dimensions to the links between agricultural productivity and nutritional well-being. Lower grain prices can stimulate livestock production and provide local markets with high-quality animal protein and highly absorbable sources of micronutrients. Ready availability of cheap grain in local markets permits farmers to specialize in growing fruits and vegetables instead of grain, with similar nutritional effect. The stimulus to small and medium enterprises in rural areas from low nominal wages, made possible by low food prices, can speed the absorption of surplus labor and set the stage for higher real wages. Nutrition knowledge, household income, and low prices for foods with high levels of micronutrients are the major determinants of micronutrient status in rural households. Agricultural productivity can influence prices directly and incomes indirectly and provide the local supplies to make nutrition knowledge effective.

Multifunctionality and agriculture

Much of the discussion of nonmarket values from farm production has focused on agriculture's "multifunctionality" as the basis for domestic policies that have clear social, environmental, or security rationale. The United States especially has been reluctant to embrace this concept, seeing it as a disguised mechanism for agricultural protection in Europe, Japan, and Korea. But the above discussion highlights the importance of nonmarket values from the agricultural sector in developing countries, where the sector's role in stimulating economic growth and reducing poverty should win U.S. applause.

Thus, it would be sensible for the United States to take the lead in the Doha Round of WTO negotiations to design rules explicitly recognizing what reasonable "multiple" functions might be for agriculture in different countries and at different stages of development. For example, environmental protection would be an acceptable role for domestic agricultural policies in all countries, whereas policies to stimulate basic grain production to enhance domestic food security would be restricted to countries with limited access to world markets or poorly developed internal marketing systems. Diversification efforts to broaden the base for improving rural productivity and reducing poverty would also be permissible where rural poverty remains a priority.

Policy approaches and the role of government

This perspective on the connections linking agriculture, economic growth, and poverty reduction suggests two policy arenas where government actions might strengthen the connections even when the starting point with respect to income and asset distribution is unfavorable. In turn, we discuss the mechanisms for "getting agriculture moving," to use Arthur Mosher's memorable phrase (Mosher 1966), and initiatives to develop human capital, especially for the rural population.

Getting agriculture moving

There is no great secret to agricultural development. Mosher (1966) and Schultz (1964) had identified the key constraints and strategic elements by the mid-1960s. New agricultural technology and incentive prices in local markets combine to generate profitable farm investments and income streams that simultaneously increase commodity output and lift the rural economy out of poverty (Hayami and Ruttan 1985). The process can be speeded up by investing in the human capital of rural inhabitants, especially through education, and by assistance in the development of new agricultural technology, especially where modern science is needed to play a key role in providing the genetic foundation for higher yields.

Beyond this level of general understanding, however, the diversity of rural circumstances has sharply impeded its implementation. At the regional level, for example, neither the agricultural technology nor the incentive prices in rural markets have been reliably available in Sub-Saharan Africa. In Asia, success in linking the nontradable sector in rural areas to urban markets and labor-intensive export growth has been mixed at best. And, in Latin America, extreme rural poverty has largely migrated to urban areas, so the poverty problem is now primarily an urban problem (Painter 2001, Haddad et al 1999). Central America and Mexico continue to face acute rural poverty, however, and rural strategies will be needed to reduce it (de Janvry and Sadoulet 2000, 2001).

The mechanisms for both technology development and provision of rural price incentives are no longer as clear as they were in the 1960s. The CGIAR system has a laudable record of important breakthroughs for many of the world's staple foods. But funding for the system has been threatened as the market prices of these crops have dropped to historic lows, under the weight of productivity gains in developing countries and publicly subsidized crop surpluses in rich countries. Few countries have the scientific resources to conduct basic crop research on their own; so, a large question looms. Where will agricultural technology come from for the additional 3 billion people expected in the next 50 years? Biotechnology holds out both promise and concern; even in the best of circumstances, it is largely a product of scientific enterprise, public and private, in advanced countries.

There is an obvious role for the rich countries in answering this question. First, starving the CGIAR centers of funding to pursue essential and basic crop research with spillovers to many countries is very short-sighted. OECD leadership in restoring budgets could have major add-on effects. Second, the Western research university system is the best in the world at training scientists in basic biology and applied agricultural fields. The opportunity exists to provide the next generation of these scientists for the entire world.

Apart from its indirect effect on funding for the CGIAR system, the sharp drop in commodity prices in world markets also has a more immediate effect (Fox 2002). Open borders and flexible markets for foreign exchange transmit these low prices directly into the markets of poor countries, often with devastating effects on local farmers (Dawe 2002, Tabor 2002). Rich countries find ways to protect their farmers against such low prices, but poor countries cannot afford the subsidies, or defend the trade interventions, that would be needed to do the same. "Agriculture-led economic growth' is impossible unless it is profitable.

Instability in food prices also remains a concern, especially with open borders and the possibility of sharp movements in exchange rates (Islam and Thomas 1996). In 1998, for example, the collapse of the Indonesian rupiah during the financial crisis caused the landed price of imported rice to increase more than fourfold. Indeed, for a time, it was profitable to export rice in the same year as one of the worst El Niño-induced droughts in history! In open economies, food price instability has macroeconomic roots as well as local supply and demand roots. If some degree of food price stability is a political imperative, new tools will be needed to provide it (Timmer 1989).

Many place their hopes for solving the problems of price levels and price instability on new rules regulating agriculture in the WTO. But negotiations leading to useful new rules are likely to be very difficult, with Europe and Japan still extremely reluctant to abandon their farmers to free markets. The United States, under great pressure from Congress not to give away its subsidy tools as mechanisms to keep U.S. farming profitable, actually increased the level of farm subsidies in the 2002 farm bill. But even within the Bush administration, there are other perspectives. The U.S. Department of Agriculture (USDA), for example, has taken a clear stance in favor of reduced subsidies and freer trade in agriculture.

> "Lowering tariffs and other barriers to trade is fundamental to expanding exports. The average food and agricultural tariff is 62%, much higher than tariffs on manufactured items. Both developed and developing countries have high tariffs. Exports to the large potential markets in South Asia (including India) and to South America must overcome tariffs of 113% and 40%, respectively. The United States has one of the lowest food and agricultural tariffs, at 12%, and thus stands to gain immensely from ambitious tariff cuts. However, the United States still maintains some high tariffs that protect specific commodities.
>
> In addition to tariffs, high levels of domestic support for agriculture and export subsidies distort agricultural markets. In contrast to tariffs that are applied by almost all countries, developed countries account for virtually all domestic support and export subsidies. The OECD estimates that, in 2000, developed countries' total support for agri-

> culture was $327 billion. In that same year, total production supports by the European Union were $90.2 billion, compared with $49 billion by the United States. The EU dominates the use of export subsidies, accounting for approximately 90% of total annual spending since the Uruguay Round Agreement on Agriculture (URAA) took effect.
>
> USDA research shows that removing all forms of agricultural protection and support could raise world prices 12%, over half of this from removing tariffs alone. Our producers and the industries they support could see the value of U.S. agricultural exports grow 19%. Global economic welfare would increase by $56 billion annually by removing existing distortions" (USDA 2001, p. 40).

The way forward on these negotiations is badly in need of leadership. The United States is increasingly seen as a hypocritical voice in this effort, emphasizing narrow domestic political interests. The developing world itself will probably have to provide a united front on liberalizing agricultural trade if any progress is to be made in the Doha Round.

In the end then, What are the components of an agricultural development strategy? First, obviously, is a supportive macroeconomic policy, one that yields low inflation, a reasonably stable exchange rate, positive real interest rates, and perhaps some monitoring of disruptive short-run capital flows. Second, "getting prices right" extends good macro policy to the trade arena, where an open economy with low barriers to internal and external trade should produce a level playing field for producers and consumers alike.

What remains after this? The externalities from rural growth outlined above argue for policy attention and budget priorities for the rural nontradable sector, once agricultural technology is in place as the basis for profitable farming. Part of the profitability for this sector will come from a labor-intensive export sector that is successfully linked into the global economy. Rapid growth in this export sector creates demand for labor directly as well as for the goods and services of the rural economy that raise demand for labor indirectly.

Improving the rural financial system, both to permit farmers to make long-run investments and as a vehicle for handling intersectoral financial flows such as savings and remittances, will take time, but is essential to a successful structural transformation. None of this is rocket science, but all of it requires talented policy analysts and government administrators.

Investing in human capital

Investments in human capital improve the distribution of assets in the early stage of economic development, and therein is a clear policy message. For "pro-poor growth," a country must invest in the human capital of its poorest citizens. At the earliest stages, this will involve primary health clinics, household food security, and access to rural schools. Policies that encourage the efficient functioning of rural financial markets can also play a role in increasing the poor's access to capital. Later, it will mean opportunities for high school education and on-the-job training as unskilled and semiskilled labor. Such investments, if broad-based and of adequate quality, will keep the distribution of income from becoming highly skewed until well into the development process, and thus lead to the near elimination of absolute poverty. Taiwan Province of China and South Korea managed such investments until middle-income status; Brazil, the Philippines, and Thailand did not.

An optimistic policy interpretation of these results is that fiscally manageable investment strategies are available for even the poorest countries to set themselves on a growth path that includes the poor. The pessimistic interpretation suggests that political forces or bad governance will keep this from happening where the "starting point" in income and asset distribution already prevents the poor from connecting to the growth process. But surely this is a result that the donor community can grasp it provides donors with a rationale for investing in the very people that countries' leaders themselves might choose, or be forced, to ignore. Then, the policy dialogue, and the resources that could be mobilized behind it, can have dramatic effects.

Investments can be in specific knowledge as well. If the striking results for rural Central Java are any indication, the economic and welfare returns to giving mothers knowledge about the sources and importance of micronutrients are extraordinarily high (Block 2002). Diversifying local agricultural production will be one way to supply these micronutrients while moving farmers out of the income trap they face when producing low-value food grains. Fortification programs may also be highly cost-effective.

Reflections on missed opportunities and the role of government

Policymakers in developing countries show an understandable impatience with academic debate. While the main points of agreement are ignored as uninteresting, controversy rages over the decimal points. Some of that is on view here. Economic growth is good for the poor. But it could be better. Agricultural development is good for food security, poverty reduction, and economic growth. But, in theory, the same or larger benefits could be achieved by importing cheaper food from world markets and investing the difference in export-processing zones. And so it goes, the best as the enemy of the good.

And yet, it is only from the perspective of theory that we know what is possible, what we have missed, and what new opportunities await. From this perspective, the major players in the global economy missed three opportunities to assist economic development over the past several decades. First, two decades intervened between the first and the second world food conferences, with little to show in terms of increased food security and reduced poverty in the most vulnerable countries—those that might have hoped that Henry Kissinger's promise in 1976 that no child would go to bed hungry within a decade actually would translate into action. Other countries, especially in East and Southeast Asia, used the two decades to improve their rural infrastructure, agricultural technology, and economic competitiveness. They were rewarded with reduced poverty, improved food security, and rapid economic growth, but the global promises figured little in this performance.

Second, subsidies to farmers in rich countries have become larger over the past two decades, not smaller, despite promises made at the Uruguay Round. The result has not just been a large budget burden in OECD countries. More importantly for developing countries, the result has been increasing surpluses dumped on world markets, depressing world prices and the incomes of farmers in poor countries who have to compete with these prices. The best guess is that every dollar of agricultural subsidies in rich countries costs farmers in poor countries a similar amount. And official development assistance is only one-quarter of this total. It is not even remotely a fair trade.

What should developing countries do about this? First, it is important to get on with the tasks of economic development, most of which involve critical domestic decisions about macroeconomic policy, trade regimes, and economic governance. Despite repeated calls for “new thinking” on how to design and implement these critical decisions, their basic elements have been known for a decade or more. There is no substitute for sound fiscal policy, with domestic expenditures close to domestic tax revenues. There is no substitute for sound monetary policy, with low and transparent rates of inflation. Investments must be profitable, whether from domestic or international lenders, and they must not depend on special favors for their success. The public sector must not disappear under some mantra of “privatization.” The right kind of public investments “crowd in” private investments. As noted earlier, this is not rocket science. It does not depend on another decade of research. It does depend on connecting domestic policymakers to what is known about the development process, and adapting it to local circumstances.

Unfortunately, the gap here is enormous. The blame lies partly with domestic policymakers, who often think that they must rely only on domestic research and analysis to justify the way forward. In fact, of course, rediscovering the wheel is a very costly exercise. But part of the blame lies with the international policy research community, which is often caught up in the publication mill and spends far too little time explaining the relevance of international experience in specific domestic settings. Finding ways to bridge this gap would pay very large dividends.

References

Acemoglu D, Johnson S, Robinson JA. 2001. The colonial origins of comparative development: an empirical investigation. Am. Econ. Rev. 91(5): 1369-1401.

Alesina A, Perotti P. 1993. Income distribution, political instability, and investment. Working Paper No. 4486. Cambridge, Mass. (USA): National Bureau of Economic Research (NBER).

Anand S, Kanbur SMR. 1993. The Kuznets process and the inequality-development relationship. J. Dev. Econ. 40(1):25-52.

Anderson K, Hayami Y, with associates. 1986. The political economy of agricultural protection: East Asia in international perspective. London: Allen & Unwin.

Barro RJ. 1997. Determinants of economic growth: a cross-country empirical study. Development Discussion Paper No. 579, Harvard Institute for International Development. 116 p.

Birdsall N, Ross D, Sabot R. 1995. Inequality and growth reconsidered: lessons from East Asia. World Bank Econ. Rev. 9(3):477-508.

Birdsall N, Londano JL. 1997. Asset inequality matters: an assessment of the World Bank's approach to poverty reduction. Am. Econ. Rev. 97(2).

Bliss C, Stem N. 1978. Productivity, wages and nutrition: parts I and II. J. Dev. Econ. 5(4):331-398.

Block S. 2002. Nutrition knowledge versus schooling in the demand for child micronutrient status. Fletcher School, Tufts University. (In mimeo.)

Chai CP. 1995. Rural human capital and economic growth in developing countries. Senior Honors Thesis. Cambridge, Mass. (USA): Department of Economics, Harvard University.

Collier P. 2001. Conflict and development. Development Research Group, The World Bank.

Datt G, Ravallion M. 1997. Why have some Indian states done better than others at reducing rural poverty? Economica 64.

Dawe D. 1996. A new look at the effects of export instability on investment and growth. World Dev. 24(12):1905-1914.

Dawe D. 2002. The changing structure of the world rice market, 1950-2000. Food Policy 27(4):355-370.

De Gregorio J, Lee J-W. 1998. Education and income distribution: new evidence from cross-country data. Department of Economics, Korea University, Seoul, Korea.

Deininger K, Squire L. 1996. A new data set measuring income inequality. World Bank Econ. Rev. 10(3):565-591. Data available at www.worldbank.org/html/prdmg/grwthweb/growth–t.htm.

Deininger K, Squire L. 1998. New ways of looking at old issues: inequality and growth. J. Dev. Econ. 57.

De Janvry A, Sadoulet E. 2000. Rural poverty in Latin America: determinants and exit paths. Food Policy 25:389-409.

De Janvry A, Sadoulet E. 2001. Concepts for an approach to rural development in Mexico and Central America: regional development and economic inclusion. Prepared for the IDB regional workshop, Desarrollando la economia rural de Puebla a Panami, Guatemala City. 5-7 March.

Easterly W. 1997. Life during growth. World Bank Development Research Group. (In mimeo.)

Easterly W. 2002. Inequality does cause underdevelopment: new evidence. Working Paper No. 1. Center for Global Development, Institute for International Economics, Washington, D.C.

Feldstein M, Horioka C. 1980. Domestic saving and international capital flows. Econ. J. 90:314-329.

Fogel RW. 1991. The conquest of high mortality and hunger in Europe and America: timing and mechanisms. In: Higonnet P, Landes DS, Rosovsky H, editors. Favorites of fortune: technology, growth, and economic development since the industrial revolution. Cambridge, Mass. (USA): Harvard University Press. p 35-71,

Fogel RW. 1994. Economic growth, population theory, and physiology: the bearing of long-term processes on the making of economic policy. Nobel Prize Lecture. Am. Econ. Rev, 84(3):369-395.

Fox JW. 2002. Development overview. Draft chapter for "Natsios Report." USAID, Washington, D.C.

Gallup J, Radelet S, Warner A. 1997. Economic growth and the income of the poor. Harvard Institute for International Development. Prepared for the CAER II Project. (In mimeo.)

Gardner BL. 2002. American agriculture in the twentieth century: how it flourished and what it cost. Cambridge, Mass. (USA): Harvard University Press.

Gugerty MK, Timmer CP. 1999. Growth, inequality and poverty alleviation: implications for development assistance. Prepared for CAER 11, USAID, Washington, D.C.

Haddad L, Rue1 MT, Garrett JL. 1999. Are urban poverty and undernutrition growing? Some newly assembled evidence. Food Policy 27(1):1891-1904.

Hayami Y, Ruttan V. 1985. Agricultural development: an international perspective. Revised and expanded edition. Baltimore, Md. (USA): Johns Hopkins University Press.

Islam N, Thomas S. 1996. Foodgrain price stabilization in developing countries: issues and experiences in Asia. Food Policy Review No. 3. Washington, D.C.: International Food Policy Research Institute.

Jamison D, Lau L. 1982. Farmer education and agricultural productivity. Baltimore, Md. (USA): Johns Hopkins University Press.

Johnson DG. 1997. Agriculture and the wealth of nations, Ely Lecture. Am. Econ. Rev. 87(2):1-12.

Johnston BF, Mellor JW. 1961. The role of agriculture in economic development. Am. Econ. Rev. 51(4):566-593.

Knack S. 1999. Social capital, growth and poverty: a survey of the cross-country evidence. World Bank, Social Capital Initiative, Working Paper #7.

Larson D, Mundlak Y. 1997. On the intersectoral migration of agricultural labor. Econ. Dev. Cult. Change 45(2):295-319.

Lewis WA. 1954. Economic development with unlimited supplies of labor. The Manchester School 22:3-42.

Lipton M. 1977. Why poor people stay poor: urban bias in world development. Cambridge, Mass. (USA): Harvard University Press.

Lipton M. 1993. Urban bias: of consequences, classes and causality. In: Varshney A, editor. Beyond urban bias. London (UK): Frank Cass. p 229-258.

Lucas RE. 1973. Some international evidence on output-inflation tradeoffs. Am. Econ. Rev. 63:326-334.

Martin W, Mitra D. 1996. Productivity growth in agriculture and manufacturing. International Trade Division, The World Bank, preliminary draft. 30 p.

Mellor JW. 1976. The new economics of growth: a strategy for India and the developing world. Ithaca, N.Y. (USA): Cornell University Press.

Mellor JW. 2000. Agricultural growth, rural employment, and poverty reduction: non-tradables, public expenditure, and balanced growth. Prepared for the World Bank Rural Week 2000, March.

Morduch J. 1999. The microfinance promise. J. Econ. Lit. 37(4):1569-1614.

Mosher AT. 1966. Getting agriculture moving: essentials for development and modernization. New York, N.Y. (USA): Praeger.

Mundlak Y. 2000. Agriculture and economic growth: theory and measurement. Cambridge, Mass. (USA): Harvard University Press.

Mundlak Y. 2001. Explaining economic growth. Am. J. Agric. Econ. 83(5):1154-1167.

Narayan D, Pritchett L. 1999. Cents and sociability: household income and social capital in rural Tanzania. Econ. Dev. Cult. Change 47:871-892.

Naylor R, Walter PF. 1995. Is the locus of poverty changing? Food Policy 20(6):501-518.

North DC. 1992. Transaction costs, institutions, and economic performance. San Francisco, Calif. (USA): ICS Press.

Olson M. 2000. Power and prosperity: outgrowing communist and capitalist dictatorships. New York, N.Y. (USA): Basic Books.

Painter D. 2001. Urban poverty and the role of USAID. Washington, D.C. (USA): USAID.

Ravallion M. 1996. Can high-inequality developing countries escape absolute poverty? Policy Research Department, World Bank, Washington, D.C. (In mimeo.)

Ravallion M. 2001. Growth, inequality, and poverty: looking beyond the averages. World Dev. 29(11):1803-1815.

Ravallion M, Datt G. 1996. How important to India's poor is the sectoral composition of economic growth? World Bank Econ. Rev. 10(1):I-25.

Ravallion M, Datt G. 2002. Why has economic growth been more pro-poor in some states of India than in others? J. Dev. Econ. 68(2):381-400.

Rock MT. 2002. Exploring the impact of selective interventions in agriculture on the growth of manufactures in Indonesia, Malaysia, and Thailand. J. Int. Dev. 14(4):485-510.

Romer PM. 1990. Endogenous technological change. J. Polit. Econ. 98:S71-S102.

Sachs J. 1997. Nature, nurture, and growth. Economist, 14 June. p 19-27.

Sarris AH. 2001. The role of agriculture in economic development and poverty reduction: an empirical and conceptual foundation. Prepared for the Rural Development Department of the World Bank, Washington, D.C.

Schultz TW. 1964. Transforming traditional agriculture. New Haven, Conn. (USA): Yale University Press.

Strauss J. 1986. Does better nutrition raise farm productivity? J. Polit. Econ. 94(2):297-320.

Strauss J, Thomas D. 1998. Health, nutrition, and economic development. J. Econ. Lit. 36(2):766-816.

Tabor SR. 2002. Indonesian rice policy and the choice of trade regimes. Prepared for the BULOG seminar on alternative options for rice trade policy. Jakarta, Indonesia.

Teranishi J. 1997. Presentation at World Bank seminar on research project documenting importance of investment in agricultural infrastructure.

Timmer CP. 1988. The agricultural transformation. In: Chenery H, Srinivasan TN, editors. Handbook of development economics. Vol. 1. Amsterdam (Netherlands): North-Holland. p 275-331.

Timmer CP. 1989. Food price policy: the rationale for government intervention. Food Policy 14(1):17-42.

Timmer CP. 1993. Rural bias in the East and Southeast Asian rice economy: Indonesia in comparative perspective. In: Varshney A, editor. Beyond urban bias. London (UK): Frank Cass. p 149-176.

Timmer CP. 1995. Getting agriculture moving: Do markets provide the right signals? Food Policy 20(5):455-472.

Timmer CP. 1997. How well do the poor connect to the growth process? Harvard Institute for International Development. (In mimeo.)

Timmer CP. 2002a. The role of foreign assistance in the economic growth of developing countries. Draft chapter for the "Natsios Report" on Foreign Assistance and the U.S. National Interest. USAID, Washington, D.C. (In mimeo.)

Timmer CP. 2002b. Agriculture and economic growth. In: Gardner B, Rausser G, editors. The handbook of agricultural economics. Vol. II. Amsterdam (Netherlands): North-Holland.

United States Department of Agriculture (USDA). 2001. Food and agricultural policy: taking stock for the new century. Washington, D.C. (USA): USDA.

Wade R. 2001. The rising inequality of world income distribution. Finance Dev. 38(4):37-39.

Westphal L, Robinson S. 2002. The state of industrial competitiveness in developing countries. New York, N.Y. (USA): United Nations Development Programme.

Woolcock M 1998. Social capital and economic development: toward a theoretical synthesis and policy framework. Theory Society 27(2): 151-208.

Woolcock M. 1999. Managing risk, shocks, and opportunity in developing economies: the role of social capital. World Bank Development Research Group. (In mimeo.)

Notes

Author's address: Professor of Development Studies, Graduate School of International Relations and Pacific Studies, University of California, San Diego, 9500 Gilman Drive, Mail Drop 0519, La Jolla, CA 92093. ptimmer@ucsd.edu.

Acknowledgment: Major elements of this paper draw on my chapter prepared for the "Natsios Report" for USAID, but the Agency has no responsibility for the views expressed here. See Timmer (2002a).

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Appendix 1

The elasticity of connection between economic growth and poverty reduction

To estimate the elasticity of connection, Timmer (1997) regressed the level of income of each quintile on overall per capita GDP. This "levels" estimation includes country and time fixed effects (dummy variables for each developing country included and for each decade from the 1960s to the 1990s). The country fixed effects allow shifts in the regression intercept for each country, but assume the same slope, or elasticity of connection, for all countries. The fixed effects for decades allow a shift in the regression intercept for each 10-year decade.

The paper also restricted the sample of countries to those that have a significant agricultural sector, are reasonably large, and are considered developing countries. For this reason, city-states such as Hong Kong and Singapore were excluded, as were most countries with populations smaller than 6 million (Costa Rica and Jamaica are the exceptions to include better representation of Latin America and the Caribbean).

To examine the effects of inequality on income levels of the poor, Timmer constructed a variable that measures the relative income gap between the rich and the poor. A dummy variable was then created that is equal to one when the gap in income between the highest and lowest quintiles is more than twice as large as average income. Timmer then disaggregated income into sectoral components from agriculture and nonagriculture to examine whether the sectoral composition of labor productivity matters to the incomes earned by each quintile.

Earlier results from asking a similar question had already indicated that growth in the agricultural sector seems to have a much larger effect on growth of incomes in the bottom quintile than growth in services or industry (Ravallion and Datt 1996, Gallup et al 1997, Mellor 2000). The question here is framed in terms of relative labor productivities. Do the per capita labor productivities of workers in agriculture and nonagriculture have differential effects on the average earnings in each income quintile? Put another way, do the poor benefit more from growth in the agricultural or the nonagricultural sector?

Timmer found that, in unequal countries, that is, where the relative income gap is large, there is a pronounced Kuznets effect: the elasticity of connection for the poorest quintile is significantly lower than for the higher quintiles; the poor appear to be nearly disconnected from the growth process in these economies. The elasticity of connection for the poorest quintile is 0.257 for agriculture and 0.449 for nonagriculture. In contrast, for those economies with better income distribution, the elasticity of connection for the poor in the agricultural sector is 1.146 and 1.01 8 for nonagriculture. This is slightly higher than the elasticities for the upper quintiles, suggesting a slight but significant "anti-Kuznets" effect in these economies. These results are illustrated in Figure 1.

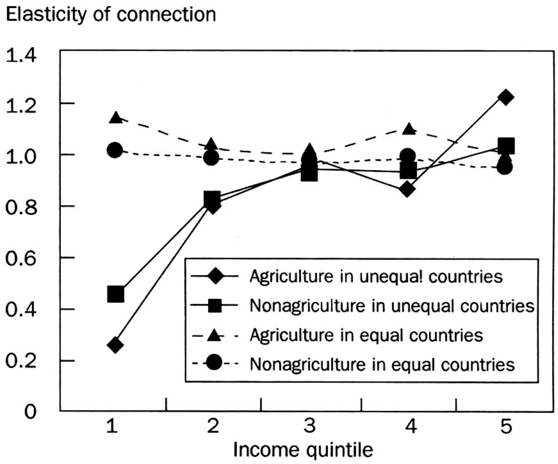


Fig. 1. Elasticity of connection in equal and unequal economies. Source: Timmer (1997).

Appendix 2

An empirical example comparing Brazil and Thailand

Building on the earlier analytical and empirical work in Timmer (1997), it is possible to use the definitions and returns to capital discussed in the text to construct crude estimates of the value of human and financial capital assets by income quintiles (for details, see Gugerty and Timmer 1999). As a particularly interesting comparison over time and space, Table 1 shows these asset values by quintile for Thailand and Brazil over a three-decade period.

Both Brazil and Thailand grew fairly rapidly during this three-decade period, Brazil from per capita income of $1,780 in 1960 to $4,272 in 1989 (3.06% annual growth), Thailand from $992 in 1962 to $3,924 in 1992 (4.69% annual growth). Income distribution in both countries, as measured by RELGAP[1], worsened, from an average level of 2.089 in Thailand at the start to a highly unequal level of 2.740 at the end. In Brazil, inequality was already very high at the start of the period, and worsened to a level of 3.135 at the end, one of the worst distributions of income in the entire Deininger-Squire sample.

Table 1. Changes in income and asset distributions over a three-decade period in Brazil and Thailand.

Quintile	Income per capita ($PPP)			Human capital per capita ($000)		Financial capital per capita ($000)	
Thailand, 1962-92	1962	1992	Annual per capita quintile growth	1962	1992	1962	1992
I	397	726	2.03%	0.64	7.22	0	0
II	427	1,491		1.24	22.52	0	0
III	600	2,276		4.70	38.22	0	0
IV	1,066	3,649		14.02	65.68	0	0
V	2,470	11,478	5.25%	42.10	120.00	0	102.26
RELGAP[a]	2.089	2.740		3.470	2.431		
Brazil, 1960-89	1960	1989	Annual per capita quintile growth	1960	1989	1960	1989
I	285	534	2.19%	0	3.38	0	0
II	614	1,047		4.98	13.64	0	0
III	970	1,965		12.10	32.00	0	0
IV	1,700	3,909		26.70	70.88	0	0
V	5,331	13,927	3.37%	99.32	120.00	0	151.24
RELGAP	2.835	3.135		3.306	2.223		

[a] See note in text.

---

[1] RELGAP is defined as the average per capita income in the top quintile minus the average per capita income in the bottom quintile, divided by the average per capita income for the society. When RELGAP is greater than two, economies have a difficult time sustaining growth and connecting the poor to it (Timmer 1997).

Not surprisingly, asset distributions in both countries also changed quite significantly, but not always in the expected direction. Levels of human capital increased dramatically for all income classes, but much faster for the poor than for the rich, who were already closer to the plateau levels used in this analysis. Increases of two to three times were the norm in Brazil; full order-of-magnitude increases occurred in Thailand. Even as income distribution worsened, the distribution of human capital became more equal, as the poor were finally included in the growth process to some extent.

This result is supported by empirical research that indicates that changes in primary school enrollment are strongly positively associated with growth in lower-income countries (Easterly 1997, de Gregorio and Lee 1998). Because of the self-limiting nature of human capital accumulation, however, this dimension of asset distribution is also limited in its potential contribution to future earnings. In addition, given the constraints on investment in human capital by the poor suggested by the theoretical literature, it is clear that government policy will play an important role in human capital accumulation at lower levels of development.

The open-ended nature of financial assets avoids the ceilings inherent in accumulation of human capital. If the distribution of financial assets is or becomes highly skewed during the growth process, at some point the income-earning potential of these assets will lead to a self-reinforcing skewing of incomes. Both Brazil and Thailand seem to have reached such a point by around 1990. In Brazil, a simple dynamic calculation shows that, if all incomes above the human capital level of $6,365 are saved and invested in financial assets that earn the assumed 5% per year, within a decade the upper quintile of income earners will receive the entire additional income produced by an economy growing at 5% per capita per year.

At some point in the development process, concentration of ownership of financial assets can lead to sharply skewed income distribution as an inevitable result of economic growth, a result that is not typically seen in the early stages of growth when the dependence on investments in human capital are far more important for the distribution of income and for lifting the poor out of absolute poverty (Ravallion 1996).

Plant breeding and genetics

Editor: D.S. Brar

New frontiers in genetics and plant breeding

Biodiversity, cytogenetics, genome analysis, 21st century biology, and crop improvement

B.S. Gill

The current plant breeding paradigm can be depicted as a continuum of disciplines involving biological diversity -> genetics/cytogenetics -> genomics -> plant biology-> crop improvement. Dr. G.S. Khush was the top practitioner of this paradigm for replenishing humanity's rice bowl on the world stage provided by IRRI. As someone who was initiated into plant cytogenetics by Dr. Khush in the late Professor Charley Rick's laboratory, we have applied this paradigm in stocking humanity's bread pantry under the auspices of the Wheat Genetics Resource Center. Brief highlights of our latest results on wheat's origins; cytogenetics and genome analyses; chromosome and genome differentiation, including recombination patterns, genomics, and transgenomics; and their application to wheat crop improvement are discussed.

I was initiated into plant cytogenetics by Gurdev Khush in the summer of 1969 while beginning my graduate studies in Charley Rick's laboratory at the University of California at Davis. Gurdev had joined the International Rice Research Institute (IRRI) the previous year as the rice breeder and was back in Davis to finish a book on aneuploidy. Gurdev patiently taught me how to make smear preparations from anthers and to identify the 12 chromosomes of tomato at the pachytene stage of meiosis. Since then, I have considered Dr. Khush as my mentor and friend. Therefore, it is a great honor for me to speak at a symposium honoring Dr. Khush on the eve of his retirement. What a great career and pleasure it has been for those who have been touched by it!

In Charley Rick's laboratory, Dr. Khush led the research integrating biodiversity, cytogenetics, and genome analysis toward the ultimate goal of crop improvement. At IRRI, Dr. Khush led a research team that used the same recipe with miraculous results for rice improvement. More important, this comprehensive basic and applied approach laid the foundation for the advances we are now witnessing in 21st century biology. It was no accident that the first disease-resistance genes were cloned in tomato (Martin et al 1993) and rice (Song et al 1995) because the genetic materials used were developed and unselfishly shared with the plant science community by Khush, Rick, and their colleagues.

Perhaps unknown to many, Dr. Khush wore two hats at IRRI, that of a rice breeder and a cytogeneticist. As a cytogeneticist, he dedicated his life to the study of chromosome structure, behavior, and manipulation. His book on aneuploidy (Khush 1973) became a classic. As a rice breeder, he understood biodiversity and cytogenetics and their critical role in crop improvement. In this review, I shall briefly touch on some biodiversity issues but will focus mainly on some of the classic questions and unsolved problems about chromosome structure, behavior, and evolution that underlie biodiversity.

Biodiversity versus biotechnology

Rather than a choice between the two, I see biotechnology as a tool to study, use, and enhance biodiversity. Biodiversity shaped by the environment is the source of germplasm for plant breeding and crop improvement. Genomics is the key discipline to unravel the biology of a fully functioning organism, how it perceives and reacts to the environment. This working knowledge of a functioning plant will have a major future effect on crop improvement. The crop improvement research enterprise is an organic whole. Although biodiversity is essential for progress in plant breeding, improved varieties and the spread of agriculture negatively affect biodiversity. We know that most agronomic genes, especially those involved in disease resistance, are fast evolving, as will be genes that may arise from other adverse effects on the environment such as global warming. So, our gene banks, while useful in the short term, are seed morgues over the long haul. We must maintain biodiversity *in situ* as "gene parks," at least for the centers of origin and diversity of our crop plants. In 2002, the United Nations hammered out plans for a sustainable world. We, the members of the plant science community, also must make long-term plans and ensure that our plant breeding enterprise is sustainable too, for the very survival of humankind hinges on it!

Biodiversity and variations in chromosome size, morphology, and number

Chromosomes package, reassort and recombine, transmit, and regulate the expression of all genes in an organism and form the material basis of biological diversity. Over thousands of millions of years of evolution, chromosome number and size diverged enormously among species. Genome size (the sum total of the size of an entire chromosome complement of an organism) can vary by the well-known mechanisms of aneuploidy and polyploidy. In addition, changes in genome size can be brought about by episodes of amplification and deletion of repeated DNA sequences. In grasses, chromosome number varies from 2n=4 (Bennett et al 1986) to 2n=200 in some sugarcane species (Gill and Grassl 1986). Similarly, the three grass crops that feed the world, rice, maize, and wheat, vary in chromosome size and number. Rice is a diploid with 2n=24 and basic chromosome number of 1x=12. Maize is a paleotetraploid with 2n=20 and 1x=5. Bread wheat is a recent allohexaploid with 2n=42 and 1x=7. The genome size also varies from 420 Mb in rice to 2,500 Mb in maize and 16,000 Mb in wheat. A typical wheat chromosome is 20 times the size of a rice chromosome and three times the size of a maize chromosome. The changes in chromosome number and size occurred over a span of 65 million years (Huang et al 2002). At the fundamental level, what mechanisms in these grass taxa produced a 20-fold variation in chromosome size and basic chromosome numbers ranging from 1x=5 to 1x=12? Advances in chromosome biology and comparative genomics have begun to yield answers to some of these questions and will be briefly discussed.

How chromosomes vary in size

The analysis of the structure of a piece of chromosome including genes *Sh2* (shrunken 2) and *A1* (anthocyaninless 1) at its boundaries in rice, maize, and wheat has shown that variation in the amount of transposable sequences (transposons and retrotransposons) is the major cause of the change in chromosome size (Fig. 1). Genes *Sh2-X1-X2-A1* span 20 kb in rice and 140 kb in maize, a sevenfold increase in size because of many rounds of amplification of transposable elements in maize (Civardi et al 1994).

In wheat, there was a break between *X1* and *X2*. The *Sh2-X1* interval spans 2 kb in rice and has a genetic length of 1.5 cM in wheat or an estimated size of 400 kb, a

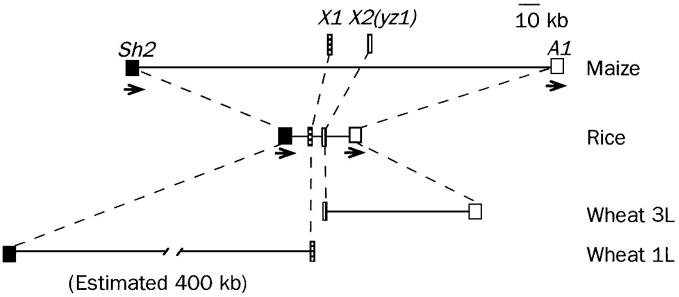


Fig. 1. Chromosome size expansion. The *Sh2* (shrunken 2)-*X1* (transcription factor)-*X2* (transcription factor)-*A1* (anthocyaninless 1) gene region has been used as a measuring scale to study genome expansion in maize and wheat vis-à-vis rice. These four genes are syntenic in rice and maize but not in wheat, where they are located on two different chromosomes. *Sh2* and *A1* are separated by only 20 kb in rice but by 140 kb in maize, a sevenfold genome expansion in maize. *X2-A1* is separated by 12 kb in rice but by 50 kb in wheat, a fourfold genome expansion in wheat. *Sh2-X1* is separated by 2 kb in rice and by an estimated 400 kb in wheat, a 200-fold expansion in wheat. In all cases, genome expansion was due to the amplification of transposable elements. For more details, see Li and Gill (2002); figure modified from Appels et al (2003).

200-fold change in size. *X2–A1* spans 12 kb in rice but 50 kb in wheat, a fourfold change in size. In the early Triticeae, the break in synteny decimated *X1* on the ancestral chromosome. A duplicated copy of *X1* on an alien chromosome, 7L, is now actually the functioning copy (Li and Gill 2002). Thus, it appears that transposons, retrotransposons, and, to a smaller extent, tandemly repeated DNA elements are the major players in chromosome size variation. In addition, transposable elements may be causal agents of chromosome repatterning, including deletions, inversions, duplications, and translocations.

How basic chromosome number changes occur

The change in basic chromosome number essentially amounts to a gain or loss of centromeres and redistribution of chromosome material. The loss of a centromere is easy to envision but, for the gain of a centromere, either the centromeres must be divisible or they have to arise *de novo.* It is known that basic chromosome number changes can arise within populations of a species. This occurs in species with mostly acrocentric chromosomes. Two acrocentric chromosomes can fuse to form a metacentric Robertsonian translocation chromosome with the loss of the genetically inert short arms, and the basic chromosome number is reduced by one. The process is reversible. Recently, Zhang et al (2001) analyzed centromere structure in experimentally produced Robertsonian translocation chromosomes and showed that centromeres are divisible. Based on this, one can easily imagine a model for basic chromosome number changes as depicted in Figure 2.

Pencentric inversions and translocations can further mold chromosome morphological diversity ranging from large to small and acrocentric to metacentric. Comparative genome analysis of rice, maize, and wheat indicates that two chromosomes (at least around the centromeres and most of the adjacent short and long arms) in the basic complement may have maintained ancestral structure. The chromosomes 1 of rice, 3 of maize, and 3 of wheat are essentially colinear (Sorrells et al 2003). The remaining chromosomes may have been derived by a process of centromere misdivision, translocations, and inversions. We do not know the ancestral basic chromosome number of the grass family. Assuming 1x=5 as the ancestral condition for the maize, wheat, and rice lineage, 1x=7 of the Triticeae can be calculated by the formula $2 \times 2 + 3 = 7$ (four derived from centromere misdivision and three have ancestral centromeres). From 1x=7, 1x=12 of rice can be obtained by the formula $5 \times 2 + 2 = 12$ (10 derived and two ancestral). This hypothesis can be tested by targeted comparative mapping of the pericentromeric regions.

What triggers chromosome change?

As mentioned earlier, transposable elements are major agents of chromosomal evolution. Early on, McClintock (1984) had argued that genome stress can activate these elements. It has been known for a long time that intra-/interspecific hybridization is also associated with genetic novelty (Rick 1967). Polyploidization has also been associated with rapid genomic changes (Leitch and Bennett 1997, Ozkan et al 2001). Certain genes are also associated with chromosomal restructuring. The well-known

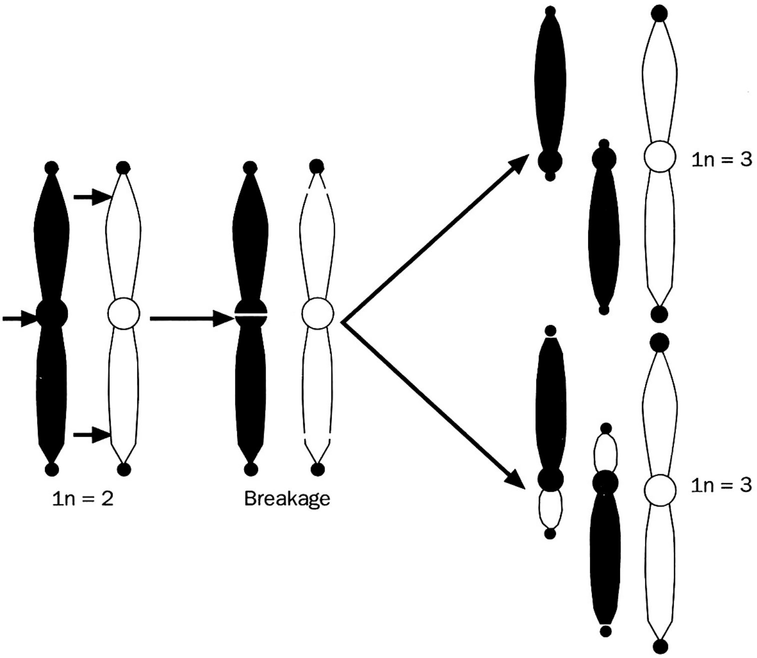


Fig. 2. Increase in basic chromosome number. A model scheme by which basic chromosome number changes may occur in nature. As demonstrated by Zhang et al (2001), the centromere may break, producing two acrocentric chromosomes that become healed by the addition of telomeres (top right). See Werner et al (1992) on the role of telomeres in chromosome healing. A break in the centromere may be accompanied by other breaks in chromosome arms; the subsequent union of half centromeres with acentric fragments will produce a rearranged karyotype accompanied by an Increase in chromosome number (bottom right). Such a scheme may explain changes in basic chromosome numbers in taxa within tribes and families as observed among rice (1x=12), maize (1x=5), and wheat (1x=7).

example is the gametocidal gene in wheat that is active only in F_1 hybrids (genotype: *Gcl–*) between a *Gc* - carrier (*Gc/Gc*) and a *Gc* - noncarrier line (–/–).The *Gc/* –plants have normal meiosis. Among the two types of gametophytes, the "-" type undergoes extensive chromosome breakage prior to the S-phase of the first mitotic division (Nasuda et al 1998). *Gc* gametophytes have normal mitosis and gametogenesis. As a result, all the progenies are *Gc*/*Gc*. *Gc* alleles with mild to strong gametocidal action have been identified. Mild forms of the *Gc* gene have been used to isolate a set of deletion stocks in wheat (Endo and Gill 1996). Because gametes with mild *Gc* action are functional, the chromosomal structural changes are heritable and, hence, can play a role in chromosome evolution.

Chromosome domain specialization

The well-known domains of chromosomes are the centromeres (organize kinetochores for chromosome movement during cell division), telomeres (maintain chromosome integrity), origins of replication (help replicate chromosomes), heterochromatin (inactive chromatin), and euchromatin (active chromatin). As reviewed earlier (Gill and Friebe 1998), there are also limitations overall size beyond which too small or too large chromosomes are unstable. Superimposed on this is overall functional specialization as dictated by the centromere-telomere axis. The centromeric regions, to a large extent, are genetically inert. They are poor in genes and recombination and the two may be causally related (see below). Most of the action is at the telomeres and some recent results are summarized below.

How chromosomes control recombination

During meiosis, pairing among homologous chromosomes begins at the telomeres, which are apparently anchored to the nuclear membrane. As meiosis proceeds, complete synapsis is established first at the telomeric ends and, as a result, recombination preferentially occurs at the distal ends of chromosomes. This hypothesis was tested in deletion chromosomes with terminal-end deficiencies. In these chromosomes, proximal poorly recombining regions are the new telomeric ends. Such deletion chromosomes showed elevated rates of recombination at their distal ends (Qi et al 2002). Recombination also is mainly restricted to gene-rich regions of chromosomes, which also are localized in the distal regions of chromosomes (Gill et al 1996, Faris et al 2002). Chromosomes also control recombination through the little understood phenomenon of interference. Both positive and negative interference are observed in regions of high and low recombination, as well as in proximal and distal ends of chromosomes (Boyko et al 2002). Then there is the enigmatic observation that, in isochromosomes, recombination preferentially occurs in *cis* isochromatids (chromatids attached to the same centromere) rather than in *trans* isochromatids (Qi et al 2000). The implications of this finding for normal recombination have not been fully explored.

Unusual recombination in wide crosses

Classical recombination studies were carried out in highly inbred strains and mutants were produced in the same strain for analyzing recombination between markers. These studies revealed that positive interference, whereby one crossover inhibits the formation of another crossover nearby, was the norm and that negative interference (one crossover is associated with another one nearby) was rare. However, mapping with restriction fragment length polymorphisms (RFLPs) mandated the use of genetically diverse parents and the genetic maps thus produced were much longer than expected based on classical recombination theory (Nilsson et al 1993, Gill et al 1995). The mapping data revealed a high frequency of so-called singletons, where a switch in data type is for one marker only, similar to a gene-conversion-type event (see Gill et al 1995, Faris et al 2000). Khush and his colleagues also observed gene

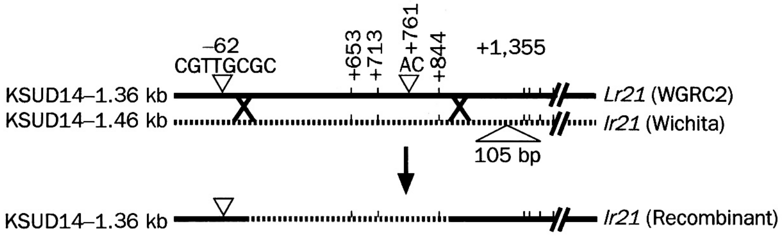


Fig. 3. Unusual recombination within a gene. Demonstration of a gene-conversion-type event (also called a noncrossover as it is not accompanied by the exchange of flanking markers) at the leaf rust resistance locus *Lr21* in wheat. The resistance (*Lr21*) and susceptible (*lr21*) alleles differ by insertion deletion (indel) polymorphisms. Note indels at position -62 (8 bp), +761(2 bp), and +1,355 (105 bp). The *Lr21* and *lr21* alleles also differed by single nucleotide polymorphisms (SNP) at positions +653, +713, +844, and others on the right border. The recombinant *lr21* allele had an 8-bp indel from *Lr21,* lost a 2-bp indei, and had three SNPs from *lr21.* It is hypothesized that indels on the left and right borders of the gene (and those beyond the gene, as it mainly consists of transposable elements) forced recombination within the gene. This kind of recombination will not lead to chiasmate associations and may be common in wide crosses.

transfer in rice interspecific hybrids, in which chiasmate associations were few (Jena et al 1992, Ishii et al 1994). There is a plausible molecular explanation for these results. The intergenic regions in highly divergent parents of either an RFLP mapping population or a wide interspecific cross are composed of mainly different transposable elements and are riddled with insertion/deletion (indel) polymorphisms. As a result, recombination is restricted to genic regions where DNA sequence homology is high, which is a prerequisite for recombination. This may sometimes force exchanges between very short pieces of DNA (less than 1,000 base pairs) that fail to support a chiasmate association. This type of recombination, which occurs in the absence of flanking markers, is called “noncrossover” (Yao et al 2002). We have recently documented and molecularly analyzed this type of unusual recombination in wheat (Huang et al 2003; see Fig. 3). The recombination occurred within the coding sequence of the rust-resistance locus *Lr21* involving the exchange of less than 1,000 bp of DNA and produced a susceptible allele (recombinant *lr21*). One can speculate that the indels on each side of the rust locus forced the recombination within the gene. In other cases, such exchanges may involve several adjacent genes or longer stretches of DNA but that are still not visible as cytological chiasmata, as was the case in rice interspecific hybrids. Anyone working with wide crosses should be alert to unusual recombination events in the progenies and should take advantage of this phenomenon for rapid genetic transfers.

Chromosome manipulation in crop improvement

There is a long history of chromosome and cytogenetics research in crop improvement. Cytogenetics facilitates gene transfer in wide hybrids, mapping of genomes, and analysis of basic chromosome structure, function, and engineering for crop improvement (for reviews, see Jiang and Gill 1994, Jiang et al 1994, Friebe et al 1996, Faris et al 2002). In wheat, deletion stocks have been used for chromosome-bin mapping of expressed sequence tags (ESTs) (Qi et al 2003, see also Web site: http://wheat.pw.usda.gov/NSF/project.html). These maps have revealed gene-rich and gene-poor regions and have facilitated map-based cloning of genes in spite of the large genome of wheat (Faris and Gill 2002, Faris et al 2003, Huang et al 2003). The homoeologous pairing gene *Ph1* (Riley and Chapman 1958) and *Ph* -inhibitor *Ph*^{1} (Chen et al 1994, Aghaee-Sarbarzeh et al 2002) genes permit recombination between homoeologous chromosomes of wheat and other Triticeae species, a reservoir of genes that is otherwise unavailable for wheat improvement. Faris et al (2002) have summarized an updated scheme for alien gene transfer using Ph genes. Parts of the alien-transfer scheme from homoeologous chromosomes (these chromosomes do not recombine with recipient crop-plant chromosomes) are relevant to all crop plants. Following interspecific hybridization, the first aim should be the introgression of single arms as compensating Robertsonian translocations (Faris et al 2002). Compensating translocations are those in which homoeologous arms are exchanged. The next step is induced recombination between the alien and the host arms, which can be done in wheat using the mutant of the *Ph1* gene or *Ph*^{1} gene. Once this gene is cloned, assuming that the *Ph* gene will be functional in heterologous systems, it should be possible to exploit it for alien transfer in all crop plants.

Conclusions

Chromosome/genome size, gene duplication, deletions, inactivation, and micro-colinearity changes are driven by transposable and retrotransposable elements. Transposon activity is often associated with interspecific hybridization and/or polyploidization. Certain genes, aneuploidy, and univalent misbehavior during meiosis in intra- or interspecific hybrids may trigger gross chromosome structural changes and aneuploid changes in chromosome number. Cycles of polyploidization and diploidization are a major driving force causing wide variation in chromosome numbers. As broken chromosomes must heal and be transmitted to the next generation, most chromosomal restructuring events occur in germ tissues, meiocytes, and especially in gametophytes. Obviously, an understanding of these processes will facilitate the engineering of plant genomes and benefit crop improvement through a more efficient harvest of genes from the biodiversity pool of our crop-plant relatives.

References

Aghaee-Sarbarzeh M, Ferrahi M, Singh S, Singh H, Friebe B. Gill BS, Dhaliwal HS. 2002. *Ph*^{1} -induced transfer of leaf and stripe rust-resistance genes from *Aegilops triuncialis* and *Ae. geniculata* to bread wheat. Euphytica 127:377-382.

Appels R, Francki M, Chibbar R. 2003. Advances in cereal functional genomics. Funct. Integ. Genom. 3: 1-24.

Bennett MD, Smith JB, Seal AG. 1986. The karyotype of the grass *Zingeria biebersteiniana* (2n=4) by light and electron microscopy. Can. J. Genet. Cytol. 28:554-562.

Boyko E, Kalendar R, Korzun V, Fellers JP, Koro A, Schulaman AH, Gill BS. 2002. A high-density cytogenetic map of the *Aegilops tauschii* genome incorporating retrotransposons and defense-related genes: insights into cereal chromosome structure and function. Plant Mol. Biol. 48:767-790.

Chen PD, Tsujimoto H, Gill BS. 1994. Transfer of *Ph*^{1} gene promoting homoeologous pairing from *Triticum speltoides* into common wheat and its utilization in alien genetic introgression. Theor. Appl. Genet. 88:97-100.

Civardi L, Xia Y, Edwards KJ, Schnable PS, Nikolau BJ. 1994. The relationship between genetic and physical distances in the cloned *a1-sh2* interval of the *Zea mays* L. genome. Proc. Natl. Acad. Sci. USA 91:8268-8272.

Endo TR, Gill BS. 1996. The deletion stocks of common wheat. J. Hered. 87:295-307.

Faris JS, Fellers JP, Brooks SA, Gill BS. 2003. A BAC contig spanning the major domestication locus *Q* in wheat and identification of a candidate gene. Genetics. (In press.)

Faris JD, Friebe B, Gill BS. 2002. Wheat genomics: exploring the polyploid model. Curr. Genomics 3:577-591.

Faris JD, Gill BS. 2002. Genomic targeting and high-resolution mapping of the domestication gene *Q* in wheat. Genome 45:706-718.

Faris JD, Haen KM, Gill BS. 2000. Saturation mapping of a gene-rich recombination hot spot region in wheat. Genetics 154:823-835.

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS. 1996. Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91:59-87.

Gill BS, Friebe B. 1998. Plant cytogenetics at the dawn of the 21st century. Curr. Opinion Plant Biol. 1:109-115.

Gill BS, Gill KS, Endo TR, Friebe B. 1995. Expanding genetic maps: re-evaluation of the relationship between chiasmata and crossovers. Chromosome Res. 3(Suppl 1):283-298.

Gill BS, Grass1 CO. 1986. Pathways of genetic transfer in sugarcane hybrids. Sugarcane 2:27.

Gill KS, Gill BS, Endo TR, Boyko EV. 1996. Identification and high-density mapping of gene-rich regions in chromosome group 5 of wheat. Genetics 143:1001-1012.

Huang L, Brooks SA, Li W, Fellers JP, Trick HN, Gill BS. 2003. Map-based cloning of a rust-resistance gene from bread wheat's large polyploid genome. Genetics. (In press.)

Huang S, Sirikhachornkit A, Su X, Faris JD, Gill BS, Hasekorn R, Gornicki P. 2002. Phylogenetic analysis of the acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the *Triticum/Aegilops* complex and the evolutionary history of polyploid wheat. Proc. Natl. Acad. Sci. USA 99:8133-8138.

Ishii T, Brar DS, Multani DS, Khush GS. 1994. Molecular tagging of genes for brown planthopper resistance and earliness introgressed from *Oryza australiensis* into cultivated rice, *O. sativa.* Genome 37:217-221.

Jena KK, Khush GS, Kochert G. 1992. RFLP analysis of rice (*Oryza sativa* L.) introgression lines. Theor. Appl. Genet. 84:608-616.

Jiang J, Friebe B, Gill BS. 1994. Recent advances in alien gene transfer in wheat. Euphytica 73:199-212.

Jiang J, Gill BS. 1994. Nonisotopic *in situ* hybridization and plant genome mapping: the first 10 years. Genome 37:717-725.

Khush GS. 1973. The cytogenetics of aneuploids. New York. NY (USA): Academic Press.

Leitch IJ, Bennett MD. 1997. Polyploidy in angiosperms. Trends Plant Sci. 2(12):470-476.

Li WL, Gill BS. 2002. The colinearity of the *Sh2/A1* orthologous region in rice, sorghum and maize is interrupted and accompanied by genome expansion in the Triticeae. Genetics 160:1153-1162.

McClintock B. 1984. The significance of responses of the genome to challenge. Science 226:792-801.

Martin GB, Brommonschenkel SH, Chunwongse J, Frary A, Canal MW, Spivey R, Wu T, Earle ED, Tanksley SD. 1993. Map-based cloning of a protein kinase gene conferring disease resistance in tomato. Science 262:1432-1436.

Nasuda S, Friebe B, Gill BS. 1998. Gametocidal genes induce chromosome breakage in the interphase prior to the first mitotic cell division of the male gametophyte in wheat. Genetics 141:721-731.

Nilsson N-O, Sall T, Bengtsson BO. 1993. Chiasma and recombination data in plants: Are they compatible? Trends Genet. 9(10):344-347.

Ozkan H, Levy AA, Feldman MW. 2001. Allopolyploidy-induced rapid genome evolution in the wheat (*Aegilops-Triticum*) group. Plant Cell 13:1735-1747.

Qi L, Echalier B, Friebe B, Gill GS. 2003. Molecular characterization of a set of wheat deletion stocks for use in chromosome bin mapping of ESTs. Funct. Integ. Genom. 3:39-55.

Qi LL, Friebe B, Gill BS. 2000. Recombination in an isochromosome preferentially occurs between *cis* isochromatids. Chromosoma 109:390-396.

Qi L, Friebe B, Gill BS. 2002. A strategy for enhancing recombination in proximal regions of chromosomes. Chromosome Res. 10:645-654.

Rick CM. 1967. Exploiting species hybrids for vegetable improvement. In: Proceedings of the XVII International Horticultural Congress. III:217-229.

Riley R, Chapman V. 1958. Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713-715.

Song WY, Wang GL, Chen LL, Kim HS, Pi LY, Gardner J. Wang B, Holsten T, Zhai WS, Zhu LH, Fauquet C, Ronald PC. 1995. A receptor kinase-like protein encoded by the rice disease resistance gene *Xa21*. Science 270:1804-1806.

Sorrells ME, La Rota CM, Bermudez-Kandianis CE, Greene RA, Kantety R, Munkvold JD, Miftahudin, Mahmoud A, Gustafson JP, Qi LL, Echalier B, Gill BS, Matthews D, Lazo G, Chao S, Anderson OD, Edwards H, Linkiewicz AM, Dubcovsky J, Akhunov ED, Dvorak J, Zhang D, Nguyen HT, Peng J, Lapitan NLV, Gonzalez-Hernandez JL, Anderson JA, Hossain KG, Kalavacharla V, Kianian SF, Choi DW. Close TJ, Dilbirligi M, Gill KS, Steber C, Walker-Simmons MK, McGuire PE, Qualset CO. 2003. Comparative DNA sequence analysis of wheat and rice genomes. Genome Res. (Submitted.)

Werner JE, Kota RA, Gill BS. 1992. Distribution of telomeric repeats and their role in the healing of broken chromosome ends in wheat. Genome 35:844-848.

Yao H, Zhou Q, Li J, Smith H, Yandeau M, Nikolau BJ. Schnable PS. 2002. Molecular characterization of a meiotic recombination across the 140-kb multigenic *a1-sh2* interval of maize. Proc. Natl. Acad. Sci. USA 99:6157-6162.

Zhang P, Friebe B, Lukazewski AJ, Gill BS. 2001. The centromere structure in Robertsonian wheat-rye translocation chromosomes indicates that centric breakage-fusion can occur at different positions within the primary constriction. Chromosoma 110:335-344.

Notes

Author's address: Wheat Genetics Resource Center, Department of Plant Pathology, Kansas State University, Manhattan, KS 66506-5502, USA.

Acknowledgments: The research summarized here was supported by grants from USDA-NRI, a USDA special grant to the Wheat Genetics Resource Center, McKnight Foundation, National Science Foundation, Kansas Wheat Commission, and Kansas Agricultural Experiment Station. I am grateful to W.J. Raupp for the artwork and editing of this manuscript and to my colleagues Bernd Friebe, Justin Faris, Li Huang, Wanlong Li, Lili Qi, and Peng Zhang for their research contributions to this review. This is contribution 03-296-A from the Kansas Agricultural Experiment Station, Manhattan, Kansas.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Genetic and physical mapping of the maize genome through radiation hybrids

R.L. Phillips, H.W. Rines, R.J. Okagaki, R.G. Kynast, R. Donahue, and W.E. Odland

Chromosome addition lines and radiation hybrids (RHs) provide powerful mapping tools. Oat x maize crosses followed by embryo rescue result in haploid oat plants with one or more maize chromosomes. Seed and/or DNA are available of monosomic or disomic additions of each of the ten maize chromosomes in an oat background. These materials are especially useful for mapping DNA sequences to chromosomes. Irradiation of monosomic addition line seed results in plants and progeny with various maize chromosome modifications, allowing physical mapping to a 5-Mb region or smaller. Use of a dispersed maize-specific retroelement, chromosome-specific markers, and genomic *in situ* hybridization (GISH) on interphase cells speeds the identification of maize chromosomes and chromosome segments. GISH has been used recently to distinguish various genomes of rice. Monosomic alien addition lines have been produced between *Oryza sativa* L. and several wild rice species. These materials will also simplify certain genetic procedures. Addition lines often have distinctive phenotypes. Correlating the phenotype and maize chromosome segments in RHs allows placement of the gene(s) controlling the trait. Chromosome 6 oat-maize addition exhibits a disease lesion mimic phenotype; data from chromosome 6 RHs indicate that the phenotype may be controlled by the *Les13* gene located in 6L.

Large and complex genomes pose special problems for gene mapping. Many markers are usually required to locate a gene to a small region of a chromosome. Because of the relatively large proportion of repeated elements, including retrotransposons (San Miguel et al 1996), complete genome sequencing generally is not financially or operationally feasible. Special methods are needed to map the thousands of DNA sequences being isolated as expressed sequence tags (ESTs) or by other means. The ability to map the new sequence to a physical location on the chromosome, as opposed to the genetic location, provides a more realistic vision of the genomic structure of a species.

Wide hybridization followed by complete or partial uniparental chromosome loss

Laurie and Bennett (1986, 1988, 1989, 1990) discovered that the pollination of wheat ovules with maize pollen followed by embryo rescue resulted in the recovery of haploid plants of wheat. They demonstrated that fertilization occurred and gave rise to an intergeneric hybrid zygote, but that the maize chromosomes were eliminated early in embryo development (Laurie and Bennett 1989). Rines and Dahleen (1990) showed that crosses of oat and maize followed by embryo rescue gave rise to haploid oat plants. Plant recovery frequency is low, with about 5-10% embryo initiation following pollination and about 5-20% plant regeneration. The overall frequency of haploid plants is therefore about 1%. The oat haploids are partially self-fertile and give rise to progenies that are euploid (doubled haploidy) or aneuploid, both arising by a process of meiotic restitution (Rines et al 1996).

About one-third of the progenies from oat by maize crosses have retained one or more maize chromosomes (Riera-Lizarazu et al 1996). We have observed from one to, in rare instances, ten maize chromosomes among these progenies. From self-pollination of oat haploids that contain maize chromosomes, some progenies are produced with the normal hexaploid complement of oat chromosomes and the expected array of maize chromosomes. Among the F_2 offspring were monosomic and disomic additions, as well as monosomic substitutions of maize chromosomes.

Easy identification of oat-maize addition lines

The selection of F_1 plants with maize chromosomes is generally performed in three steps: (1) PCR F_1 DNA using Grande 1 primers. Grande 1 is an LTR-type retrotransposon that is distributed throughout maize chromosomes, but absent from oat chromosomes; (2) count maize chromosome(s) via genomic *in situ* hybridization (GISH) using FITC-labeled maize genomic DNA on root meristem cells; the presence of one or two chromosomes can be readily distinguished in interphase cells, which are numerous enough to make this cytological step quite simple; (3) identify individual maize chromosome(s) by polymerase chain reaction (PCR) with maize chromosome-specific simple sequence repeat (SSR) primers. We use a set of markers for each maize chromosome that was selected from the MaizeDB at www.agron.missouri.edu/ and tested against oat. The maize chromosome markers are either absent from oat or show polymorphisms.

Behavior of addition chromosomes

Transmission frequencies of the maize chromosome(s) in the oat background are usually as predicted for interspecies chromosome additions in plants (Riley 1960). Disomic oat-maize additions with chromosomes 2, 3, 4, 6, and 9 generally show nearly 100% transmission of the maize chromosome. Monosomic oat-maize additions with maize chromosomes 2,3,8, and 9 show, as expected, 6-10% transmission. The disomic oat-maize additions with maize chromosome 7 had irregular transmission (0–66%) among the panicles of F_2 and F_3 progenies. After selection in favor of stable transmission, nearly 100% transmission was attained by the F_5 generation. Monosomic oat-maize additions with maize chromosomes 1 or 5 gave irregular transmission among the panicles; transmission varied from 0 to 3%. Disomic additions recovered in the F_2 transmitted the maize chromosome at higher frequencies. In these cases, transmission frequencies are irregular and indicate some somatic sectoring activity.

Availability and use of addition lines

We now have produced oat-maize addition lines for all 10 maize chromosomes (Kynast et al 2001), mostly in two or more different oat genetic backgrounds. All maize chromosomes have been recovered as disomic additions to oat, except for maize chromosome 10. The haploid chromosome 10 oat-maize addition line is vegetatively maintained. Table 1 gives a summary of the lines and the availability of seed and/or DNA.

These materials are extremely efficient for mapping DNA sequences to their respective physical chromosome. PCR for a particular sequence will indicate whether or not that sequence is present in the DNA being tested. Using DNA from the set of 10 addition lines, the PCR reaction quickly shows on which chromosome or chromosomes the sequence resides. The mapping of duplicate genes or gene families is

Table 1. Oat-maize chromosome addition lines.

Added maize chromosome(s)	Maize (donor)	Oat (host)	Addition type	Genomic status	Number of lines	Available	
						DNA	Seed
1	Seneca 60	Starter	Disomic	Diploid	1	+	+
1	Seneca 60	Preakness	Monosomic	Haploid	1	+	–
2	Seneca 60	Starter	Disomic	Diploid	7	+	+
2	Seneca 60	Sun II	Disomic	Diploid	1	+	+
3	Seneca 60	Sun II	Disomic	Diploid	1	+	+
3	Seneca 60	Preakness	Disomic	Diploid	1	+	+
4	Seneca 60	Starter	Disomic	Diploid	5	+	+
4	A188	Starter	Disomic	Diploid	2	+	+
5	Seneca 60	Starter	Disomic	diploid	1	+	+
5	Seneca 60	F_1 hybrid	Disomic	Diploid	1	+	+
6	Seneca 60	Starter	Disomic	Diploid	2	+	+
6	Seneca 60	F_1 hybrid	Disomic	Diploid	1	+	+
7	Seneca 60	Starter	Disomic	Diploid	3	+	+
7	Seneca 60	GAFPark	Disomic	Diploid	1	+	+
8	*bz1-mum9*	Starter	Disomic	Diploid	1	+	–
8	Seneca 60	GAFPark	Monosomic	Diploid	1	+	+
9	Seneca 60	Starter	Disomic	Diploid	7	+	+
9	Seneca 60	GAFPark	Disomic	Diploid	1	+	+
10	Seneca 60	GAFPark	Monosomic	Haploid	1	+	–
1 + 9	Seneca 60	Starter	Double disomic	Diploid	1	+	+
4 + 6	Seneca 60	Starter	Double disomic	Diploid	1	+	+

readily possible with this technology. No polymorphisms need to be identified in this procedure for mapping genes. Table 2 shows the mapping of various duplicate (or more) EST sequences to chromosome using this approach.

Production of radiation hybrid lines

The oat-maize additions provide the opportunity to produce—via gamma irradiation of monosomic additions—lines that possess only a portion of the individual maize chromosome (Riera-Lizarazu et al 2000, Vales et al 2000). This approach allows the mapping of sequences to a more precise location than a whole chromosome. The hexaploid nature of the oat genome makes this approach feasible since the oat plant-whose genome no doubt also is rearranged because of the radiation—shows little effect. The polyploid nature of oat allows various cytogenetic events to occur without significantly reducing fertility.

Our laboratory is in the process of producing up to 100 lines for each of the 10 maize chromosomes derived from irradiated monosomic additions. These lines are called radiation hybrids (RHs). The idea arises from the radiation hybrid method being used extensively for mapping human DNA sequences (Cox et al 1990). In that case, human cells are irradiated to break the human chromosomes; these cells are fused with mouse or Chinese hamster cells. Cell lines are produced that carry the diploid set of rodent chromosomes and pieces of human chromosomes. DNA hybridization or PCR with DNA from these lines using a DNA sequence to be mapped will reveal the human chromosome segment to which the sequence belongs. The theory is that the probability that radiation (gamma rays) will break a chromosome between two markers is directly related to the physical distance between the two markers. Using software called RHMap (Boehnke et al 1996), one can determine the physical map location of a sequence. The high-resolution radiation hybrid set of cell lines for mapping the human genome allows the location of sequences to within a 100-kb DNA segment (Stanford Human Genome Center Web site at http://shgc-www.stanford.edu/). A high-resolution RH panel usually contains about 90 RH lines in humans and animals (Stewart et al 1997, Womack et al 1997).

Candidate RH lines produced from irradiated oat-maize additions are those retaining maize Grande 1 and/or CentA sequences, but not yet fully characterized with markers (Kynast et al 2002). Currently we have more than 600 candidate RHs for four chromosomes: 239 for chromosome 2, 202 for chromosome 9, 101 for chromosome 6, and 78 for chromosome 4. The RH panel for chromosome 9 allows the mapping of a sequence to an approximately 5-Mb region of chromosome 9 based on the assumption of random breakage induced by the gamma radiation (Riera-Lizarazu et al 2000, Kynast et al 2000). A high-resolution RH mapping panel is also under development for chromosome 2. Lines are available for use in low-resolution mapping (involving 10 RH lines that divide chromosome 9 into eight segments), which quickly allow the placement of a DNA sequence to a portion of a chromosome 9 arm (Okagaki et al 2001). A chromosome 2 low-resolution mapping panel is being

Table 2. Identifying and locating duplicated genes to chromosome.

EST [a]	Member of contig [b]	Primary blast hit [c]		Secondary BLAST hit [d]		Chromosome [e] location
AI737658	TUC05-31-1950.1	TUC01-12-19-523.1	6.00E-11			4 and 6
AI737739	TUCO2-04-28-8895.1	TUC02-04-28-1858.3	e-151	TUC01-09-30-9171.1	e-149	4 and 5
AI737779	TUCO2-02-07-20211.1	TUC02-04-28-9099.1	e-157			9 and 10
AI737782	TUC02-02-07-18886.1	TUC02-02-07-13013.1	6.00E-39	TUC02-04-28-4506.0	4.00E-18	4 and 7
AI737789	TUC02-042811016.1	TUC02-04-28-5731.1	E = 0	TUC02-04-28-439.4	E = 0	1, 2, and 10
AI737814	TUC0531-1635.1	TUC02-01-02-361.1	E = 0	TUC0405-1117.1	1.00E-14	1 and 6
AI737827	TUC02-04288340.1	TUC02-04-28-11524.1	e-119			1 and 3
AI737851	TUC02-0428165.1	TUC02-0428-6503.1	E = 0			1, 2, and 7
AI737827	TUC02-0428140.1	TUC01-26-813.1	e-168			2 and 7
AI941974	TUC02-04284490.1	TUC0405-7008.1	e-132			2 and 7
AI941535	TUC02-02-07-18754.1	TUC02-02-07-17279.1	e-156			1 and 9
AI941604	TUC02-01-02-179.1	TUC02-04-28-10007.1	1.00e-30	TUC02-04-28-8590.1	9.00E-25	2, 3, 7, and 8

[a] EST sequences were used to search ZmDB (Gai et al 2000) for related sequences. [b] These contigs include the starting ESTs. Contigs are taken from ZmDB. [c] These contigs were identified as related to the starting EST by BLAST searches. [d] In some cases, additional contigs were identified in BLAST searches. [e] Mapping data are from Okagaki et al (2001).

Table 3. Phenotype differences of oat-maize chromosome additions in comparison to their parental oat.

Added maize chromosome	Phenotype	
	Morphological characters	Physiological characters
1	Reduced plant height, thick stalk, thick leaf with erect blade, compact spike-like panicle, fine hair-like roots	Neutral photoperiod response for flowering, Reduced seed set under long-day regime, corn chromosome transmission under short-day regime only
2	Waxy stalk, bluish leaf with long blades	Elongated vegetative growth, late maturing
3	Liguleless, crooked panicle	-
4	Light green leaf, small seeds	Early maturing
5	Branched stalk	Reduced susceptibility to oat crown rust pathogens
6	Disease lesion mimic	Reduced seed set
7	Small stature	-
8	Reduced plant height, open panicle	Elongated vegetative growth, low fertility
9	-	Erratic premature senescence, reduced seed set
10	Small stature, grassy type, multi-floral spikelets	Ovule and pollen sterility

prepared, as well as medium-resolution panels involving 20-30 RH lines for chromosomes 2 and 9.

Addition-line phenotypes

The phenotype of the oat-maize addition lines varies depending on the particular maize chromosome present. Table 3 gives the latest description of phenotypes associated with each addition line.

Mapping gene(s) controlling addition-line phenotypes

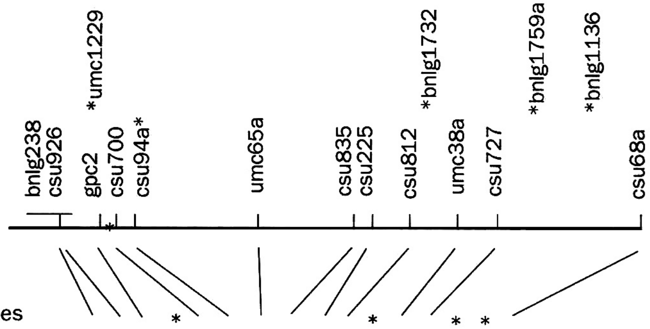
Five of the original set of six chromosome 6 F_1 monosomic addition plants in the haploid oat background had a phenotype known as a disease lesion mimic. A newly recovered disomic addition of maize chromosome 6 in a different genetic background than the previous six also shows the disease lesion mimic phenotype. The plants show necrotic lesions but no pathogenic organism appears to be present. Such mutants inducing spontaneous cell death have been identified in several species such as *Arabidopsis,* barley, maize, and rice (Iwata et al 1978, Johal et al 1995). The fact that not all of the plants showed the typical phenotype of a particular addition line is also seen with other oat-maize additions. A chromosome 3 addition, depending on the genetic background, usually possesses a crooked panicle and abnormal ligules on the upper leaves. This phenotype has been shown to be due to the ectopic expression of the *Liguleless 3* gene on maize chromosome 3 (Muehlbauer et al 2000). Addition-line plants for maize chromosome 9 often show a premature senescence syndrome when the plant is stressed. This sensitivity is not understood now. Assuming the phenotype of the oat-maize addition line is expressed at a consistent frequency level, the occurrence of the phenotype among the radiation hybrids should allow the placement of the genetic factor(s) involved in producing the phenotype. Those RHs with the responsible genetic region may exhibit the phenotype, whereas those RHs without the respective chromosome segment will possess a normal phenotype. The chromosome 6 oat-maize addition showed the disease lesion mimic phenotype five out of six times (83%). Figure 1 shows the results of genotyping 13 RHs with the disease lesion mimic phenotype and 7 healthy RH plants. We used 16 markers spread across chromosome 6, 11 Invader probes from Third Wave Inc., Madison, Wisconsin (Kwiatkowski et al 1999), and 5 PCR probes. Markers from the proximal region of the long arm were present in 12 of the 13 plants showing a disease lesion mimic phenotype, and these markers were absent in half of the plants that did not express the lesion trait. This indicates that the gene(s) producing the disease lesion mimic phenotype is associated with the proximal half of 6L. For a standard genetic map of maize, see Davis et al (1999).

In surveying the literature on the map locations of disease lesion mimic mutations (known as Les mutants), we discovered that *Les13* has been mapped to the same general region on chromosome 6 (Neuffer 1992). Thus, the phenotype exhibited by the chromosome 6 oat-maize addition line may be due to the abnormal expression of *Les13*.

Genetic mapping studies determined that *Les13* is tightly linked to one of the markers, csu94a, mapped on the RH lines. The csu94a marker also cosegregated with the disease lesion mimic phenotype in most of the RH plants tested (Fig. 2). There were four exceptions. Plant 6.1.004.3-04 showed the lesion phenotype but was missing all tested markers, and plants 6.1.006.3-04, 6.1.01 8.3-03, and possibly 6.1.014.4-04 were healthy but carried csu94a. We therefore planted 10 seeds from each of the 20 RH plants to test the progenies for the lesion phenotype and we tested additional markers. Progenies retaining maize sequences were recovered from 11 of the 20 original RH lines. Fourteen SSR markers were placed on this material, including bnlg2191, which is tightly linked to *Les13.*

Screening the progenies offers two benefits. First, it provides an independent test for the disease lesion mimic phenotype. Because of the incomplete penetrance of the trait, plants identified as healthy may actually carry the sequences responsible for the lesion phenotype. Conversely, plants identified as having lesions could have had lesions caused by senescence. Second, screening progenies can uncover segregation of markers. Lines 6.1.003.02 and 6.1.003.05 apparently carried both parts of a reciprocal translocation. The translocated chromosomes segregated in their progenies (Fig. 2). Scoring the lesion phenotype in these plants should help confirm the location of sequences responsible for the lesion trait.

Although these data are not highly definitive, they do serve to demonstrate the idea of mapping the genetic control of addition-line phenotypes using radiation



RH lines				*							*			*	*		
6.1.014.1-04	+	−	+	+	+				+		+	+	+	+	+	+	RH lines with mild lesion symptoms
6.1.004.6-04	−	−		−			+		+		−			−	−		
6.1.010.2-05	+	−	+	+							−	−	−	−	−	−	
6.1.003.3-01			+	−	+	+	+	+	+							+	RH lines with severe lesion symptoms
6.1.003.3-02	+	−	+	+		+	+		+		−	−	−	−	−	−	
6.1.003.3-03	+	+	+	+	+	+	+	+	+	+		−		−	+	−	
6.1.003.3-05	+	−	+	+	+	+	+	+	+		+	+	+	+	+	+	
6.1.003.1-01	+	−	+	+	+	+	−	−	+	+	−	−	−	−	−	−	
6.1.003.1-02	+	+	+	+		+	+	+	+		+	+	+	+	+	+	
6.1.014.5-03	+	+	+	+	+	+	+	+	−		+	+	+	+	+	+	
6.1.003.2-04	+	−	+	+	+	+	+	+	+		−	−		−	−	−	
6.1.010.2-02	−	−	−	+	+	+	+	+	+		−	−	−	−	−	−	
6.1.004.3-04	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	
6.1.006.3-04	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	RH lines with no apparent lesions
6.1.018.3-03	+		+	+	+	+		−	+		+			+	+	+	
6.1.014.4-04	+	−	+	+			+	+	+		+	+	+	+	+	+	
6.1.014.1-01	+	+	+	+	+	−		−	+	+	+	+	+	+	+	+	
6.1.012.7-01	−		−	−	−	−	+		−			−	−	−	−	−	
6.1.010.2-03	−	+	−	−	−	−	−	−	−	−		−	−	−	−	−	
6.1.004.7-04	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	

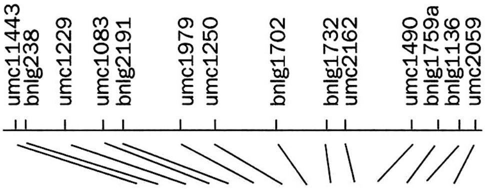
+ Marker present

☐ Not tested, or ambiguous data

− Marker absent

Fig. 1. Placing markers on the chromosome 6 radiation hybrid lines. Presence of a marker indicates that that region of the chromosome is present in the line. The location of markers on the UMC98 map is shown. The approximate positions of markers not placed on the UMC98 map are shown above. Marker csu94a has been tightly linked to *Les13.*

hybrids. Although the gene product of *Les13* is not known, we do know that another disease lesion mimic mutant *(Lls1)* in maize encodes for two conserved binding motifs such as are found in aromatic-ring-hydroxylating dioxygenases implicated in cell death (Gray et al 1997). In rice, a spotted leaf gene *(Spl7)* similar in appearance



6.1.003.1-01-04	+	+	+	+	+	+	+	−	−	−	−	−	−	−
6.1.003.1-01-10	+	+	+	+	+	−	+	+	−	−	−	−	−	−
6.1.003.1-01-07	+	−				+	+		−	−	−	−	−	−
6.1.003.3-02-01	+			+		+	+	+	+	+	+	−	+	+
6.1.003.1-02-02	+	+	+	+	+	+	+	+	−	−	−	−	−	−
6.1.003.1-02-03	+	+	+	+	+	+	+	+	−	−	−	−	−	−
6.1.003.1-02-06	−	−	−	−	−	−	−	−	+	+	+	+	+	+
6.1.003.2-04-03	+	+		−	+	+	+	+	−	−	−	−	−	−
6.1.003.2-04-07	+	+	+	+	+	−	−		−	−	−	−	−	−
6.1.003.2-04-08	+	+	−	+	+	−	−	+	−	−	−	−	−	−
6.1.003.3-01-05	+	+		+	+	+	+	+	+		+		+	−
6.1.003.3-01-07		−	−	−	−	−	−	−	−	−	−	+	−	−
6.1.003.3-01-08	+	+	+	+	+	+	+	+	+	+	+	+		+
6.1.003.3-01-10	−	+	+	+	+		+	−	−	−	−	−	−	−
6.1.003.3-02-01	+	+		+	+	+	+	+	−	−	−	−	−	−
6.1.003.3-02-08	+	+		+	+	+	+	+	−	+	−	−	−	−
6.1.003.3-02-09	+	+		−	+	+	+	+	−	−	−	−	−	−
6.1.003.3-03-08	+	−		+		+	+	+	−	−	−	−	−	−
6.1.003.3-05-02	−	−		−		−	−	−	+	−	+	+	+	+
6.1.003.3-05-03	+	+		+	+	+	+	+	−	−	−	−	−	−
6.1.003.3-05-09	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6.1.010.2-05-01	+	+		+	−	−	−	−	−	+	−	−	−	
6.1.010.2-05-02	+	+	+		−	−	−	−	−	−	−	−	−	−
6.1.010.2-05-03	+	−		+	−	−	−	−	−	+	−	−	−	−
6.1.010.2-05-05	+	−			−	−	−	−	−	−	−	−	−	−
6.1.014.4-04-08	+	+	−	+	+	+	+	+	+	−	+		+	+
6.1.014.4-04-09	+	+	+	+	+	+	+	+	+	+	+	−	+	+
6.1.014.5-03-02	+	+	+	+	+	+	+	+	+	+	+	+	−	
6.1.018.3-03-06	+	+	+	+	+		+	+	+	+	+	+	+	

+ Marker present
☐ Not tested, or ambiguous data
− Marker absent

Fig. 2. Placement of markers on progeny of radiation hybrid lines for maize chromosome 6. The location of markers on the IBM map is shown. Marker bnlg2191 is closely linked to *Les13.*

to a disease lesion mimic was identified by map-based cloning to encode a heat-stress transcription factor (Yamanouchi et al 2002).

Is there value in considering RHs for rice?

The typical use of a radiation hybrid map is to provide physical mapping information in lieu of a genome sequence or to assist with the sequencing effort. The recent sequencing of the rice genome (Yu et al 2002, Goff et al 2002) suggests that developing a radiation hybrid map for rice would be unnecessary. This would be true for radiation hybrid maps based on the standard approach of cell fusion. But producing radiation hybrid lines through wide hybridizations—such as oat with maize as demonstrated here, or perhaps *Oryza sativa* with a wild rice species — produces unique biological materials that have many other uses.

If the sequence is duplicated or part of a multigene family, the whole-genome sequence should allow the sequences to be located relative to any other sequence. Whole-genome sequencing, however, still does not reflect the entire genome; the centromeres and other highly repeated regions are not usually sequenced. RHs would include these regions, although we generally have a limited number of markers to identify the breaks in such regions. Of course, the phenotype of addition lines cannot be predicted from the genome sequence data.

The genus *Oryza* has nine different genomes among the 24 species. Hybrids have been made between elite breeding lines and wild rice species representing all nine genomes. Opportunities therefore exist to create numerous alien addition lines using wild species and GISH is a powerful technique to detect various combinations of chromosomes from such species. GISH has been used successfully to differentiate parental genomes in hybrids containing the A genome of *O. sativa* (Abbasi et al 1998a,b, Asghar et al 1998, Brar, personal communication, Yan et al 2001). The wild species hybrids involve *O. minuta* (BBCC), *O. officinalis* (CC), *O. eichingeri* (CC), *O. australiensis* (EE), *O. brachyantha* (FF), *O. ridleyi* (HHJJ), *O. granulata* (GG), and *Porteresia coarctuta* (HHKK). No blocking DNA was needed to differentiate F, G, and HJ from the A genome, whereas it was needed to distinguish the BC, C, and E genomes from the A genome of rice. The genomes of the hybrids between *O. latifolia* (CCDD) and *O. ridleyi* (HHJJ), as well as *O. australiensis* (EE) and *O. ridleyi* (HHJJ), have been differentiated by GISH. Li et al (2000) used GISH to demonstrate considerable differentiation between the E genome and the C and D genomes of wild rice. Interestingly, the B genomes in *O. minuta* and *O. punctata* could be distinguished by GISH (Li C et al 2001). GISH analysis of meiotic metaphases of *O. sativa* × *O. australiensis* was used to reveal autosyndetic pairing of 1–2 bivalents among A genome chromosomes and allosyndetic pairing between 1–4 homoeologues of A and E chromosomes (Abbasi et al 1999). Although the differences in GISH hybridization may mostly reflect repeated sequences, polymorphisms might be required to map rice genes.

Monosomic alien addition lines (MAALs) with 2n = 25 chromosomes have been produced in a rice background. MAALs for 6 to 12 of the chromosomes, depending on the species, have been produced; there are 12 MAALs (Jena and Khush 1989) for *O. officinalis* (CC), 7 (Brar and Khush 1996) for *O. minuta* (BBCC), 11 (Multani et al, unpublished) for *O. latifolia* (CCDD), 8 (Multani et al 1994) for *O. australiensis* (EE), 7 (Brar and Khush, unpublished) for *O. brachyantha* (FF), and 6 (Brar et al, unpublished) for *O. granulata* (GG). Eleven groups of monosomic alien addition lines were reported by Yasui and Iwata (1991) in *O. punctata* (BB).

Such addition-line materials have many uses. The oat-maize addition lines, for example, were used to isolate sequences in the centromeric region of a particular maize chromosome and to determine their distribution across the other maize chromosomes (Ananiev et al 1998). The isolation of genome-specific DNA probes in oat allows the A/D genome to be clearly differentiated from the C genome, and translocations between the A/D and C genomes are obvious (Ananiev et al 2002). Sorting of individual chromosomes may be possible with addition lines depending on the size differential between the parents (Li L et al. 2001). Horizontal transfer of resistance genes becomes feasible based on the finding of new resistance factors from alien chromosomes. We tested the oat-maize additions with pathogens for oat crown rust and observed reduced susceptibility in maize chromosome 5 additions in two oat backgrounds.

Is there value in mapping rice sequences using oat-maize addition lines or RHs?

This might give some interesting data on the syntenic relationship between rice and maize. Rice is increasingly used as a reference for the identification of candidate genes and map-based cloning. Greater knowledge of microsynteny between rice and maize should prove helpful in such activities, especially relative to the duplicated nature of maize as an ancient tetraploid.

Summary

Oat x maize crosses generate both haploid oat plants and oat-maize partial hybrids. Oat haploids produced by this procedure are partially self-fertile and provide both aneuploids and doubled haploids among the progenies. All ten addition lines of individual maize chromosomes in oat have been recovered, and these allow for the easy mapping of sequences to maize chromosomes. Radiation hybrids are being developed for the fine mapping of maize DNA sequences to 5-Mb regions. The genetic control of the phenotype of the addition lines may be mapped to the chromosome segment by phenotyping the RH lines derived from that particular oat-maize chromosome addition.

How will work of this type facilitate plant breeding in the 21st century? Plant breeders will likely be using the new molecular genetic technologies and information to assess the parental origin of numerous short DNA segments across the entire genome. Information will be available on which molecular markers are closely linked to QTLs for the traits of interest, or the actual gene will be available to determine the presence of a factor influencing a trait. Having genes carefully mapped will facilitate the approach. Map-based cloning will be made much easier in those cases in which the genome has not been sequenced. The extensive background work in plant breeding and biotechnology provided by scientists such as Gurdev Khush has formed the framework for such future advances.

References

Abbasi F, Brar D, Carpena A, Fukui K, Khush G. 1999. Detection of autosyndetic and allosyndetic pairing among A and E genomes of *Oryza* through genome *in situ* hybridization. Rice Genet. Newsl. 16:24-25.

Abbasi F, Brar D, Carpena A, Fukui K, Khush G. 1998a. Characterization of parental chromosomes in an anther culture derived plant from *O. sativa* x *O. australiensis* Comin through genomic *in situ* hybridization. Rice Genet. Newsl. 15:84-86.

Abbasi F, Brar D, Carpena A, Khush G. 1998b. Molecular cytogenetic analysis of *O. sativa* L. x *O. brachyantha* A. Chev. et Roehr. derivatives. Rice Genet. Newsl. 15:86-87.

Ananiev E, Phillips R, Rines H. 1998. Chromosome-specific molecular organization of maize (*Zea mays* L.) centromeric regions. Proc. Natl. Acad. Sci. USA 95:13073-13078.

Ananiev E, Vales M, Phillips R, Rines H. 2002. Isolation of A/D and C genome specific dispersed and clustered repetitive DNA sequences from *Avena sativa.* Genome 45:431-441.

Asghar M, Brar D, Hernandez J, Ohmido N, Khush G. 1998. Characterization of parental genomes in a hybrid between *O. sativa* and *O. officinalis* Wall ex Watt. through fluorescence in situ hybridization. Rice Genet. Newsl. 15:83-84.

Boehnke M, Lunetta K, Hauser E, Lange K, Uro J, Vander Stoep J. 1996. RHMAP: statistical package for multipoint radiation hybrid mapping: Version 3.0, available at www.sph.umich.edu/group/statgen/software/rhmap.html.

Brar D, Khush G. 1996. Wide hybridization for rice improvement: alien gene transfer and molecular characterization of introgression. In: Jones M, Dingkuhn M, Johnson D, Fagade S, editors. Interspecific hybridization: progress and prospects. Bouake (Côte d'Ivoire): West Africa Rice Development Association. p 21-29.

Cox D, Burmeister M, Price E, Kim S, Myers R. 1990. Radiation hybrid mapping: a somatic cell genetic method for constructing high-resolution maps of mammalian chromosomes. Science 250:245-250.

Davis G, McMullen M, Daysdorf C, Musket T, Grant D, Staebell M, Xua G, Polacco M, Kosterd L, Melia-Hancock S, Houchins K, Chao S, Coe Jr E. 1999. A maize map standard with sequenced core markers, grass genome reference points and 932 expressed sequence tagged sites (ESTs) in a 1736-locus map. Genetics 152:1137-1172.

Gai X, Lal S, Xing L, Brendel V, Walbot V. 2000. Gene discovery using the maize genome database ZmDB. Nucl. Acids Res. 28:94-96.

Goff S, Ricke D, Lan T-H, et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Gray J, Close P, Briggs S, Johal G. 1997. A novel suppressor of cell death in plants encoded by the IISI gene of maize. Cell 89:25-31.

Iwata N, Omura T, Satoh H. 1978. Linkage studies in rice (*Oryza sativa*) on some mutants for physiological leaf spots. J. Fac. Agric. Kyushu Univ. 22:243-251.

Jena K, Khush G. 1989. Monosomic alien addition lines of rice: production, morphology, cytology and breeding behavior. Genome 32:449-455.

Johal G, Hulbert S, Briggs S. 1995. Disease lesion mimics of maize: a model for cell death in plants. BioEssays 17:685-692.

Kynast R, Okagaki R, Odland W, Russell C, Livingston S, Rines H, Phillips R. 2000. Towards a radiation hybrid map for maize chromosomes. Maize Genet. Coop. Newsl. 74:60-61.

Kynast R, Okagaki R, Rines H, Phillips R. 2002. Maize individualized chromosomes and derived radiation hybrid lines and their use in functional genomics. Funct. Integr. Genomics 2:60-69.

Kynast R, Riera-Lizarazu O, Vales M, Okagaki R, Maquieira S, Chen G, Ananiev E, Odland W, Russell C, Stec A, Livingston S, Zaia H, Rines H, Phillips R. 2001. A complete set of maize individual chromosome additions to the oat genome. Plant Physiol. 125:1216-1227.

Kwiatkowski R, Lyamichev V, de Arruda M, Veri B. 1999. Clinical, genetic, and pharmacogenetic applications of the Invader assay. Mol. Diagn. 4:353-364.

Laurie D, Bennett M. 1986. Wheat x maize hybridization. Can. J. Genet. Cytol. 28:313-316.

Laurie D, Bennett M. 1988. Chromosome behaviour in wheat × maize, wheat × sorghum and barley x maize crosses. In: Brandham PE, editor. Kew Chromosome Conference 3. Her Majesty’s Stationary Office, London. p 167-177.

Laurie D, Bennett M. 1989. The timing of chromosome elimination in hexaploid wheat × maize crosses. Genome 32:953-961.

Laurie D, O’Donoughue L, Bennett M. 1990. Wheat × maize and other wide sexual hybrids: their potential for genetic manipulation and crop improvement. In: Gustafson J, editor. Gene manipulation in plant improvement II. New York (USA): Plenum Press. p 95-126.

Li C, Zhang D, Ge S, Hong D. 2000. Relationships among the CC, DD, and EE genomes in the *Oryza officinalis* complex detected by two-probe genomic *in situ* hybridization. Intl. Rice Res. Notes 253: 18-20.

Li L, Arumuganathan K, Rines H, Phillips R, Riera-Lizarazu O, Sandhu D, Zhou Y, Gill K. 2001. Flow cytometric sorting of maize chromosome 9 from an oat-maize chromosome addition line. Theor. Appl. Genet. 102:658-663.

Li C, Zhang D-M, Ge S, Lu B-R, Hong D-Y. 2001. Identification of genome constitution of *Oryza malampuzhaenisi, O. minuta,* and *O. punctata* by multicolor genomic *in situ* hybridization. Theor. Appl. Genet. 103:204-211.

Muehlbauer G, Riera-Lizarazu O, Kynast R, Martin D, Phillips R, Rines H. 2000. A maize-chromosome 3 addition line of oat exhibits expression of the maize homeobox gene *Liguleless 3* and alterations of cell fate. Genome 43:1055-1064.

Multani D, Jena K, Brar D, de los Reyes B, Angeles E, Khush G. 1994. Development of monosomic alien addition lines and introgression of genes from *Oryza australiensis* Domin. to cultivated rice *O. sativa* L. Theor. Appl. Genet. 88:102-109.

Neuffer M. 1992. Location and designation of 8 dominant mutants from chemical mutagenesis and spontaneous origin. Maize Genet. Coop. Newsl. 66:39-40.

Okagaki R, Kynast R, Livingston S, Russell C, Rines H, Phillips R. 2001. Mapping maize sequences to chromosomes using oat-maize chromosome addition materials. Plant Physiol. 125:1228-1235.

Riera-Lizarazu O, Rines H, Phillips R. 1996. Cytological and molecular characterization of oat x maize partial hybrids. Theor. Appl. Genet. 93:123-135.

Riera-Lizarazu O, Vales M, Ananiev E, Rines H, Phillips R. 2000. Production and characterization of maize chromosome 9 radiation hybrids derived from an oat-maize addition line. Genetics 156:327-339.

Riley R. 1960. The meiotic behaviour, fertility and stability of wheat-rye chromosome addition lines. Heredity 14:89-100.

Rines H, Riera-Lizarazu O, Maquieira S, Phillips R. 1996. Wide crosses for haploids. In: Scoles G, Rossnagel B, editors. Proceedings 5th International Oat Conference and 8th International Barley Genetics Symposium. Saskatchewan, Canada. p 207-212,

San Miguel P, Tikhonov A, Jin Y-K, Motchoulskaia N, Zakharov D, Melake-Berhan A, Springer P, Edwards K, Lee M, Avramova 2, Bennetzen J. 1996. Nested retrotransposons in the intergenic regions of the maize genome. Science 274:765-768.

Stewart E, McKusick K, Agagrwal A, et al. 1997. An STS-based radiation hybrid map of the human genome. Genome Res. 7:422-433.

Vales M, Riera-Lizarazu O, Yoon E, Okagaki R, Rines H, Phillips R. 2000. Maize-chromosome 9 translocations and deletions in progenies of oat-maize chromosome 9 radiation hybrids. Am. Soc. Agron. Abstr. p 113.

Womack J, Johnson J, Owens E, Rexroad C, Schlapfer J, Yang Y. 1997. A whole-genome radiation hybrid panel for bovine gene mapping. Mamm. Genome 8:854-856.

Yamanouchi U, Yano M, Lin H, Ashikari M, Yamada K. 2002. A rice spotted leaf gene, *Sp17,* encodes a heat stress transcription factor protein. Proc. Natl. Acad. Sci. USA 99:7530-7535.

Yan H, Liu G, Cheng Z, Min S, Zhu L. 2001. Characterization of euploid backcross progenies derived from interspecific hybrids between *Oryza sativa* and *O. eichingeri* by restriction fragment length polymorphism (RFLP) analysis and genomic *in situ* hybridization (GISH). Genome 44236-95.

Yasui H, Iwata N. 1991. Production of monosomic alien addition lines of *Oryza sativa* having a single *O. punctata* chromosome. In: Rice genetics 11. Manila (Philippines): International Rice Research Institute. p 147-155.

Yu J, Hu S, Wang J, et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science 296:79-92.

Notes

Authors' address: Department of Agronomy and Plant Genetics, Plant Molecular Genetics Institute, University of Minnesota, 1991 Upper Buford Circle, St. Paul, MN 55108, USA.

Acknowledgments: This material is based upon work supported by the National Science Foundation under Grant nos. 9872650 and 0110134. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Applying agricultural biotechnology produce salt- and drought-tolerant rice plants

A. Garg, V. Sangwan, C. He, M. Dey, F. Duan, F. Li, J. Su, and R. Wu

Transgenic approaches offer new opportunities to improve tolerance for dehydration stress in plants by incorporating genes that are involved in stress tolerance. As an example, we transformed rice separately with two binary plasmids, each containing a fusion gene consisting of two *Escherichia coli* trehalose biosynthetic genes (*otsA* and *otsB*). We found that, in several transgenic lines, regulated overexpression of the fusion gene resulted in high levels of tolerance for salt, drought, or low-temperature stresses. Compared with nontransgenic rice, transgenic lines containing either fusion gene exhibited sustained plant growth, a more favorable mineral balance, and less photo-oxidative damage under stress conditions. With the insertion-mutagenesis approach, the functions of many new genes from rice can be discovered. We expect that some of the new genes related to abiotic stress tolerance may be useful for transformation. We have recently developed a strategy to systematically produce a nonredundant, indexed, insertion-mutant rice library. Our approach is unique in that it can readily produce an evenly spaced transposon-tagged population of 150,000 sublines, each at a known chromosomal location, without the need to determine the flanking sequence of each subline.

Agricultural productivity is profoundly influenced by abiotic stresses such as drought, salinity, and low temperature. In many organisms, compatible solutes such as trehalose, proline, and betaines are synthesized to protect enzymes, membranes, and other cellular components from damage from these abiotic stresses, even though the exact mechanism of stress tolerance is not yet fully understood. Transgenic approaches offer new opportunities to improve tolerance for dehydration stress in plants by incorporating genes that are involved in stress tolerance. As an example, we transformed rice separately with two binary plasmids, each containing a fusion gene consisting of two *Escherichia coli* trehalose biosynthetic genes (*otsA* and *otsB*). We found that, in several transgenic lines, regulated overexpression of the fusion gene resulted in high levels of tolerance for salt, drought, or low-temperature stresses.

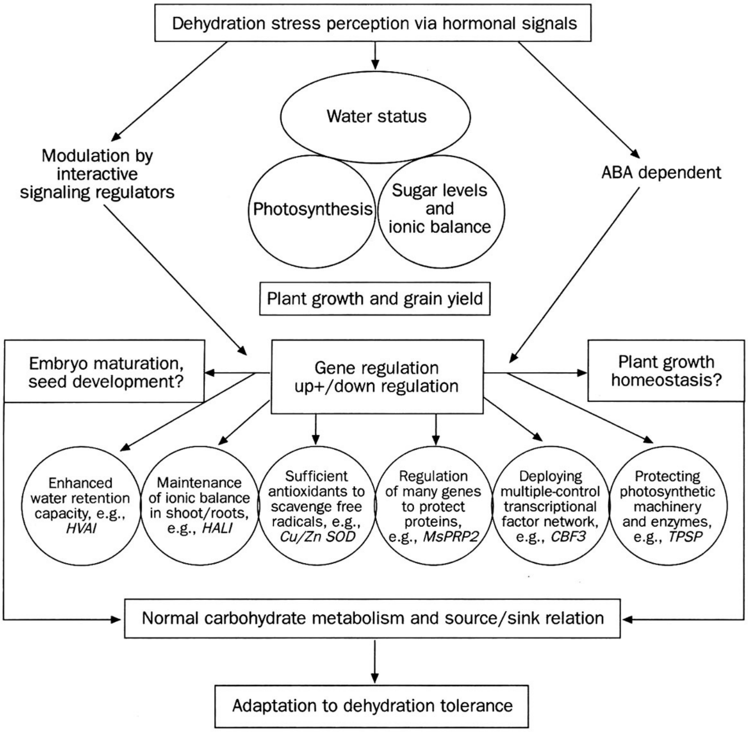
Compared with nontransgenic rice, transgenic lines containing either fusion gene exhibited sustained plant growth, a more favorable mineral balance, and less photo-oxidative damage under stress conditions. These findings demonstrate the feasibility of engineering rice for abiotic stress tolerance, which can minimize the loss of grain yield and thus increase farm income.

With the insertion-mutagenesis approach, the function of many new genes from rice can be discovered. We expect that some of the new genes related to abiotic stress tolerance may be useful for transformation. We have recently developed a strategy to systematically produce a nonredundant, indexed, insertion-mutant rice library. Our approach is unique in that it can readily produce an evenly spaced transposon-tagged population of 150,000 sublines, each at a known chromosomal location, without the need to determine the flanking sequence of each subline. This population is ideal for gene discovery via functional genomics because it will save a great deal of time by not having to screen the entire mutant population to find the desired mutant that matches the gene of interest.

Abiotic stresses on plants

Abiotic stresses, such as drought, excessive salinity, and low temperature, are major environmental factors that severely affect global agricultural production by altering plant metabolism, growth, and photosynthesis (Bray 1997). Plants have evolved a broad spectrum of strategies to cope with various abiotic stresses by displaying complex quantitative traits involving coordinated and differential expression of a network of genes to ensure their own survival and the prosperity of their progenies. These responses result in a wide variety of biochemical and physiological adaptive changes, such as the accumulation of compatible solutes (trehalose, glycine betaine, proline, and polyamines), synthesis of different late embryogenesis abundant (LEA) proteins, activation of several detoxification enzymes, and producing molecular chaperones and many other regulatory gene products (Bajaj et al 1999, Ramanjulu and Bartels 2002). Even though the exact number of genes that coordinate and regulate the process has yet to be determined, transgenic approaches still offer new opportunities to elucidate the functions of many useful candidate genes from different organisms, and to improve abiotic stress tolerance in plants and combat world hunger (Borlaug 2000).

As a first step toward improving stress tolerance in crop plants, understanding the underlying regulatory gene(s) governing the stress-signaling pathways is an essential component of basic and applied research. Different genes and a network of pathways are regulated in different organisms for sustained growth during prolonged exposure to environmental stresses (Fig. 1). Drought or osmotic stress can directly or indirectly affect plant water status. A common response to these types of stress is the metabolic changes in carbohydrate levels, ionic balance, and photosynthetic efficiency of the plant. However, our current understanding of the genes regulating these functions is far from complete. Therefore, a major challenge is to assess the relative contribution of each gene to abiotic stress tolerance in model plants. This



HVA1: group 3 LEA protein gene; *HAL1*: promotes K^+Na^+ selectivity; *Cu/Zn SOD*: superoxide dismutase; *MsPRP2*: transcription factor; *CBF3*: transcription factor; *TPSP*: trehalose-6-phosphate synthase/phosphatase fusion gene (trehalose synthesis).

HVA1: group 3 LEA protein gene; *HAL1:* promotes K^+Na^+ selectivity; *Cu/Zn SOD:* superoxide dismutase; *MsPRP2:* transcription factor; *CBF3:* transcription factor; *TPSP:* trehalose-6-phosphate synthase/phosphatase fusion gene (trehalose synthesis).

Fig. 1. The complex network of pathways that are affected when plants are subjected to environmental stresses.

will allow us to identify the pathways and sets of genes that interact within a network of genes. The mutant libraries being produced for forward and reverse genetics and the availability of sequence information from *Arabidopsis,* rice, and several other organisms hold the key to our missing knowledge about the mechanism(s) of abiotic stress tolerance in plants. The key is in the design of experiments that will direct us to the appropriate genes to elucidate their function.

Recently, several reports have been published related to the improvement of abiotic stress tolerance in plants via genetic engineering and the need to use functional genomic approaches to enhance grain yield (Xu et al 1996, Apse et al 1999, Kasuga

Table 1. Comparison of abiotic stress tolerance in transgenic rice lines transformed with different agronomically useful genes.

Over-production of	Promoter/gene	Plasmid	Levels of protection			References
			Salt [a]	Drought [b]	Low temperature [c]	
LEA III	Act1/ *Hva1*	pBY520	Medium	Medium	ND	Xu et al (1996)
LEA II, LEA I	Act1/ *PMA80* Act1/ *PMA1959*	pJPM44 pJPM45	Medium	Medium	ND	Cheng et al (2002)
Proline	Act1/ *p5cs* ABRC/ *p5cs*	JS102 JS112	Medium/ high	Medium/ high	ND	Cheng et al (2001)
Polyamines	ABRC/*ADC*	pMR43	Medium	Medium	ND	Royand Wu (2001)
Polyamines	ABRC/*SAMDC*	pMR10	Medium	Medium	ND	Royand Wu (2002)
Trehalose	ABRC/*TPSP*	pSB109-TPSP	High	High	High	Garg et al (2002)
Transcription factor	ABRC/ *Atmyb2*	pVS105	Medium	Medium	ND	Sangwan and Wu (2003), unpublished

[a]100 mM NaCl for 7 to 30 d. [b] No watering for 6 d, twice. [c] 10 °C for 3 d; ND = not done. High-level protection: control/transgenic = 20-30%/80-90%. Medium level = 20–30%/50-60%.

et al 1999, Saijo et al 2000, Roy and Wu 2001). Also, new insights and direction into the molecular and physiological basis of dehydration tolerance have been studied using the tools of molecular markers, microarray, and proteomics (Oztur et al 2002, Reddy et al 2002, Salekdeh et al 2002). However, there is still a gap between what has been achieved and what needs to be achieved in terms of abiotic stress tolerance in plants. This gap could have a significant effect on agricultural productivity (Khush 1999, Surridge 2002).

The first part of this chapter is devoted to describing the progress that our laboratory has been making with the goal of increasing dehydration-stress tolerance in rice. Over the last seven years, we have individually introduced eight potentially beneficial genes into rice and observed improved stress tolerance in each case (see Table 1). We now use one example to illustrate that regulated overexpression of trehalose biosynthetic genes in transgenic rice plants can substantially increase tolerance for drought, high salinity, and low temperature. We also briefly discuss the future prospects of this line of research to increase rice yield.

The second part of this chapter is devoted to briefly summarizing our preliminary work in producing an indexed, nonredundant, insertion-mutant rice library. This library can be used in the future to aid in the discovery of the functions of many new genes, some of which are expected to be related to abiotic stress tolerance. These

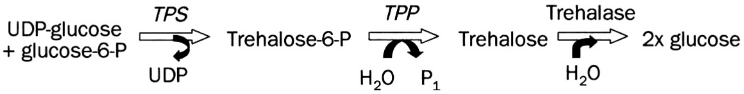


Fig. 2. Trehalose synthesis and degradation pathway in bacteria and plants.

genes can then be linked to suitable promoters and transferred into rice plants to further enhance stress-tolerance levels.

Transgenic plants engineered to synthesize trehalose for enhanced abiotic stress tolerance

Trehalose (α -D-glucopyranosyl- 1,1 - α -D-glucopyranoside) is a nonreducing disaccharide of glucose (Fig. 2) that occurs in a large variety of organisms ranging from bacteria, fungi, and nematodes to invertebrate animals. In addition to its function as a storage carbohydrate and transport sugar, trehalose plays an important role in stress protection (Crowe et al 1992). Trehalose has been shown to possess the unique feature of reversible water absorption capacity to protect biological structures from damage during desiccation (Sussich et al 2001). When water dissipates from the water shell of macromolecules during severe dehydration, trehalose can act as a water substitute by satisfying the hydrogen-bonding requirement of polar groups on the surface of the dried protein (Crowe et al 1992). Thus, the native folding and biological activity of proteins are maintained and denaturation and aggregation are prevented. Furthermore, trehalose remains stable at elevated temperatures and at low pH and does not undergo Maillard browning with proteins. These protective properties of trehalose are clearly superior to those of other sugars, such as sucrose, making trehalose an ideal stress protectant. The protective property may include serving as an osmolyte, regulating other genes or pathways, and protecting different macromolecules in the cells.

Despite the wide distribution of trehalose in microorganisms and invertebrates, trehalose had until recently been found only in a few plant species, notably highly desiccation-tolerant, resurrection plants (clubmosses *Selaginella lepidophylla* and *S. sartorii* and the angiosperm *Myrothamnus flabellifolius*), so named because of their unique ability to fully recover from a state of almost complete loss of water. These resurrection plants accumulate trehalose at levels approaching 1% of dry weight under nonstress conditions, whereas the majority of plants do not appear to accumulate easily detectable amounts of trehalose (Wingler 2002). However, genes encoding enzymes of trehalose synthesis, that is, trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP), have been identified in *Arabidopsis* (Leyman et al 2001). TPS and TPP homologs have also been found in rice, soybean, and potato (Table 2). Given the apparent lack of a significant amount of trehalose accumulation, which may be due to low levels of expression of the endogenous

Table 2. Selected list of putative genes that are likely to be involved in trehalose biosynthesis and degradation in plants.

Accession no.	Gene name	Homology	Organism	TPS domain [a]	TPP domain [b]	P boxes [c]
At1g78580	*AtTPS1*	TPS	*Arabidopsis thaliana*	+	+	-
At1g16980	*AtTPS2*	TPS	*A. thaliana*	+	+	-
At1g17000	*AtTPS3*	TPS	*A. thaliana*	+	+	-
At4g27550	*AtTPS4*	TPS	*A. thaliana*	+	+	-
At4g17770	*AtTPS5*	TPS	*A. thaliana*	+	+	+
At1g68020	*AtTPS6*	TPS	*A. thaliana*	+	+	+
At1g06410	*AtTPS7*	TPS	*A. thaliana*	+	+	+
At1g70290	*AtTPS8*	TPS	*A. thaliana*	+	+	+
At1g23870	*AtTPS9*	TPS	*A. thaliana*	+	+	+
At1g60140	*AtTPS10*	TPS	*A. thaliana*	+	+	+
At2g18700	*AtTPS11*	TPS	*A. thaliana*	+	+	+
At5g51460	*AtTPPA*	TPP	*A. thaliana*	-	+	+
At1g78090	*AtTPPB*	TPP	*A. thaliana*	-	+	+
AF056946	Unnamed	TPS	*Gossypium hirsutum*	+	?	?
BAB21172	Unnamed	TPS	*Oryza sativa*	+	+	+
BAB56048	Unnamed	TPS	*O. sativa*	+	+	+
AAG13478	Unnamed	TPP	*O. sativa*	-	+	+
AAD00829	Unnamed	TPS	*Selaginella lepidophylla*	+	+	+
AAL91978	Unnamed	TPS	*Solanum tuberosum*	+	+	+
AAF22127	*T19F06.15*	Trehalase	*A. thaliana*	-	-	-
AAD22970	*GMTRE1*	Trehalase	*Glycine max*	-	-	-
CAB50901	*TRE1*	Trehalase	*Medicago truncata*	-	-	-
AAG13442	Unnamed	Trehalase	*O. sativa*	-	-	-
CAA03401	Unnamed	Trehalase	*S. tuberosum*	-	-	-

[a] TPS/ [b] TPP domains and P boxes were identified using clustalW sequence analysis from EMBL-EBI. [c] P boxes = phosphatase boxes.

genes or to the presence of trehalase activity, the question arises whether trehalose synthesis is a common phenomenon in higher plants and whether the increase in trehalose levels in crop plants might confer abiotic stress protection.

Recently, several research groups have been attempting to study the role of trehalose in abiotic stress protection and plant metabolism, including sugar sensing in crop plants via genetic engineering (Holmstrom et al 1996, Goddijn and van Dunn 1999, Paul et al 2001). However, in most cases, constitutive overexpression of TPS and/or TPP encoding genes from yeast or *Escherichia coli* in model dicot plants (tobacco or potato) resulted in enhanced trehalose levels, but also caused stunted plant growth and altered metabolism under normal growth conditions (Goddijn et al 1997, Romero et al 1997, Pilon-Smits et al 1998).

As an alternative approach to engineer increased trehalose accumulation in rice, we used a fusion gene (*TPSP*) that consists of the *E. coli otsA* and *otsB* genes that encode TPS and TPP, respectively (Seo et al 2000), by fusing them with a short linker without deleting any amino acids of either protein moiety. The fusion gene has the dual advantages of necessitating only a single transformation event to introduce both genes simultaneously into the rice genome, while at the same time imitating naturally occurring putative bipartite TPS/TPP-like genes in plants (Table 2). Two binary plasmids (pSB109-TPSP and pSB-RTSP) were constructed (Garg et al 2002), each driving the *TPSP* fusion gene either by an ABA stress-inducible ABRC promoter (Su et al 1998) for cytosolic expression or by a light-regulated rice rbcS promoter with a transit peptide (Kyozuka et al 1993) for chloroplast targeting. The T-DNA was introduced into indica rice (Pusa Basmati 1) by *Agrobacterium*-mediated gene transfer (Garg et al 2002). In contrast to previous reports in dicot plants, all 90 independent primary transformants (T_0) that we produced showed a normal vegetative phenotype and were completely fertile. Southern blot analysis showed that about 40% of the transgenic plants transformed with either of the plasmids harbored a single copy of the transgene. The homozygous fifth generation (T_4) transgenic plants were used to conduct several physiological experiments.

Most of the independent transgenic lines harboring low copies of the transgene showed markedly enhanced salt tolerance after 4 weeks of continuous 100 mM NaCl treatment under both hydroponic and soil-grown experiments. All 25 experimental plants from each transgenic line (three independent experiments) survived after prolonged exposure to salt stress and displayed vigorous root and shoot growth; over the same treatment period, all the nontransgenic stressed (NTS) plants were dead or nearly dead because of severe salt damage of leaves and concomitant loss of chlorophyll. Transgenic plants developed longer and thicker roots than NTS plants during the salt stress and showed dry weight similar to that of nontransgenic, nonstressed control (NTC) plants (Garg et al 2002).

The results described above suggest that increased trehalose levels in transgenic plants might be acting as a positive regulator of salt tolerance. To evaluate this hypothesis, the levels of trehalose and other nonstructural carbohydrates were measured in the shoots of transgenic and nontransgenic lines. A low amount of endogenous trehalose was detected in the shoots of nontransgenic plants without stress and a marginal increase under salt stress (<25 μg g^{-1} FW) was detected. In contrast, the transgenic plants exhibited elevated trehalose levels in shoots under nonstress conditions (50-200 μg g^{-1} FW). After salt stress, the transgenic lines showed 3- to 8-fold higher trehalose in the shoots than nontransformed plants. Transgenic lines with a stress-inducible promoter (ABRC) showed a larger stress increase in trehalose accumulation in shoots compared with plant lines harboring the light-regulated rbcS promoter. The range of trehalose accumulation was 80-530 μg g^{-1} FW in shoots from ten independent transgenic lines during salt stress. The identity of trehalose in the plant extracts was confirmed by incubating samples with porcine-kidney-derived trehalase enzyme (Sigma, USA) followed by chromatographic analysis (Garg et al 2002).

Clearly, many factors in addition to endogenous trehalose levels function to regulate plant stress responses. In nontransgenic salt-stressed plants, a considerable decline in soluble carbohydrates was observed in the shoots vis-a-vis nontransgenic, nonstressed plants. In contrast, transgenic plants showed a significant increase in the accumulation of trehalose, glucose, sucrose, and soluble starch in the shoot tissue in response to abiotic stresses (data not shown). The level of stress-induced trehalose accumulation in the transgenic rice plants was far below that observed in resurrection plants and other drought-stress-tolerant organisms. These data indicate that the enhanced stress tolerance we observed in our transgenic plants was not a direct effect of trehalose acting only as an osmoprotectant. Rather, the correlation with total soluble carbohydrate levels suggests that trehalose may be acting as a general regulator of carbon metabolism, as has been reported in some microorganisms (Thevelein and Hohmann 1995). However, the role of trehalose as a signaling molecule in the regulation of carbohydrate metabolism and stress responses appears to be a complex one (Table 3).

The reduction of photosynthesis and subsequent production of reactive oxygen species are thought to be of major importance in decreasing plant performance and leading to photo-oxidative damage during abiotic stress (Saijo et al 2000). The effects of increased trehalose accumulation on photosynthesis during salt stress were assessed by measuring the quantum yield of photosystem II (PS II) photochemistry using *in vivo* chlorophyll fluorescence techniques. After 4 weeks of continuous 100 mM NaCl treatment, the quantum yield of PS II photochemistry in nontransgenic plants was

Table 3. Complex role of trehalose biosynthesis in the regulation of carbon metabolism in transgenic or mutant plants.

Active molecule [a]	Regulated pathway/ mechanism	Testing method	References
Tre-6-P	Sugar accumulation during drought stress	Transgenic tobacco plants constitutively expressing the *E. coli TPS* gene	Pilon-Smits et al (1998)
Tre-6-P	Photosynthetic capacity	Transgenic tobacco plants constitutively expressing the E. coli *TPS* or *TPP* genes	Paul et al (2001)
Tre-6-P	Embryo maturation	*Arabidopsis* mutant with disruption in *TPS1* by dSpm transposable element	Eastmond et al (2002)
Trehalose	Higher levels of soluble carbohydrates in leaves and increased capacity for photosynthesis	Transgenic rice plants with inducible overexpression of the *E. coli TPS* and *TPP* genes as a fusion gene (*TPSP*)	Garg et al (2002)

[a] Tre-6-P = trehalose-6-phosphate.

only 16%, whereas the activities of the best-performing transgenic lines were more than 78% of those of their nonstressed controls. Similarly, salt-induced decreases in the fluorescence parameter Fv/Fm, which is a measure of accumulated damage to PS II, were considerably smaller in the transgenic lines compared with much larger decreases in the NTS plants. In another independent experiment, similar results were obtained from drought and low-temperature stresses, indicating the common role that maintenance of photosynthetic capacity plays in tolerance for abiotic stress (Garg et al 2002).

It is known that dehydration stress is a complex trait and that many genes are involved in stress. However, our results in overproducing a single compound, trehalose, resulted in high levels of abiotic stress tolerance in rice compared to the use of other genes (Table 1). However, direct comparison of the extent of abiotic stress tolerance in different studies using different genes and promoters, even in our own laboratory, cannot be made. This is because the experimental conditions used (e.g., differences in rice varieties, duration and severity of the applied stress, and the age of the plants in stress experiments) vary significantly. Abiotic stress tolerance in rice is likely due to an interplay of several survival mechanisms, some of which are operating simultaneously depending upon the severity and duration of the stress. However, it is not yet fully understood how trehalose is involved in the stress tolerance of the individual cell, organelle, or whole plant.

In conclusion, we have demonstrated that engineering trehalose overproduction in rice can be achieved by stress-inducible or tissue-specific expression of the bifunctional TPSP fusion gene without detrimental effects on plant growth or grain yield. During abiotic stress, transgenic plants accumulated increased amounts of trehalose and showed high levels of tolerance for salt, drought, and low-temperature stresses compared with nontransgenic plants. These results demonstrate the potential use of our transgenic approach in developing improved rice cultivars with increased abiotic stress tolerance and enhanced rice productivity. Moreover, we believe that a higher level of abiotic stress tolerance can be achieved by introducing several beneficial genes into the same rice plant.

The discovery of trehalose metabolism in higher plants, and its role in carbon metabolism and stress protection, has led to a new series of scientific surprises and challenges for the future in this field. Analysis of the tissue-specific expression of trehalose biosynthesis and degradation might shed light on its role in sugar sensing and signaling, plant metabolism, plant-pathogen interactions, abiotic stress tolerance, and seed development. A major task ahead is to pinpoint all the functions of trehalose in plants.

Insertion-mutagenesis approach for gene discovery in rice

A major challenge in the postgenomic era is to identify the functions of the predicted 60,000 genes present in the rice genome (Yu et al 2002, Goff et al 2002). A multipronged strategy, combining analysis of mutant phenotypes, sequence similarities, and expression profiles, offers new opportunities to determine the functions of a large number of genes.

A direct method for determining gene function in a plant is to analyze the changes that occur when a particular gene is inactivated by mutation. A convenient way of determining the functions of all the genes in a plant genome is to disrupt each gene by insertion of a plasmid. The number of transposons or T-DNA inserts needed to approach saturation depends on the size of the gene of interest and the size of the genome. To achieve a 99% probability of tagging all the genes in rice by inserting a plasmid at 3-kb intervals in the rice genome, constructing a random-saturation, insertional-mutant library of rice would require the production of 660,000 tagged plant lines (Krysan et al 1999). Each line represents a loss-of-function mutant. Transposable elements provide a convenient means of disrupting many plant genes without the need to produce a very large number of primary transformants.

So far, all the published reports describing attempts to construct a saturation, insertion-mutant library in any plant have used the random approach, which is very time-consuming, especially for rice (Sundaresan et al 1995, Enoki et al 1999, Jeon et al 2000). Furthermore, once the mutant library is constructed, all the mutant lines need to be screened to find the desired mutant that matches a specific gene of interest. This is time-consuming and labor-intensive, even to determine the function of a single gene. Therefore, determining the functions of all 60,000 predicted genes in the rice genome would require tremendous amounts of time and effort.

To speed up gene discovery, we have developed a systematic approach to construct a nonredundant, indexed, near-saturation, insertion-mutant rice library. The approach is unique in the production of an evenly and precisely transposon-tagged insertional-mutant rice population, which is ideal for functional genomics in speeding up gene discovery. We have constructed three novel plasmids that all contain maize *Ds* elements and two clusters of strategically designed enzyme cleavage sites within the T-DNA. These plasmids, which differ in other aspects, are briefly described in a later section. For illustration, we use a gene-trap plasmid (Fig. 3) for transformation of rice variety Nipponbare. In our experimental design, we plan to produce approximately 15,000 primary transformants (T_0) and choose only those transgenic plants (around 5,000) that harbor a single copy of the T-DNA. By determining the flanking sequence of each of the 5,000 transgenic plants and finding the chromosomal location of each plant, approximately 2,000 *Ds*-T-DNA-containing anchor lines can be produced. These anchor lines are selected so that the average distance between adjacent anchors is approximately 200 kb. The next step in using plasmid 1 (a gene-trap plasmid, as shown in Fig. 3) is to cross each *Ds*-containing anchor line with two different *Ac*-containing rice lines. After transposition, a large number of newly transposed sublines can be derived from each anchor line and easily selected by resistance to both Basta and hygromycin.

Next, DNA from each subline is digested with I-*Ppo*I endonuclease, followed by Southern blot analysis. The desired DNA fragment released by the digestion is then identified by probing separately with a portion of the RB and LB sequences present in the plasmid. The approximate size of the DNA fragment is estimated by comparing

I. *Ds* - containing T-DNA from a gene-trap plasmid after integration into the genome of transgenic rice before transposition

A B

∼∼∼∼LB-*bar*-5′ *Ds*-*hpt*-Ip1-Gus-GPIn-3′ *Ds*-UbP-Ip2-CN-RB∼∼∼∼

where Ip1 and Ip2 are I- *Ppo*I recognition sequences; CN is a rice sequence for rapid copy number analysis by PCR; UbP is maize ubiquitin promoter; GPIn is GPA1 intron; LB and RB are left and right borders of the T-DNA; bar is the phosphinotricin acetyl transferase gene; *hpt* is the hygromycin phosphotransferase gene; Gus is *uidA;* wavy lines are rice genomic DNA. Only essential components are included in this figure.

II. T-DNA in transgenic rice after transposition to the right

A B C

∼∼∼∼LB-*bar*-UbP-Ip2-CN-RB∼∼∼∼5′ *Ds*-*hpt*-Ip1-Gus-GPIn-3′ *Ds*∼∼∼∼

III. After cleavage of rice genomic DNA (in step II) by I- *Ppo*I endonuclease

A B C

∼∼∼∼LB-*bar*-UbP + Ip2-CN-RB∼∼∼∼5′ *Ds*-*hpt* + Ip1-Gus-GPIn-3′ *Ds*∼∼∼∼

By Southern blot analysis, the size (up to 120 kb) of fragment 5 containing DNA can be determined by comparing with DNA size marker.

Fig. 3. Analysis of a subline derived from a specific anchor plant line.

it with DNA markers up to 120 kb, and a more precise size is determined by polymerase chain reaction (PCR). Alternatively, the distance of transposition can be determined solely by a modified PCR approach developed in our laboratory without the need for Southern blot analysis. In our strategy, we keep only those sublines that have transposed up to 120 kb away, both to the left side and right side of the anchor position. Next, we choose approximately 80 sublines such that the average distance between adjacent sublines is 3 kb. To achieve a 99% probability that every rice gene has been tagged, we need to produce only 150,000 ordered insertion-mutant lines instead of 600,000 randomly produced mutant lines (Krysan et al 1999). Our approach is especially advantageous over the published methods, which produce the insertion-mutant plant lines by the random shotgun approach. In our new approach, at an early stage, we use two rapid and simple biochemistry-based procedures to preselect (from approximately 1,200 sublines derived from each anchor line) 80 plant lines that are approximately 3 kb apart from neighboring tagged lines, thereby converting a randomly tagged library into an ordered, linked, nonredundant library. However, some of the redundant lines are saved to serve as allelic mutants. The resulting transposon-tagged rice library will be suitable for simultaneously analyzing the function of large numbers of different genes using the reverse-genetic approach. The major advantage of our systematically produced mutant sublines is that we know the chromosomal location of the transposon-mediated insertion in every subline. Therefore, if scientists wish to obtain mutant lines that correspond to a specific gene at a known chromosomal location, they need to analyze only a few mutant sublines. If the gene of interest is a quantitative trait locus (QTL), they need to screen only several hundred mutant sublines that surround the specific QTL instead of all 600,000 sublines in any randomly produced saturation-mutant library.

By using the *Ds*-containing gene-trap plasmid (plasmid 1), we have produced approximately 1,000 primary transformants. Copy-number determination was carried out by a rapid PCR method (Li et al 2003) and 350 transformants were found to contain a single copy of the *Ds*-containing plasmid. Next, we determined the flanking sequence by either the TAIL PCR method (Liu et al 1995) or a modified ligation-mediated PCR method (Balzergue et al 2001). Approximately 200 samples produced flanking sequences containing the right border of plasmid 1 and a readable DNA sequence of at least 250 nt. Out of the 200 samples, 50 matched the rice DNA sequence from the public database. Thus, we now have 50 anchor plants. As more of the genomic sequence is released to the public database, we expect that most of the remaining 150 samples will become useful anchor lines. We estimate that, within two years, we will produce approximately 2,000 anchor plants, which will serve our needs. Some of the anchor plants will be produced by transforming rice with a related plasmid, referred to as plasmid 2, which is also a gene-trap plasmid but includes a glucocorticoid-inducible promoter (Pieter et al 2001) to drive the expression of the maize transposase gene in the same plasmid. In this case, we do not need to cross a *Ds*-plant with an *Ac*-plant, but simply need to induce the promoter with dexamethasone to activate the transposase gene. Additional anchor plants will be produced by transforming rice with another plasmid, referred to as plasmid 3, which is an activation-trap plasmid. We have already separately transformed rice with plasmids 2 and 3. The 2,000 anchor plants will include those produced by using all three plasmids. All 150,000 sublines produced from these anchorlines are loss-of-function mutants. In addition, the sublines produced from plasmid 3 also serve as gain-of-function mutants.

References

Apse MP, Aharon GS, Snedden WA, Blumwald E. 1999. Salt tolerance conferred by overexpression of a vacuolar Na+/H+ antiport in *Arabidopsis.* Science 285:1256-1258.

Bajaj S, Targolli J, Liu L-F, Ho-T-HD, Wu R. 1999. Transgenic approaches to increase dehydration-stress tolerance in plants. Mol. Breed. 5:493-503.

Balzergue S et al. 2001. Improved PCR-walking for large-scale isolation of plant T-DNA borders. BioTechniques 30:496-503.

Bray EA. 1997. Plant responses to water deficit. Trends Plant Sci. 2:48-54.

Borlaug NE. 2000. Ending world hunger: the promise of biotechnology and the threat of antiscience zealotry. Plant Physiol. 124:487-490.

Cheng ZQ, Targolli J, Su J, He CK, Li F, Wu R. 2001. Transgenic approaches for generating rice tolerant of dehydration stress. In: Khush GS, Brar DS, Hardy B, editors. Rice genetics IV. IRRI, Science Publishers, Inc. p 423-438.

Cheng Z, Jayaprakash TL, Huang X, Wu R. 2002. Wheat LEA genes, *PMA80* and *PMA1959,* enhance dehydration tolerance of transgenic rice (*Oryza sativa* L.). Mol. Breed. 10:71-82.

Crowe JH, Hoekstra FA, Crowe LM. 1992. Anhydrobiosis. Annu. Rev. Physiol. 54:579-599.

Eastmond PJ, van Dijken AJ, Spielman M, Kerr A, Tissier AF, Dickinson HG, Jones JD, Smeekens SC, Graham IA. 2002. Trehalose-6-phosphate synthase 1, which catalyses the first step in trehalose synthesis, is essential for *Arabidopsis* embryo maturation. Plant J. 29:225-235.

Enoki H, Izawa T, Kawahara M, Komatsu M, Koh S, Kyosuka J, Shimamoto K. 1999. *Ac* as a tool for the functional genomics of rice. Plant J. 19:605-613.

Garg AK, Kim JK, Owens TG, Ranwala AP, Choi YD, Kochian LV, Wu RJ. 2002. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. Proc. Natl. Acad. Sci. USA 99:15898-15903.

Goddijn OJ, van Dunn K. 1999. Trehalose metabolism in plants. Trends Plant Sci. 4:315-319.

Goddijn OJ, Verwoerd TC, Voogd E, Krutwagen RW, de Graaf PT, van Dunn K, Poels J, Ponstein AS, Damm B, Pen J. 1997. Inhibition of trehalase activity enhances trehalose accumulation in transgenic plants. Plant Physiol. 113: 181-190.

Goff S et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Holmstrom KO, Mantyla E, Welin B, Mandal A, Palva ET, Tunnela OE, Londesborough J. 1996. Drought tolerance in tobacco. Nature 379:683-684.

Jeon J-S et al. 2000. T-DNA insertional mutagenesis for functional genomics in rice. Plant J. 22:561-570.

Kasuga M, Liu Q, Miura S, Yamaguchi-Shinozaki K, Shinozaki K. 1999. Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. Nat. Biotechnol. 17:287-291.

Khush GS. 1999. Green revolution: preparing for the 21st century. Genome 42:646-655.

Krysan PJ, Young JC, Sussman MR. 1999. T-DNA as an insertional mutagen in *Arabidopsis.* Plant Cell 11:2283-2290.

Kyozuka J, McElroy D, Hayakawa T, Xie Y, Wu R, Shimamoto K. 1993. Light-regulated and cell-specific expression of tomato *rbcS-gusA* and rice *rbcS-gusA* fusion genes in transgenic rice. Plant Physiol. 102:991-1000.

Leyman B, Van Dijck P, Thevelein JM. 2001. An unexpected plethora of trehalose biosynthesis genes in *Arabidopsis thaliana.* Trends Plant Sci. 6:510-513.

Li F, Dey M, He CK, Sangwan V, Wu XZ, Wu R. 2003. Rapid PCR-based determination of transgene copy number in rice. Plant Mol. Biol. Rep. (In press.)

Liu YG, Mitsukawa N, Oosumi T, Whittier RF. 1995. Efficient isolation and mapping of *Arabidopsis thaliana* T-DNA insert junctions by thermal asymmetric interlaced PCR. Plat J. 8:457-463.

Oztur ZN, Talame V, Deyholos M, Michalowski CB, Galbraith DW, Gozukirmizi N, Tuberosa R, Bohnert HJ. 2002. Monitoring large-scale changes in transcript abundance in drought- and salt-stressed barley. Plant Mol. Biol. 48:551-573.

Paul M, Pellny T, Goddijn 0. 2001. Enhancing photosynthesis with sugar signals. Trends Plant Sci. 6:197-200.

Pieter B, Ouwerkerk F, de Kam RJ, Harry J, Hoge C, Meijer AH. 2001. Glucocorticoid-inducible gene expression in rice. Planta 213:370-378.

Pilon-Smits EAH, Terry N, Sears T, Kim H, Zayed A, Hwang S, van Dunn K, Voogd E, Verwoerd TC, Krutwagen RW, Goddijn OJM. 1998. Trehalose-producing transgenic tobacco plants show improved growth performance under drought stress. J. Plant Physiol. 152:525-532.

Ramanjulu S, Bartels D. 2002. Drought- and desiccation-induced modulation of gene expression in plants. Plant Cell Environ. 25:141-151.

Reddy AR, Ramakrishna W, Sekhar AC, Ithal N, Babu PR, Bonaldo MF, Soares MB, Bennetzen JL. 2002. Novel genes are enriched in normalized cDNA libraries from drought-stressed seedlings of rice (*Oryza sativa* L. subsp. *indica* cv. Nagina 22). Genome 45:204-211.

Romero C, Belles JM, Vaya JL, Serrano R, Culianez-Macia FA. 1997. Expression of the yeast trehalose-6-phosphate synthase gene in transgenic tobacco plants: pleiotropic phenotypes include drought tolerance. Planta 201:293-297.

Roy M, Wu R. 2002. Overexpression of S-adenosylmethionine decarboxylase gene in rice increases polyamine level and enhances sodium chloride-stress tolerance. Plant Sci. 163:987-992.

Roy M, Wu R. 2001. Arginine decarboxylase transgene expression and analysis of environmental stress tolerance in transgenic rice. Plant Sci. 1602369-875.

Saijo Y, Hata S, Kyozuka J, Shimamoto K, Izui K. 2000. Over-expression of a single Ca^{2+}-dependent protein kinase confers both cold and salt/drought tolerance on rice plants. Plant J. 23:319-327.

Salekdeh GH, Siopongco J, Wade LJ, Ghareyazie B, Bennett J. 2002. Proteomic analysis of rice leaves during drought stress and recovery. Proteomics 2:1131-1145.

Seo HS, Koo YJ, Lim JY, Song JT, Kim CH, Kim JK, Lee JS, Choi YD. 2000. Characterization of a bifunctional enzyme fusion of trehalose-6-phosphate synthetase and trehalose-6-phosphate phosphatase of *Escherichia coli.* Appl. Environ. Microbiol. 66:2484-2490.

Su J, Shen Q, Ho T-HD, Wu R. 1998. Dehydration-stress-regulated transgene expression in stably transformed rice plants. Plant Physiol. 117:913-922.

Sundaresan V, Springer P, Volpe T, Haward S, Jones JDG, Dean C, Ma H, Martienssen R. 1995. Patterns of gene action in plant development revealed by enhancer trap and gene trap transposable elements. Genes Develop. 9: 1797-1810.

Sunidge C. 2002. Agricultural biotech: the rice squad. Nature 416:576-578.

Sussich F, Skopec C, Brady J, Cesaro A. 2001. Reversible dehydration of trehalose and anhydrobiosis: from solution state to an exotic crystal? Carbohydr. Res. 334:165-176.

Thevelein JM, Hohmann S. 1995. Trehalose synthase: guard to the gate of glycolysis in yeast? Trends Biochem. Sci. 20:3-10.

Wingler A. 2002. The function of trehalose biosynthesis in plants. Phytochemistry 60:437-440.

Xu D, Duan X, Wang B, Hong B, Ho T-HD, Wu R. 1996. Expression of a late embryogenesis abundant protein gene, *HVAI,* from barley confers tolerance to water deficit and salt stress in transgenic rice. Plant Physiol. 110:249-257.

Yu J et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. indica). Science 296:79-92.

Notes

Authors' address: Department of Molecular Biology and Genetics, Cornell University, Ithaca, NY 14853, USA. ray.wu@cornell.edu.

Acknowledgments: This research work on overproduction of trehalose was supported in part by the Rockefeller Foundation Grant RF 98001-606 (to R.J.W.). We thank Dr. Yang Do Choi and Dr. Ju-Kon Kim for providing the *TPSP* fusion gene and the plasmid constructs. We thank Dr. T. Nagamine of Japan for high-quality rice seeds, variety Nipponbare, which were used for the transposon-tagged population.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Creation of and new developments in the ecological breeding system for super rice

Yao Xiang Huang

The "Rice Ecological Breeding Science System" has gone through several stages. In the 1950s-'60s, dwarf breeding involved the creation of the world's first artificially bred dwarf rice variety, Guang Chang Ai (1959), using the dwarf gene *Sd-1.* In the 1970s, the new dwarf gene *Sd-g* was used to breed Gui Chao Shuang Gui.

The cross combination and population selection method was invented, resulting in a shortening of the breeding time and improving the efficiency and success rate of rice breeding.

In the 1980s, semidwarf and early growth, super-high-yield breeding led to the breeding of Te Qing (which yielded 15.26 t ha^{-1}) and Sheng You (15.36 t ha^{-1}). In the 1990s, semidwarf, early growth, deeprooted, super-high-yield, (very) highquality breeding led to the breeding of Sheng Tai and the Jin Ke Zhan series (including Guang Chao 6).

Super ascendancy rice ecological breeding is described. The new cross combination and population selection method with emphasis on two sources is introduced and discussed in detail.

Scientific research and field production practices have proven that the performance of developed varieties is the overall expression of their superior genes. Plant phenotype is the result of genotypic expression in particular ecological environments. Stable and high yields of rice varieties are determined by their superior germplasm and genetic potential and their adaptability to their ecological environment. The rice ecological breeding strategy is based on this fact (Yao Xiang Huang 1990).

The yield of a crop is related to the growing structure of the population. The ideal population structure is developed by a good plant type under good cultivation conditions. Therefore, the objective of ecological breeding is based on ecological characters in different geographical locations to develop the ideal plant type to bring out the full potential of a variety. The key is to develop a plant type with ideal shape, population structure, and physiological and ecological characters. The emphasis here is that the plant type must combine all of the above synthetic characters, not just plant shape.

The establishment of the rice ecological breeding system did not start with a full and well-analyzed plan. Instead, it is developed like all other science disciplines: facing the highest-priority issues, coming up with new ideas and practices, and evaluating them continuously. Its establishment marks success in combining basic and applied research.

The rice ecological breeding system

Semidwarf breeding

Southern China has frequent storms and torrential rains, causing rice to lodge and resulting in very low yields. I therefore established the following rice breeding targets: semidwarfs; combining higher ability to use nitrogen, higher resistance to lodging, resistance to diseases, resistance to low temperature; a good root, stem, leaf, and panicle structure; and higher yielding ability.

Beginning in 1955 (Yao Xiang Huang 1959), using my earlier selected local farming semidwarf Ai Zi Zhan 4, which bears the *sd-1* gene, I developed the first artificially bred semidwarf variety Guang Chang Ai in 1959. It was rapidly distributed to different areas for evaluation and adoption. In the 1960s, I developed a series of new semidwarf varieties, which resulted in a shift to semidwarf breeding and high-yielding cultivars. With these varieties, China entered an era of semidwarf rice production, which has been a major contribution to China, its first "Green Revolution." This created enormously expanded social and economic benefits. The semidwarf rice breeding program in China was seven to ten years ahead of other similar programs in the world.

The semidwarf character of varieties such as Ai Zi Zhan 4 and Guang Chang Ai is due to the multiple effect of the main dwarf gene. It is closely related to important characters such as plant type, biomass, harvest index, nitrogen use, and lodging resistance. The creation and widespread adoption of the dwarf varieties formed the foundation for hybrid rice research and the basis for the high yield potential of hybrid rice. The varieties Guang Chang Ai and Zheng Zhu Ai and their descendants are used extensively to develop hybrid rice in China.

Dense growth breeding

High temperature, high humidity, small variation between day and night temperature, and frequent cloudy days are the weather characteristics of Guangdong Province. In the 1970s, I began breeding rice plants with dense panicles and compact tillers (Yao Xiang Huang 1983) to develop a new plant type that can maintain higher yields under high humidity and low sunlight. I discovered an especially dense-growing rice plant in a late generation of crossbreeding material. This material was used to develop the new variety Gui Yang Ai, which bears a new semidwarf gene, *sd-g*. Using Gui Yang Ai and another high-light-efficiency variety, Chao Yang Zhao 18, as parents, I successfully developed the famous rice varieties Gui Chao and Shuang

Gui, using hybrid breeding, repetitive hybridizing, and my newly invented cross combination and population selecting method (Yao Xiang Huang 1980, Zhong Yong Hu et al 2001).

Chinese geneticists Chong Qing Xie and Li Hong Zhu (1989) pointed out that varieties Gui Chao and Shuang Gui were planted on more than 1.67 million hectares, indicating their outstanding adaptability and high yield. The panicle grain count, panicle grain density, and single-plant yield characters of these varieties have a higher combining ability than the varieties bearing the *sd-1* gene. This development of discovering and using a new dwarf gene to avoid repetitively using the same gene, resulting in narrowing the genetic background, and to avoid the potential danger of lowering the adaptability of varieties was highly valued.

Breeding semidwarf, early maturing, and super-high-yielding varieties

If the source and sink (storage) in rice are not balanced, the rice tillers will have low biomass in the nutrition growth period, which will have a negative effect on the production of large panicles. In the 1980s, after analyzing the variety Gui Chao and finding the source and sink relationship between early growth and large panicles, a new scheme for creating a super-high-yielding rice plant type with dense and early growth was formed. The goal for semidwarf and early growth, super-high-yield breeding is to create rice varieties that will rapidly produce the sheath and longer, thicker, and larger leaves and high biomass before the nutrition growth period. At the same time, these varieties should keep the overall desirable characters of the semidwarf type, especially well-developed roots, lodging resistance, efficient fertilizer use, and a high number of effective panicles. This is the third stage of the ecological breeding program and the famous rice varieties Te Qing and Sheng You were successfully developed (Yao Xiang Huang 1999).

The main scheme is to select as parents excellent dwarf and semidwarf types that are compact, fast-growing, and high- and ultra-high-yielding. It is necessary to select for a relatively high number of panicles, increased panicle weight, strong culms, and increased leaf area index to enable a large amount of carbohydrates to be synthesized, accumulated, and transferred to provide for the heavy panicle weight and large panicles. Following this guideline, the following varieties were developed:

Te Qing 2
  15.26 t ha^{-1}, single cropping (Yunnan Province)
  12.00 t ha^{-1}, one planting in double cropping (Guangdong Province)
Sheng You 2
  15.36 t ha^{-1}, single cropping (Guizhuo Province)
  12.86 t ha^{-1}, one planting in double cropping (Guangdong Province)

These varieties are evidence of the success of the theory of super-high-yield breeding.

Breeder Charles Bollich (Bollich 1991) said, “When I think about rice varieties needed over the next ten years and even beyond the year 2000, I think about the Chinese varieties Gui Chao and Te Qing. Their plant type has changed some of my beliefs about where the next yield advances may be hidden. They will likely have more early season vigor and more biomass. They will be able to store more carbohydrates prior to development of the panicle." He also mentioned that the right way to breed new high-yielding, high-quality varieties would be by stressing yield first and then correcting for grain type (Bollich 1991).

Breeding semidwarf, early maturing, deeprooted, super-high-yielding varieties with improved grain quality

A thorough study of the early growth and super-high-yielding variety Te Qing showed that its large panicle, high grain count on each panicle, and plump grain are directly related to its healthy, vigorous, and strong root system, which is deeply and widely distributed without premature senility. Based on this study, the scheme for developing semidwarf, early growing, deep-rooted, super-high-yielding, and very high-quality rice varieties was established (Yao Xiang Huang 1999, 2001).

The characteristics of an ideal root system enable nutrients to be readily absorbed and transferred to develop healthy green leaves and a high harvest index (grain:straw ratio). Also, they advance and activate plant functions all the way to the latest growth stages. An ideal root system provides the conditions to use high fertilization rates efficiently to produce well-filled grains and strong sturdy plants that resist lodging.

We analyzed the compact and fast-growing variety Shuang Gui, the semidwarf, early growth variety Gui Chao, the IRRI super rice, and other early growing, ultra-high-yielding deep-rooted varieties and concluded that

1. Varieties with ultra high yield and good grain quality have a well-developed root system. The root length is 25% to 50% longer than that of varieties with a high number of panicles at the tillering stage and they maintain the same number to the later stages. Also, the root weight of a single culm is much higher.
2. The newly bred ultra-high-yielding high-quality varieties Sheng Tai 1 and Qi Miao Xian 2 are equal to or better than the earlier ultra-high-yielding, large-panicle, early growth variety Te Qing 1 in panicle weight of a single plant, panicle weight of a single culm, grain number per panicle, and number of filled grains.

Therefore, the semidwarf, early growth, deep-rooted, super-high-yielding, (very) high-quality breeding system has a bright future. Sheng Tai 1 and Qi Miao Xian 2 could be used as the preferred gene source for super rice.

Rice varieties with a high panicle count tend to have shorter roots than the large-panicle varieties and their root count is higher than that of the large-panicle varieties. However, crossbreeding using the high-panicle-count variety Shuang Gui 36 as the female parent produced the large-panicle variety Jin Gui Zhan, which also has a very high root count. Shuang Gui 36 perhaps has strong genetic combining ability so that high root count and long root length are combined.

Our research group has already developed some varieties with good potential such as the Qi Miao Xiang series Qi Miao Xiang 12, Sheng Tai 1, and Gao Ke 13 (early growth, large panicles, and good grain quality) and the Jin Ke Zhan series (including Guang Chao 6; early growth, deep roots, large panicles, and good grain quality). Also, we used the combining technique to develop the Guang Chao series varieties, including Guang Chao 1, 2, 3, and 4, which all have high yield and good quality.

In summary, the success of the ecological breeding theory is based on the following methodology:

1. Targeted ultra high yield, good grain quality, multiple disease resistance, and wide adaptability;
2. Based on ecological breeding objectives, primarily use crossbreeding, combine with other standard techniques such as tissue culture, radiation, and chemically induced mutations, and any suitable biotechnology tools;
3. Create a new ideal plant type with rich ecological targeting;
4. Create a new ideal rice plant type based on the fundamental principles of heredity, that is, segregation, independent assortment, linkage, and crossing over, and pay special attention to detecting outcrossing and mutations;
5. In evaluating new segregating populations, use state-of-the-art methods to conduct functional appraisals;
6. Use the cross combination and population selection method and genealogical methods in making selections;
7. When a promising selection is relatively homozygous, conduct yield trials and mid-term adaptability tests to release the new variety as early as possible to contribute to increased rice production in the country;
8. Continue selecting better variants from the released variety to achieve a better performance and obtain the full potential of the genotype.

The development of the ecological breeding system

China is currently facing a new situation: a large population with a diminishing area for crop production, particularly in the south, where Guangdong Province is located. As an experienced rice breeder, I believe that varieties must be developed that will require less planting area but will produce high yields with superior grain quality that will increase farm income, such as super rice. With such varieties, less field area would be required to produce the same total yield as before. These varieties would require only one planting annually and could be grown at the optimum time for maximum production and grain quality. They would allow other crops to be grown when the single rice crop has been harvested. To develop such varieties is a formidable challenge and I am therefore establishing a new approach for super rice breeding by cross combination and population selection.

After studying and analyzing the population dynamics of rice under the ecological conditions in southern China, particularly Guangdong Province, our objective is to develop varieties with large and ultra-large panicles to achieve higher yields. However, based on past experience, varieties with large panicles normally have many problems. The view is that large panicles are associated with poor fertility, poor grain filling, and irregular small and large panicles on the same plant.

Based on my 1990-91 studies of the root systems of early growth, ultra-high-yielding varieties with large panicles, I believe that emphasis must be on improving the root system of varieties, that is, obtaining roots that are vigorous, deep, and strong so that the root system is in balance with the aboveground portion of the plant to achieve maximum efficient use of both sources.

This has been demonstrated with varieties such as Chi Xiu Zhan 3 and Sheng Tai 1, which have high fertility and well-filled grains and well-developed root systems that are deep, thick, and strong, and grow fast. These results are opposite to the view that a high grain count will result in low fertility. Under the new system of breeding, the significant point is to give equal emphasis to the root system and the aboveground plant.

Besides crossbreeding, our program cooperated with the biotechnology breeding program headed by Mei Fang Li at the Chinese Academy of Agricultural Sciences (Beijing) for many years (Mei Fang Li 2000). In the current super rice research program, we have already achieved early results. New varieties such as Zu Pei 127, Guang Hua 416, and San Te and the Jin Ke Zhan series 63305, 6320, and 6418, and Guang You Zhan form a strong base for further advances.

New cross combination and population selection method with emphasis on two sources

At this stage of ecological breeding, based on root research, I improved my cross combination and population selection method to turn it into the two-source cross combination and population selection method. The most important step is to observe both sources, the root system and the aboveground plant, in the F_1 generation to measure the combining ability of the parents to choose superior parent combinations.

Another approach in this new breeding method is to select in the F_3 generation for superior characteristics in the selected panicle lines to develop ideal varieties with multiple homogeneous advantages. Begin testing relatively superior homozygous lines early in the targeted production areas while at the same time continue to select for further improvement.

The cross combination and population selection method is based on the fundamental theory of heredity and the laws of segregation and independent assortment. In a simplified way, according to statistical probability, the F_2 recombination of genes is as follows:

Number of pairs of hybrid gene = n
Number of genotypes in $F_2 = 3^n$
Number of new homozygous types in $F_2 = 2^n - 2$
Number of heterozygous types in $F_2 = n \times 2^{n-1}$

When three pairs of genes participate in crossbreeding, this can be expressed as (AA,BB,CC) × (aa,bb,cc) => (AA,aa,Aa) × (BB,bb,Bb) × (CC,cc,Cc)

Number of pairs of hybrid gene = $n = 3$
Number of genotypes in $F_2 = 3^n = 27$
Number of new homozygous types in $F_2 = 2^n - 2 = 6$

AABBcc AabbCC Aabbcc aaBBCC aaBBcc aabbCC

Number of heterozygous types in $F_2 = n \times 2^{n-1} = 12$

AABBCc AabbCc aaBBCc aabbCc AABbCC AABbcc
AaBbCC aaBbcc AaBBCC AaBBcc AabbCC Aabbcc

When 10 pairs of genes participate in crossbreeding:

Number of pairs of hybrid gene $= n = 10$

Number of genotypes in $F_2 = 3^n = 59{,}049$

Number of new homozygous types in $F_2 = 2^n - 2 = 1{,}022$

(Ratio to total number of genotypes = 1,022/59,049 = 1.7%)

Number of heterozygous types in $F_2 = n \times 2^{n-1} = 1{,}536$

(Ratio to total number of genotypes = 1,536/59,049 = 2.6%)

From the above calculations, one can see that, by choosing parents with complementary characters, there is a possibility for the desired type variety to appear in the F_2. However, from the ratios shown above, it is hard to identify the basically stable selections in early generations. To do so requires very large F_2 populations and must include all individuals showing good overall performance.

The following is a simple explanation of the operation of the new cross combination and population selection method.

Parental selection is a very important step in crossbreeding. In our guideline, we emphasize targeting high and stable yield based on an excellent plant type, guided by complementary characters and assisted by variation surpassing that of the parents. To enrich the hybrid gene base, to widen the variation in later generations, and to obtain new superior characters, we often make crosses between different ecological types or between indica and japonica types. Repeat crossbreeding and combined crossbreeding are also used. Considering cytogenic inheritance, combined forward and backward crossbreeding could be performed together. Observe both the root system and plant body in observation plots in the F_1 generation and investigate thoroughly to observe the combining ability of the parents in order to select superior parental combinations. The F_1 character composition and the F_2 character recombination determine the combining ability. The F_1 character composition can appear again in the F_2 and the F_2 character recombination determines the limits of variation.

Procedures:

F_1 field experiment: Single seed planting.

F_1 selection: Observe both sources, the root and plant body, in the F_1 generation to determine the combining ability of the parents to select parents and cross combinations.

F_2 field experiment: Plant 10,000 to 20,000 individuals for each cross combination. Plant in pairs of two rows per selected panicle, with each row containing five individual plants.

F_2 selection: Select one or a few outstanding cross combinations, make many individual selections from the superior combination population, and pick an average of one panicle from four plants, which provides about 3,000 to 7,000 selected panicles from each cross combination.

For those combinations with poor population characters, perform individual plant selection and follow traditional breeding procedures with them.

F_3 field experiment: Plant panicle lines, two lines for each panicle, with each line containing 8 to 10 individuals.

In the F_3, emphasize superior characters and stability. It can be divided into four stages:

1. Tillering period: Observe the whole-panicle line for plant type, leaf type, leaf color, and tillering ability.
2. Vegetative growth period: Observe the whole-panicle line for plant type, leaf type, leaf color, and growth habit.
3. Heading period: Observe the whole-panicle line for initial heading, final heading, and panicle type for consistency.
4. Maturity period: Refer to the observations of the first three earlier stages and appraise plant height, plant type, leaf color, panicle type, grain type, fertilization rate, maturing color, high and stable yielding ability, and uniformity of maturity to determine panicle line selection.

Also, based on panicle line performance in the F_3, consider conducting transmigration selection (crossbreeding using F_3 plants), tissue and cell culture, and radiation- and chemically induced mutations. These techniques are key processes in developing super rice. However, these techniques are suitable for different periods of the rice plant so they should be planned early. If it is impossible to perform them in the F_3 they can be done in the F_4.

F_4 selection and appraisal: Perform preliminary yield trials, regional adaptability tests, and disease resistance tests. For relatively stable panicle lines with overall superior characters, continue panicle selection for further appraisal. For the selected F_3 panicle lines, continue selecting the best lines because some variation will continue.

To verify the ability to obtain good, stable varieties in the F_3 generation, from 1978 to 1980 the Guangdong Academy of Agricultural Sciences conducted a study on the subject. The study involved 15,527 panicle lines from 21 crossbreeding combinations. The results showed that 600 out of the 15,527 panicle lines (4.24%) were basically stable or tended to be stable. To further certify the reliability of this result, individual plants were selected from five panicle lines within the basically stable panicle lines, and planted in the F4 by plant line. Variance analysis was used to measure the differences between the plant lines that originated from the same F_3 panicle line. The items measured were plant height, panicle length, total grain count, and 1,000-grain weight, and the results indicated no significant difference.

At first glance, the cross combination and population selection method may give the impression of a huge workload, but the crucial and effective work is concentrated in the early part of the breeding process. Other breeding selection methods may have a lower workload in the early part, but the total amount of work would not be less. More important is that the cross combination and population selection method has a high success rate, good results, and advantages for rice crossbreeding.

References

Bollich C. 1991. Future rice varieties will change directions. Rice J. Feb.1991:10-14.

Chong Qing Xie, Li Hong Zhu. 1989. Genetic studies on dwarfism in indica rice: the inheritance of semi-dwarfism of varieties Shuang Gui and Cong Gui 36. J. Nanjing Agric. Univ. 12(3):1-6.

Mei Fang Li. 2000. Utilizing bio-tech rapid high efficiency to develop super rice. China Super Rice Research Project Report 1997-1999. Crop Breeding and Cultivation Institute, Chinese Academy of Agricultural Sciences.

Yao Xiang Huang. 1959. Breeding for creating "dwarf type" rice varieties. Proceedings of the China National Crop Breeding Conference, Nov. 1959, Beijing, China. p 1-10.

Yao Xiang Huang. 1980. Research on cross combination and population selection method in rice cross breeding. Guangdong Agric. Sci. 15-13.

Yao Xiang Huang. 1983. Rice dense growing breeding. Guangdong Agric. Sci. 1:1-8.

Yao Xiang Huang. 1990. Ecological breeding: crop breeding strategy decision. Guangdong Agric. Sci. 4:3-7.

Yao Xiang Huang. 1999. Formation and new development of ecological breeding science system. Guangdong Agric. Sci. 5:2-6.

Yao Xiang Huang. 2001. Semi-dwarf, early growth, deep root, super high yield, (very) high quality China super rice breeding. Guangdong Agric. Sci. 3:2-6.

Zhong Yong Hu, Yao Gui He, Yong Hong Wan. 2001. Progress in super and high quality rice breeding. In: China seed industry: new opportunity, new challenge, new strategy. Beijing (China): Agriculture Press. p 391-394.

Notes

Author's address: Researcher, Guangdong Academy of Agricultural Sciences, and chief scientist, Guangzhou Institute of Agricultural Sciences, 101 Building 4, East Section, Guangdong Academy of Agricultural Sciences, Wushan, Guangzhou, China 510640. hyxys@yahoo.com.cn.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Physiological traits associated with high yield potential in rice

T. Horie, I. Lubis, T. Takai, A. Ohsumi, K. Kuwasaki, K. Katsura, and A. Nii

The rapidly increasing world population requires the creation of new rice genotypes that surpass current yield potential under optimum management practices. It is therefore important to identify yield-limiting processes of rice and associated traits and to quantify their genetic variability. Field experiments conducted at Kyoto, Japan, for three years and a brief review of previous studies revealed that the genotypic difference in rice yield is most closely related to the crop growth rate (CGR) during the late reproductive period (14 to 0 d before full heading). CGR at this stage has critical effects on final spikelet number by regulating spikelet degeneration and potential single-grain weight by determining husk size. It also has strong effects on grain filling through the formation of active sinks by way of pollen grain and husk development and determining endosperm cell number by way of the reserve substrate supply in initial grain filling. A large genotypic variability in CGR during the late reproductive period was associated with that in radiation-use efficiency, but not with radiation interception rate. Genotypes having a higher CGR during this period had a cooler canopy temperature and higher maximum leaf photosynthetic rate, and they accumulated more nonstructural carbohydrates in the culms and leaf sheaths. A considerably large genotypic difference in the photosynthetic rate in this period could be viewed as a function of leaf nitrogen percentage in g g^{-1} and stomatal diffusive conductance or carbon isotope discrimination rate. The large variability in these traits observed among the existing rice genotypes, their wild relatives, and progenies of their hybrids suggests that there is still much scope for breeding new rice genotypes that surpass current yield potential by accumulation of the genes controlling these traits.

Although rapidly increasing world population, especially in developing countries, requires more rice production, the availability of fertile land and water for rice production is decreasing. This necessitates increased rice production per unit land area, that is, higher yield. But increases in rice yield have slackened considerably since the mid-1980s in many countries (Hossain 1999). One of the causes for the stagnation in yield is the slower rate of yield potential improvement in rice under optimum management practices. In the tropics, rice yield potential has not increased substantially in the past three decades since the Green Revolution began and the gap between yield potential and farmers' yield has narrowed (Peng et al 1999). Recognizing this, intensive and extensive work has been done to create new high-yielding rice genotypes, which includes the breeding work on new plant types (NPTs; Khush and Peng 1996) and F_1 hybrids (Yuan 1994). The hybrids showed a mean yield advantage of about 15% over the best inbred cultivars in China (Yuan 1994) and 9% at the International Rice Research Institute (Peng et al 1999). NPTs showed significantly higher yield than the elite inbred cultivar IR72 in the tropical wet season, but yield similar to that of IR72 in the dry season (Peng et al 1999). In Japan, indica-japonica crossbred cultivars Milyang23 and Takanari showed 36% to 47% higher yield than Nipponbare, a standard cultivar (Horie 2001). For the requirement of 70% more rice production in 2025 than in 1995 in Asia (Peng et al 1999), more efforts clearly have to be made to break the barrier to increases in yield potential in rice.

The design of rice genotypes with higher yield potential has been made based mainly on plant type (plant height, tiller number, panicle size, leaf length, leaf thickness and nitrogen content, leaf angles, stem and root thickness, etc.) (Tsunoda 1959, Yoshida 1972, Peng et al 1994, Yuan 2000). Contrary to this, physiological traits such as leaf photosynthetic rate, stomatal conductance, and respiration rate have rarely been used for the design of cultivars and in breeding programs, despite the enormous amount of work that has been done in crop physiology. To surpass the current yield potential of rice, physiological traits as well as the traditional plant type should be incorporated in breeding programs with the aid of molecular markers. For this, it is important to identify yield-limiting processes of rice and associated traits and to quantify their genetic variability.

This paper first reviews the yield formation processes that were improved for the past increase in rice yield potential to understand what is left for further improvement. Then, it describes the results of field experiments conducted in Kyoto, Japan, to identify yield-limiting processes of rice and associated crop physiological traits. Finally, it discusses important traits for high yield potential in rice and their genetic variability.

Understanding the past increase in yield potential

To understand which processes of yield determination were improved for the past increase in rice yield potential forms a basis for developing strategies for a further increase in yield potential. Here, we briefly review yield determination processes and associated traits that were improved mainly in the Green Revolution period.

Crop yield (Y, kg ha^{-1}) is most simply expressed as the product of biomass production (W) during the entire growth duration and harvest index (h):

$$Y = h\,W \qquad (1)$$

Crop yield potential is the maximum yield of a crop genotype under no biotic and abiotic stresses with an optimum supply of resources. For the yield potential of a specific grain crop such as rice, equation 1 can be transformed into

$$Y= \frac{W_{AF} + f\,W_{BF}}{W_{BF} + W_{AF}} (W_{BF} + W_{AF}) \qquad (2)$$

where W_{BF} and W_{AF} indicate biomass production before and after the flowering of a crop, respectively, and f the fraction of W_{BF} that is translocated to the grain after flowering. It is well accepted that the yield increase of grain crops up to now has been achieved mostly by increasing the harvest index (h), while the increase in total biomass production (W) was small or none (Holliday 1976, Evans 1993). This was also shown for rice (Takeda et al 1984, Akita 1989). This fact suggests that the increase in crop yield potential has been achieved through the increase in biomass production after flowering (W_{AF}) and/or translocation percentage (f) of preflowering biomass to grain, while W_{BF} remains unchanged or decreases. Evans (1993), based on his thorough review of the effect of preflowering crop growth rate (CGR) on yield, concluded that we lack evidence that the improvement of yield potential in any crop has been associated with higher preflowering CGR. This was also confirmed for rice between old and new genotypes (Takeda et al 1983, 1984, Akita 1989, Saito et al 1993). Akita (1989) describes that the ideal way to maintain a high CGR during the grain growth period and better ripening is to reduce the crop dry weight of rice at heading to as low as possible without sacrificing sink capacity. The above review suggests that the increase in rice yield potential in the Green Revolution period was achieved through the increase in biomass production in the postflowering period but not in the preflowering period.

Since leaf photosynthesis is the primary process for crop biomass production, extensive and intensive studies have been made on genetic and environmental effects on this process with the belief (or hope) that its improvement leads to better crop yields. Those studies revealed that a considerably large genotypic difference exists in maximum leaf photosynthetic rate (P_n) in many crops (c.f. the review of Evans 1993), including rice (Murata 1961, Ohno 1976, Cook and Evans 1983, Sasaki and Ishii 1992). In rice, the higher rate of maximum leaf photosynthesis (P_n) was shown to be associated with higher leaf nitrogen (N) content per unit leaf area (Takano and Tsunoda 1971, Hayami 1982, Sinclair and Hone 1989) and higher specific leaf weight (Murata 1961, Yoshida 1972). However, no clear evidence has been presented that higher P_n is directly associated with higher yield except for the grain growth period. Kuroda and Kumura (1990a,b,c) and Sasaki and Ishii (1992) found that the genotypic difference in P_n was associated with higher yield only in the grain growth period, but not so in the preflowering period in the historical series of Japanese rice cultivars. This implies that the higher yield of modem rice genotypes is associated with a slower decline in leaf P_n during the grain growth period, but not with P_n at its maximum in crop development. Similar results have also been obtained in many other grain crops (Evans 1993, Evans and Fischer 1999). These previous studies on P_n coincide with the abovementioned view that the increase in crop yield potential was associated with W_{AF} but not with W_{BF}.

It has been shown that the increases in postflowering biomass production of high-yielding rice genotypes are associated with the traits of maintaining a larger green leaf area (Murata 1961, Shiga and Sekiya 1976, Son et al 1979), higher single-leaf P, (Hayami 1982, Saito et al 1981, Kuroda and Kumura 1990a, Sasaki and Ishii 1992), and erect leaf canopy (Ishihara and Takigawa 1981, Saito et al 1993) during the grain growth period. Semidwarf genes played important roles in creating such characteristics for increased canopy photosynthesis and CGR during the grain growth period. Those genes functioned to suppress leaf elongation and maintain high N content per unit leaf area and erect leaf canopy under high N applications, resulting in enhanced postflowering biomass production (W_{AF}), while suppressing excessive vegetative growth.

Widely different values were reported for the percentage contribution to the yield of stored carbohydrates in vegetative organs during the preflowering period in rice: 26% (Cock and Yoshida 1973), 37% (Sumi et al 1996), and about 40% (Akita 1989) depending on genotype and cultivation conditions. Akita (1989) and Song et al (1990b) showed that F_1 hybrid rice had a significantly higher percentage contribution of stored carbohydrates to yield than inbred cultivars. This suggests that a genotypic difference also exists in the fraction (f) of preflowering biomass translocated to grain. Hiraoka et al (1986) showed a negative correlation between nonstructural carbohydrate percentage in biomass at flowering and culm length for different genotypes, suggesting an effect of semidwarf genes on the yield increase in potential through the increase in f.

The arguments so far are on the source side of yield determination and past achievement in sink enlargement in rice must be reviewed as well. Rice sink size is proportional to the numbers of spikelets per unit area. It is well recognized that the number of spikelets or their potential is proportional to the plant N content in the early reproductive period (Murayama 1969, Wada 1969, Shiga and Sekiya 1976, Hasegawa et al 1994, Kobayashi and Horie 1994, Hone et al 1997). Hasegawa et al (1994) analyzed the effect of plant N on spikelet number (m^{-2}) for different rice genotypes grown in different areas of Japan by separating the plant N into its two components, N concentration ($g\ g^{-1}$) and aboveground biomass (W) at the early reproductive stage. They found that the spikelet number increased linearly with the increase in N concentration and curvilinearly, in a saturation type, with the increase in plant biomass, suggesting that the increased sink size in high-yielding rice was achieved through increasing plant N concentration. A similar result was also shown by Akita (1989). Thus, semidwarf genes also contributed to enlarging sink size through increasing plant N concentration. It should be noted, however, that the plant N content at the early reproductive stage determines the potential sink size and the actual sink size is determined by subtracting from it the spikelet number degenerated during the late reproductive period (Wada 1969, Kobayashi and Horie 1994). Spikelet degeneration is shown to depend on the availability of carbohydrates during the late reproductive period (Wada 1969).

It becomes clear from the above review on the increase in yield potential in the Green Revolution that the enlargement in sink size was achieved through the increase in plant N concentration, and that in the source size by increased postflowering biomass production (W_{AF}) and fraction (f) of preflowering biomass translocated to grain, while preflowering biomass itself (W_{BF}) remained unchanged or even decreased in comparison with older genotypes. If enlargements of W_{AF} and f would be the only ways to enlarge source size and hence yield, the room left for a further increase in rice yield potential, without an extension of grain growth duration, would be limited because grain growth duration is only about 30 days in the tropics and about 50 days even in cool temperate regions. Under such a situation, simple enlargement of the photosynthetic capacity of single leaves as attempted by Ku et al (1999) would not improve yield potential, unless it is restricted in the grain growth period.

However, evidence is being accumulated to show the substantial contribution to the yield increase of enlarged preflowering biomass production in Chinese F_1 hybrid cultivars (Song et al 1990a,b) and indica-japonica crossbred cultivars (Horie 2001). This suggests that a different mechanism from that of the yield increase in the Green Revolution may exist in the high yield potential of those genotypes. In the subsequent sections, we will reexamine the yield determination process of rice and associated traits based on field experiments with widely different genotypes, including high-yielding indica-japonica crossbreds.

Field experiments conducted in Kyoto

To identify the most critical processes for yield determination of rice genotypes and associated factors, genotype comparison experiments were conducted in Kyoto for three years, 1999,2000, and 2001. Rice genotypes having a wide genetic background were used for the experiments (Table 1): those included indica, japonica, javanica (tropical japonica), new plant type (NPT) of IRRI, indica-japonica crossbreds, and *O. sativa* × *O. glaberrima* hybrids (WAB, now called NERICA). Although the composition of genotypes used for the experiments was different among the years, three genotypes, Takanari, Nipponbare, and IR65564-44-2-2 (NPT1), were adopted throughout the three years.

The cultivation conditions of those genotypes were slightly different among the years. Planting densities (hills m^{-2}) were 50 for NPTs and 22.5 for other genotypes in 1999, 50 for NPTs and 25 for others in 2000, and 22.2 for all the genotypes in 2001. The amounts of fertilizer applied ($N:P_2O_5:K_2O$ in g m^{-2}) were 15: 10: 10 for all genotypes in 1999, 12:10:10 for all genotypes in 2000, and 5:12:12 for Ch86 and Banten (to avoid lodging) and 12:12:12 for others in 2001. While P_2O_5 and K_2O were given all as basal, N was applied in four splits (1999 and 2000) and five splits (2001) to provide an optimum N condition for rice. Weeds, diseases, and insects were strictly controlled throughout the entire growth periods in the three years. The experiments were conducted in a randomized block design with two (1999 and 2000) and three (2001) replications with genotype as the factor. Each plot size differed in different years, but was more than 22 m^2. Thus, the experiments were considered to provide close to the potential yield of genotypes.

Periodic plant harvesting was done seven times for each genotype at about 2-wk intervals. The harvesting occasions included the stages of panicle initiation (PI), 14 d before full heading, full heading, and 14 d after full heading for each genotype. Nonstructural carbohydrate (NSC) and N content, dry weight of each organ, and leaf area were determined for harvested plants. At maturity, plants on 1 m^2 were harvested and measured for yield and yield components as well as for growth attributes mentioned above. In the periodic sampling of 2001, the fully expanded uppermost two leaves of each three plants from each replication of each genotype underwent ^{13}C isotope composition (d) analysis by a mass spectrometer (MAT252, Finigan MAT). During the PI to full heading period of each cultivar, remote-sensing measurements of canopy surface temperatures and microclimate measurements were frequently made for all genotypes in the three years to obtain canopy diffusive (r_c) and aerodynamic (r_a) resistances by a newly developed method (Horie 2001). In this method, simultaneous measurements of canopy temperatures and net radiation fluxes under full sunlight and sudden shade enable us to solve energy budget equations on the canopy to give r_a, r_c, and transpiration rate under field conditions. A thermal image analyzer (Thermotracer, type TH 5104, NEC San-ei Co. Ltd.) was used for the remote-sensing of canopy surface temperature.

In 2001, measurements of single-leaf photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (E) were also made for all the cultivars. Measurements of P_n, g_s, and E were frequently made from 0900 to 1300 on clear days in the PI to maturity period. On each occasion, a portable-type apparatus was used for photosynthesis and transpiration measurements (LI-6400, LICOR) on a fully expanded uppermost leaf from three plants each in each replication of each genotype. The data thus obtained were averaged over measurements during a 2-wk period for each cultivar. More than 20 leaves of each cultivar were measured in each growth stage.

Significantly different yields were obtained among the genotypes used for the three years of field experiments (Table 1). In each year, the yield of the highest-yielding cultivar nearly doubled that of the lowest. The genotypic difference in yield was consistent among the years: Takanari, an indica-japonica crossbred, showed the highest yield, followed by Milyang23, Shanguichao, and IR72. The improved japonica Nipponbare and NPTs showed an intermediate yield. Banten (native javanica), Ch86 (native indica), and WAB (interspecific hybrid between *O. sativa* and *O. glaberrima*) yielded the lowest. Takanari outyielded Nipponbare by 35-48% and IR72 by 15-27%. Thus, the data on the yield and associated growth attributes from the field experiments provided a good database for the analysis of yield potential determination processes in the subsequent sections.

Table 1. Genotypic difference in yield, its components, and biomass production obtained from field experiments at Kyoto.

Year/genotype	Type	Growth duration (d)	Spikelets m^{-2} (000)	Filled spikelets (%)	Single grain wt. (mg)	Yield[a] (t ha^{-1})	Total dry wt. (t ha^{-1})	Harvest index (%)
1999								
Takanari	Indica × japonica	146	50.4	71.6	23.4	9.82	17.7	47.6
Nipponbare	Japonica	143	33.9	72.6	23.5	6.71	15.4	37.5
Milyang23	Indica × japonica	143	41.0	74.4	25.6	9.07	15.2	51.5
NPT1[b]	Indica × japonica	154	44.6	45.9	23.8	5.66	16.2	29.9
NPT2[b]	Indica × japonica	154	32.8	58.8	23.9	5.36	13.5	34.0
2000								
Takanari	Indica × japonica	143	45.8	84.4	24.9	11.21	18.9	50.9
IR72	Indica	143	40.7	84.3	22.1	8.80	15.3	49.4
Shanguichao	Indica	139	56.0	85.7	16.3	9.08	19.1	41.0
Nipponbare	Japonica	139	31.0	87.4	24.0	7.54	16.7	38.8
NPT1[b]	Indica × japonica	146	36.9	66.1	25.0	7.09	16.2	37.7
Takenari	Japonica	148	34.7	81.8	21.1	6.97	15.0	39.9
Milyang23	Indica × japonica	140	40.8	86.0	25.3	10.32	17.6	50.5
Banten	Javanica	146	27.6	78.6	23.1	5.83	14.0	35.7
2001								
Takanari	Indica × japonica	155	50.2	76.7	23.3	10.44	19.5	46.1
IR72	Indica	146	51.1	67.7	22.6	9.09	18.4	42.6
Shanguichao	Indica	137	59.5	79.3	17.1	9.36	17.6	45.7
Nipponbare	Japonica	143	33.0	83.7	24.1	7.76	17.0	39.3
NPT1[b]	Indica × javanica	153	34.5	72.9	24.1	7.06	17.1	35.5
Koshihikari	Japonica	129	35.6	74.7	22.4	6.92	15.1	39.5
Takenari	Japonica	156	37.1	76.4	21.4	7.06	17.1	35.5
WAB[b]	*glaberrima* × *sativa*	135	32.0	63.8	25.0	5.94	12.9	39.5
Ch86[c]	Indica	143	25.4	73.3	22.6	(4.90)	14.7	(28.8)
Banten	Javanica	150	20.2	8.7	24.1	4.75	12.4	33.0

[a] 14% water is contained in yield. [b] NPT1, NPT2, and WAB stand for IR65564-44-2-2, IR65600-127-6-2-3 and WAB450-1-EP-38HB. [c] Excluded from yield analysis because of lodging.

The period and process of yield potential determination

Contrary to the previous view that the most important process for rice yield determination is postflowering biomass production (Takeda et al 1983, 1984, Akita 1989, Saito et al 1993), Horie (2001) proposed the hypothesis that rice yield potential depends on biomass production during the late reproductive stage (2-wk period preceding full heading). In this section, we will examine the validity of this hypothesis based on the results of the three years of field experiments.

Most critical period for yield determination

Figure 1 gives changes with growth stages in aboveground biomass, leaf area index (LAI), and nitrogen (N content per unit leaf area) for three representative cultivars, Takanari (the highest-yielding cultivar), Nipponbare (an intermediate-yielding one), and Banten (the lowest-yielding). It shows that until 2 wk before heading those three cultivars showed a similar biomass growth (Nipponbare even showed a slightly higher biomass) and thereafter their biomass growth deviated. The poor growth of Banten from 2 wk before full heading was associated with its low LAI and leaf N content. Figure 1 indicates that the difference in rice yield potential became apparent in the biomass growth from 2 wk before full heading.

To examine in which stage biomass production is closely associated with the genotypic difference in yield, correlation coefficients between the crop growth rate (CGR) and final yield were calculated for different growth periods (Fig. 2). The correlation coefficient between CGR and yield changed with rice growth in a W-shaped pattern in all three years: the coefficient was relatively high during midtillering (MT) to PI, low from PI to 2 wk before full heading (2WBH), consistently high from 2WBH to full heading (FH), extremely low from FH to 2 wk after full heading (2WAH), and high from 2WAH to maturity (MAT). Thus, the genotypic difference in rice yield was consistently and most closely related to that in CGR during the 2-wk period preceding full heading or the late reproductive period. The regression lines between CGR during the late reproductive period and yield for different cultivars are shown in Figure 3 for each year. Although the regression lines differed among years for different cultivars grown under different environments, the regressions were all significant (r = 0.990, $P < 0.001$ for 1999; r = 0.937, $P < 0.001$ for 2000; and r = 0.818, $P < 0.01$ for 2001) and the high-yielding genotypes had consistently higher CGRs during this period and vice versa.

The smaller or even negative correlation coefficients between yield and CGR immediately before the late reproductive period may be interpreted as “overgrowth” (Akita 1989): a growth too large around this period results in a growth decline in the later stages, presumably because of increased maintenance respiration. The very low or negative correlation coefficients between yield and CGR during the 2-wk period after full heading may be explained by the phenomenon of marked growth retardation that occurred in the initial grain growth phase of high-yielding rice (Ohnishi 1999, Sheehy, personal communication). Ohnishi (1999) showed that japonica cultivar Koshihikari grown under extremely high solar radiation and

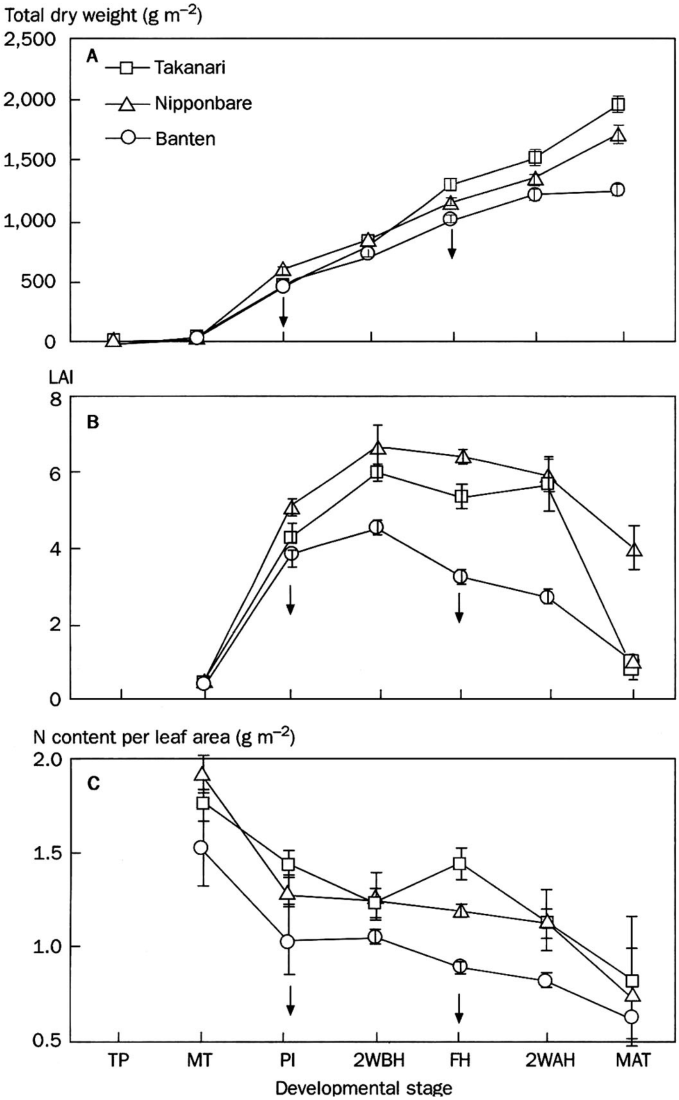


Fig. 1. Changes in aboveground biomass (A), leaf area index (LAI) (B), and leaf N content (C) with developmental stage for three representative rice cultivars having different yield potential grown in Kyoto in 2001. TP, MT, PI, PWBH, FH, 2WAH, and MAT represent transplanting, midtiliering, panicle initiation, 2 wk before full heading, full heading, 2 wk after full heading, and maturity stages, respectively.

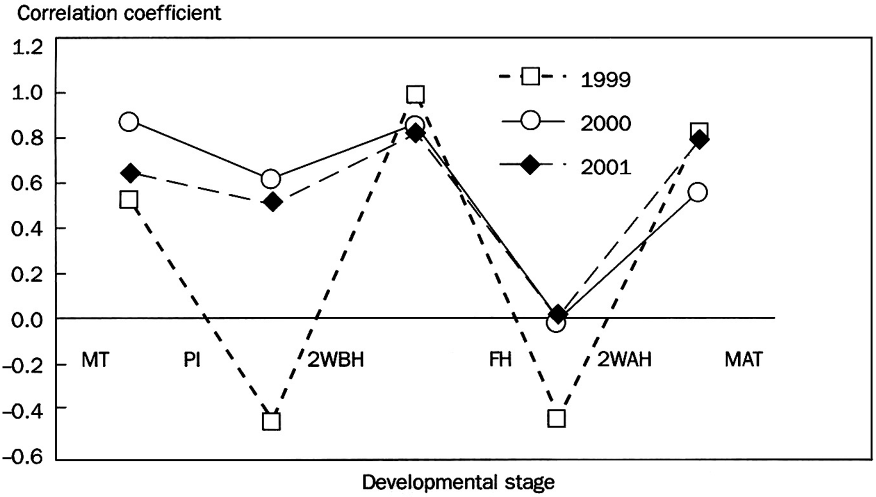


Fig. 2. Correlation coefficient between crop growth rate (CGR) at different growth stages and final grain yield for different rice genotypes given in Table 1 grown in three different years (Katsura et al 2002). Symbols are the same as in Figure 1.

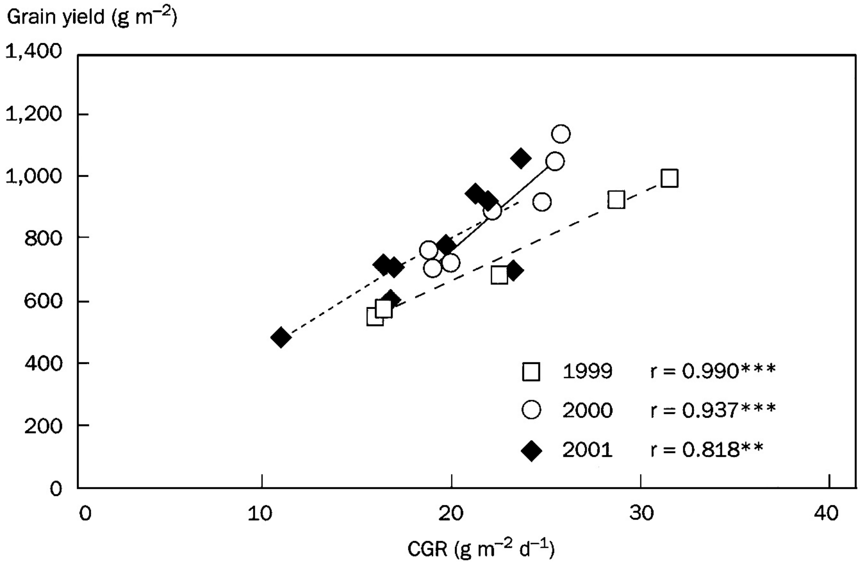


Fig. 3. Relationship between crop growth rate (CGR) during the 2-wk period preceding full heading and final yield for different genotypes given in Table 1 grown in three dlfferent years (Katsura et al 2002). *** and ** denote significance at 0.1% and 1%, respectively.

moderate temperature in Yanco, Australia, showed 53% higher yield than if it was grown in Kyoto; thereby, the Yanco crop accumulated about three times as much NSC as the Kyoto crop (Fig. 4). The marked growth retardation in the initial grain growth phase in the Yanco crop is likely to be due to the increased respiration associated with rapid mobilization of NSC stored in culms and leaf sheaths.

Almost half a century ago, Matsushima mentioned the late reproductive period as the most sensitive stage to environments for rice yield. This and our results that a genotypic difference in rice yield is most closely related to CGR during that period suggest that a higher CGR during the late reproductive period is a prerequisite for higher yield.

The process through which CGR during the late reproductive period determines yield

Rice usually terminates its spikelet differentiation at around 16 d before heading. In the subsequent reproductive period, the process of spikelet development proceeds toward anthesis, which includes the differentiation and development of anthers and pistils, meiosis, and the formation of pollen grains, etc. During this period, many spikelets degenerate and husk size is determined by carbohydrate supply (Matsushima 1957, 1976, Wada 1969, Kobayashi and Horie 1994). Also, extensive accumulation of NSC takes place during this period, with the NSC being remobilized in the subsequent grain-filling phase. Therefore, dry matter production during the late reproductive period of rice has significant effects on final yield through the following three processes: (1) determination of sink capacity (product of spikelet number per unit area and husk size), (2) accumulation of NSC necessary for successful grain filling, and (3) determination of sink activities for grain filling. Since the significant effects of biomass production during the late reproductive period on these three processes have been reviewed in depth by Horie (2001), only a brief description of these effects is given here with additional evidence.

Sink capacity formation. Sink capacity is defined as the product of the number of spikelets per unit area (sink size) and average size of a single spikelet, and represents the potential capacity of vessels that receive assimilates during the grain-filling phase. The amount of carbohydrates produced during the late reproductive period has crucial effects on both components of sink capacity. The spikelet number per unit area is the difference between the number of spikelets that differentiated and that degenerated. It is well established that the number of differentiated spikelets is proportional to plant N uptake until the spikelet differentiation stage (Wada 1969, Murayama 1969, Akita 1989, Hasegawa et al 1994, Kobayashi and Horie 1994, Horie et al 1997). Further, Akita (1989) and Hasegawa et al (1994) indicated that spikelet number was influenced by N concentration at the panicle formation stage as well as by total uptake. However, in the period after the spikelet differentiation period, namely, in the late reproductive stage, extensive spikelet degeneration occurs. Kobayashi and Horie (1994) showed that the number of degenerated spikelets reached as many as 37% of differentiated spikelets for cv. Nipponbare grown under different N applications. Importantly, Wada (1969) showed a strong negative correlation (r = -0.63,

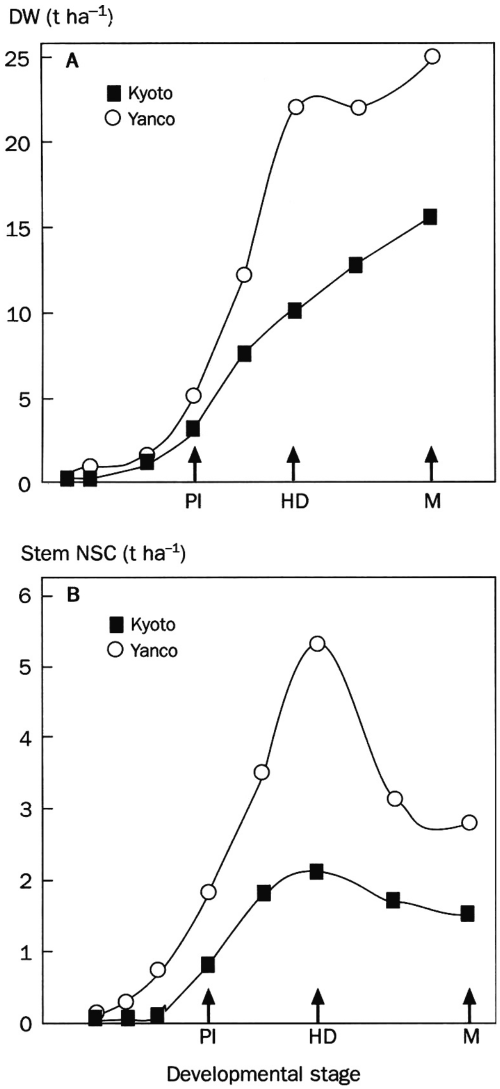


Fig. 4. Change with developmental stage in above ground biomass and nonstructural carbohydrate accumulation in Koshihikari grown in Yanco, Australia (A), and Kyoto, Japan (B) (drawn with data from Ohnishi 1999). PI, HD, and M represent panicle initiation, full heading, and maturity, respectively.

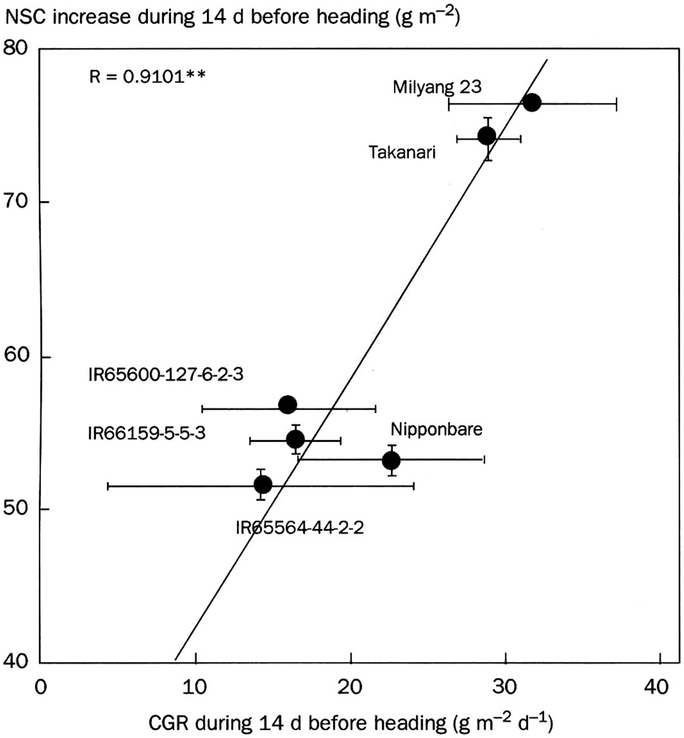


Fig. 5. Relationship between crop growth rate (COR) during the 2-wk period preceding full heading and nonstructural carbohydrate (NSC) accumulation in that period for different rice genotypes grown in Kyoto in 1999 (Nishio et al 2000). ** indicates significance at 1%.

$P < 0.001$) between the number of degenerated spikelets per unit area and dry matter production per spikelet during the late reproductive period. These facts suggest that "self-thinning" of spikelets occurs in rice depending on the availability of carbohydrates during the late reproductive period, especially at meiosis. This implies that rice has the ability to differentiate the excess number of spikelets that are to be filled so as to regulate the number in response to the availability of carbohydrates around the meiosis stage. Reflecting this, a close relationship ($r = 0.634$, $P < 0.01$) existed between CGR during the late reproductive period and the actual spikelet number per unit area for different cultivars grown in the three different years in Kyoto (Fig. 5). One cultivar, Shanguichao, apparently surpassed the other cultivars in the number of spikelets per CGR, but this seemed to reflect its smaller spikelet size (see Table 1). A similar relation as in Figure 5 was also obtained for indica genotypes by Kropff et al (1994).

Rice grain weight is limited by husk size, which is also determined by the availability of assimilates during the late reproductive stage (Matsushima 1957, 1976,

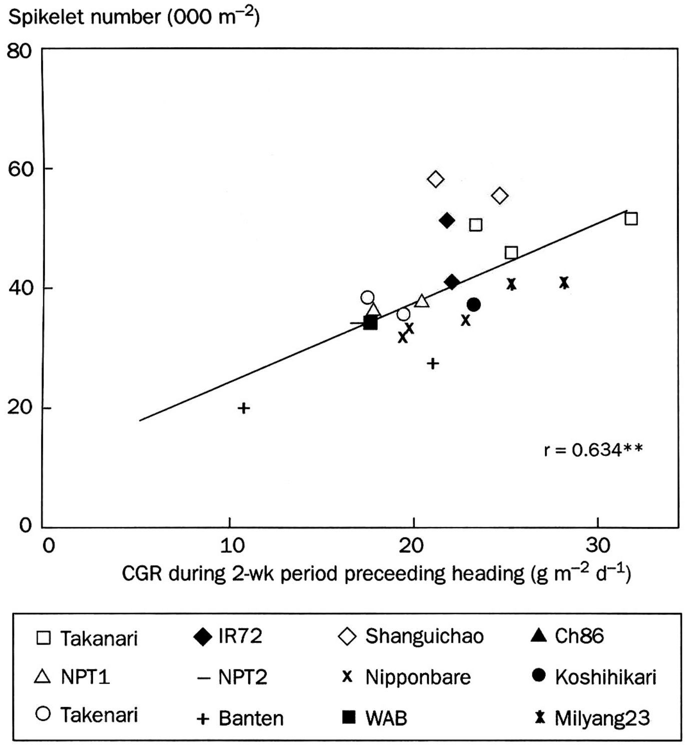


Fig. 6. Relationship between crop growth rate (CGR) during the 2-wk period preceding full heading and final spikelet number per unit area for different rice cultivars grown in three different years in Kyoto, Japan. ** denotes significance at 1%.

Seo and Ota 1983). For this reason, it may well be accepted that CGR during the late reproductive period determines the sink capacity of rice.

Grain filling. A substantial portion of the biomass produced during the late reproductive period is stored in culm and leaf sheaths as NSC. The amount of NSC stored during this period is proportional to the CGR during the same period genotypes having a higher CGR during this period accumulate more NSC (Fig. 6). Hiraoka et al (1986) showed that the percentage NSC storage in biomass was larger as culm length became shorter. No clear genotypic difference can be seen in this percentage in the results given in Figure 6. This may be because the genotypes in Figure 6 had a similar culm length. Generally, the contribution of NSC stored before heading for final grain yield is about 30% (Cock and Yoshida 1973), but, under unfavorable environments in the grain-filling period, it reaches as much as or more than 40% (Akita 1989). However, much evidence has been accumulated to indicate that NSC accumulated before the onset of grain filling plays a more important role in rice grain filling than merely the compensation for a shortage of assimilation during the grain-filling period (Yamada 1972, Takeda et al 1980, Seo and Ota 1983, Akita 1989, Nakamura et al 1992, Sumi et al 1996, Tsukaguchi et al 1996, Horie et al 1997, Moriwaki 1999). One such role of NSC is recognized in the findings (Nakamura et al 1992, Tsukaguchi et al 1996) that percentage filled grains in rice strongly depend on carbohydrate supply to spikelets during the initial 10 days of grain filling in which endosperm cell number is determined (Hoshikawa 1967). Photosynthetic production during the initial 10 d of grain filling is usually not enough to supply the necessary amount of carbohydrate for all the spikelets in a panicle for their full development in endosperm cell number, and it is more so in rice with a large sink capacity. Tsukaguchi et al (1996) showed that, although the grain-filling percentage of rice had no relation to total availability of carbohydrates (NSC + dry matter production) during the grain growth period, it was closely related to the availability during the initial 10 d after full heading. These previous studies suggest that higher CGR during the late reproductive stage enables more accumulation of NSC, which in turn contributes to a higher grain-filling percentage by determining endosperm cell number.

There are indications that sink activity of rice spikelets is predetermined before flowering through carbohydrate supply for developing husks and/or pollen grains. Seo and Ota (1983) showed that a limited supply of carbohydrate for spikelets during their development increased the number of malformed spikelets, which became either infertile or half-filled grains. Yamada (1972) and Moriwaki (1999) indicated that excessive plant N and reduced carbohydrate content around meiosis resulted in an abnormal development of pollen grains, which caused spikelet sterility. The above results suggest that CGR during the late reproductive period has a critical effect on rice grain filling by forming effective sinks through carbohydrate supply for developing husks, pollen grains, and endosperm cells. Akita (1989) has also reported a critical effect of CGR before grain filling on filling percentage in rice.

Overall effects of CGR during the late reproductive period on yield potential determination

The above review clarified the critical effects of CGR during the late reproductive period on rice yield by determining sink capacity, active sink, and grain filling. Of course, CGR at any stage in rice development influences yield. However, rice grown under intensive nutrient management has a higher LAI, leaf N content, and biomass before the middle of the reproductive period, which often causes growth stagnation in the subsequent stage, presumably because of increased maintenance respiration and mutual shading of leaves. Akita (1989) termed such a phenomenon “overgrowth.” It is for this reason that CGR during the late reproductive period has critical effects on yield.

The fact that rice genotypes having higher CGR during the late reproductive period had higher final yields (Figs. 2 and 3) indicates that those genotypes also maintained higher photosynthetic capacity in the grain growth period, as shown in

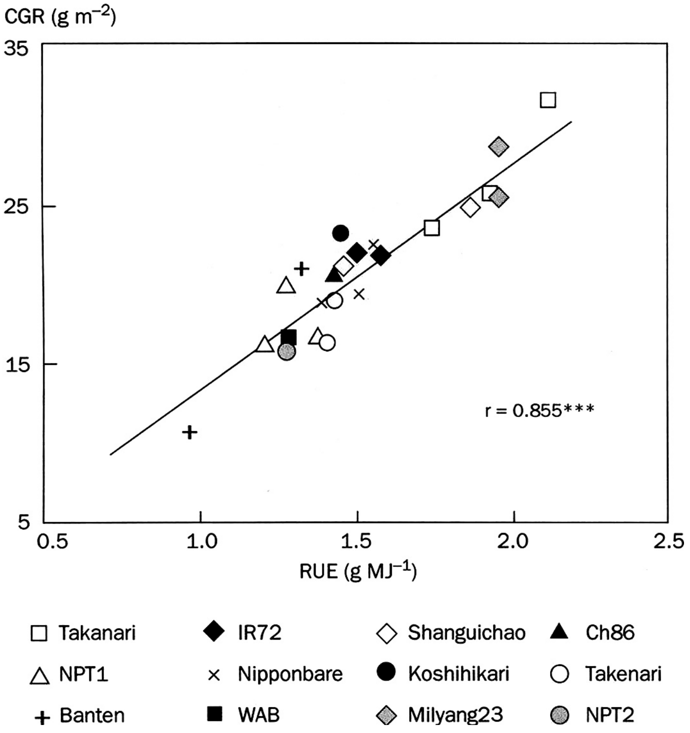


Fig. 7. Relationship between radiation-use efficiency (RUE) and crop growth rate (COR) for the 2-wk period preceding full heading for different cultivars grown in three different years in Kyoto, Japan (Katsura et al 2002). ***shows significance at 0.1%.

the subsequent sections. On the basis of that evidence, we conclude that yield potential in rice is substantially determined by the CGR during the late reproductive period.

Factors associated with genotypic difference in CGR during the late reproductive period

The field experiment results in Kyoto and the review of the previous work on yield potential determination processes in rice described earlier indicate that rice yield potential is substantially determined by CGR during the late reproductive period (the 2-wk period preceding full heading). As CGR is the product of the solar radiation interception rate and radiation-use efficiency (RUE), we examined which component affected genotypic difference in CGR. Genotypic variation in CGR during the late reproductive period was closely related to the variation in RUE (r = 0.855, *P* <0.001; Fig. 7), while having no relation to radiation interception rate. This indicates that genotypic difference in LAI is not the cause for that in CGR, but those in canopy photosynthetic rate and/or respiration rate are factors for the difference in CGR.

Genotypic difference in leaf photosynthesis, nitrogen content, and stomatal conductance

First, we will examine the genotypic difference in single-leaf photosynthetic rate at light saturation (P_n) and its relation to leaf N content and stomatal conductance (g_s). Figure 8 shows changes with developmental stage from PI afterward in leaf P_n, N content (g g^{-1}, %), and g_s for the genotypes grown in the 2001 field experiment in Kyoto. The genotypic difference in P_n was small in the early reproductive period (PI to 2 wk before full heading) and thereafter became large. Considerably large differences were observed in leaf N and g_s among the genotypes throughout the whole period investigated. Although P_n and N content declined with developmental stage, the g, of all cultivars showed a fairly stable value throughout the whole period, except for the late grain growth period. Figure 8 shows that high-yielding cultivars Takanari, Shanguichao, and IR72 had a higher P_n, N content, and g_s from PI to the early grain-filling stage and poor-yielding Banten, Ch86, and Takenari had lower values in these physiological traits, indicating that P_n and the associated traits are apparently involved in the genotypic difference in CGR during the late reproductive stage.

Investigation of what physiological traits are associated with the observed genotypic difference in P, showed that leaf thickness had no relation to it, for genotypes such as Shanguichao had a high photosynthetic rate, but its specific leaf weight (44 g m^{-2}) at the late reproductive period was much lower than that (57 g m^{-2}) of NPTl (IR65564-44-2-2). For this reason, P_n data shown in Figure 8 had a higher correlation with leaf N in g g^{-1} (%) than that in g m^{-2}. However, leaf N percentage alone could not well explain the genotypic difference in P_n, especially in the preflowering period, but P_n could change with plant development for all the genotypes. Contrary to leaf N percentage, g_s had a highly significant relationship with P_n at any stage of plant development (data not shown). As a consequence of these results, the variation in P_n among both different genotypes and development stages could well be explained by the product of g_s × N percentage ($r = 0.911$, $P < 0.001$ Fig. 9).

Many studies on genotypic difference in P_n among Japanese rice genotypes indicate that the difference was none or small before heading and became conspicuous after that (Hayami 1982, Kuroda and Kumura 1990, Sasaki and Ishii 1992). Cook and Evans (1983), investigating P_n of different indica, japonica, and javanica genotypes and their wild relatives, showed a large difference among them both at seedling and around the heading stage. The results in Figure 8 also show that a large difference exists in P_n among rice genotypes from the mid-reproductive stage onward.

Much evidence shows the stomatal regulation of leaf photosynthetic rate in rice under field conditions as well as N content (Ishihara et al 1971, 1981, Kuroda and Kumura 1990b,c). Kuroda and Kumura (1990b,c) showed that cultivar difference in P_n after heading was closely related to that in g_s, and that the difference in g_s is related to aerenchyma conductance for the supply of oxygen from leaves to roots, and thus to root activities. The results in Figure 8 and these previous studies indicate that leaf N percentage and stomatal conductance from the mid-reproductive stage onward are important physiological traits for yield potential determination in rice.

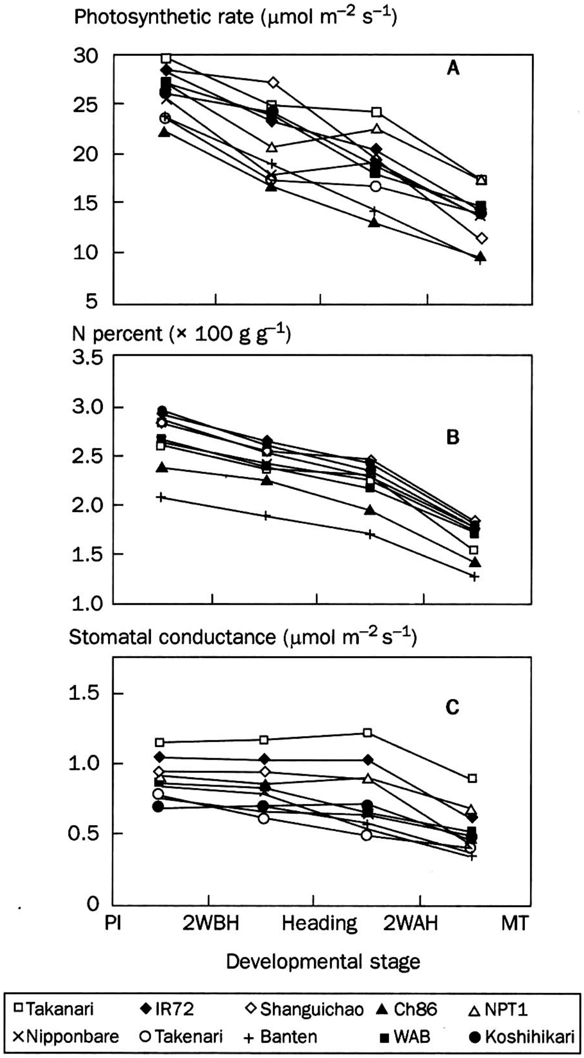


Fig. 8. Changes with developmental stage in leaf photosynthetic rate (A), N percent (B), and stomatal conductance (C) for 10 different rice cultivars grown in Kyoto in 2001 (Ohsuml et al 2002). Notations for developmental stages are the same as in Figure 1.

The above analysis suggests that a higher leaf photosynthetic rate (P_n) at least from the mid-reproductive stage onward is evidently associated with higher yield potential in rice and that considerably large differences in P_n exist among rice genotypes and their wild relatives. Recently, Uchida et al (2002) showed a marked transgressive segregation in leaf P_n, Rubisco, and Rubisco activase contents in

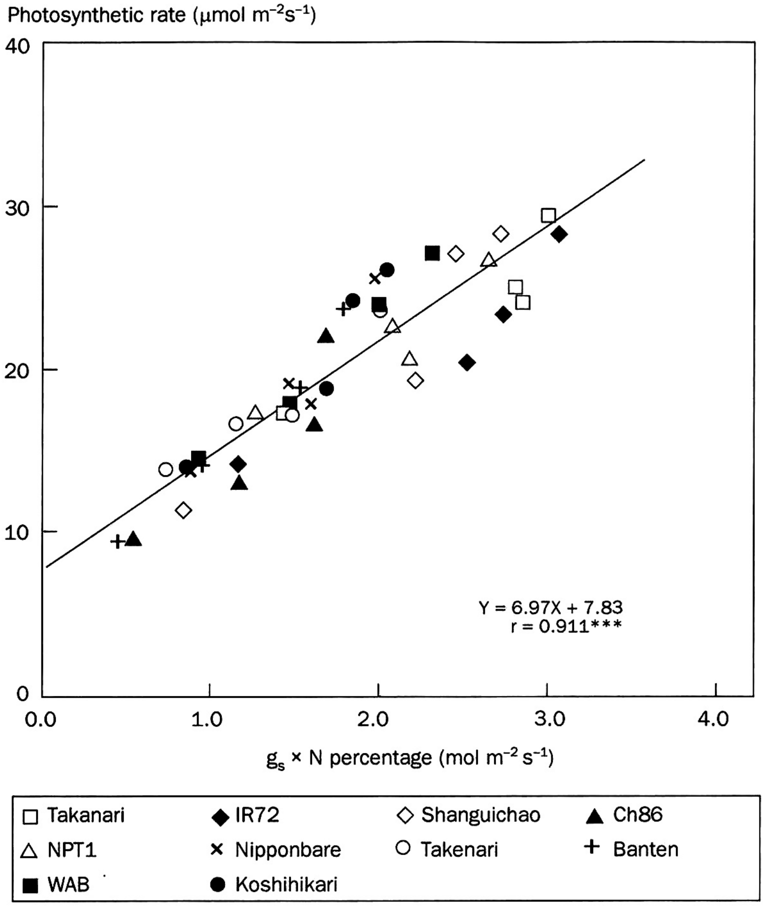


Fig. 9. Leaf photosynthetic rates as a function of N percentage and stomatal conductance (g_S) for 10 different rice cultivars measured at four different stages from panicle initiation to maturity in 2001 in Kyoto, Japan. ***shows significance at 0.1%.

progenies of an interspecific hybrid between *O. sativa* and *O. glaberrima.* Use of these genes involved in increased photosynthesis will lead to increased yield potential in rice.

Genotypic difference in P_n and its relation to carbon isotope discrimination

Carbon isotope (^{13}C) discrimination (D) is defined by

$$\Delta = \frac{\delta_{air} + \delta_{plant}}{1 + \delta_{air}/1{,}000}$$

where δ_{air} and δ_{plant} are carbon isotope compositions of air (approximately –8.0%)and plant relative to the standard Pee Dee belemite (Keeling et al 1979). Farquhar et al (1982) showed that A is related to leaf-air CO_2 concentration ratio (C_i/C_a) as

$$\Delta = a + (b - a)\, C_i/C_a \qquad (4)$$

where a and b are parameters related to ^{13}C discriminations in the boundary layer and stomatal diffusion and carboxylation processes, respectively.

Since A is related to leaf internal CO_2 concentration, we examined whether the genotypic difference in P_n observed has some relation to A. A fairly consistent genotypic difference in the carbon isotope composition (6) was observed throughout the development stages investigated (Fig. 10). Peng et al (1998) also reported such a genotypic difference in δ in rice. The genotypic difference in δ had a fairly close relation to that in P_n: the genotypes having higher P_n had lower δ and vice versa, except for one genotype, Ch86, an old indica cultivar. Since P_n is also related to leaf N percentage (N), we can assume that

$$P_n = KNC_i \qquad (5)$$

where K is an empirical constant.

From equations 4 and 5, we can obtain

$$P_n = KNC_a \frac{\Delta - a}{b - a} \qquad (6)$$

Equation 6 suggests that P_n is proportional to the product NC_a r .The validity of equation 6 for explaining variation of rice leaf P_n among both different genotypes and development stages was examined by giving the following values: a = -4.4%, b = –27.0%(Farquhar et al 1982), C_a = 350 μmol mol^{-1}, with K an unknown parameter. From the regression analysis between measured and estimated P_n by equation 6, we obtained 0.0349 mol m^{-2} s^{-1} for the value of the parameter K. Equation 6 with this parameter value explained well the variation in leaf P_n as shown in Figure 8 (Fig. 11). This suggests that leaf A as well as N percentage are traits associated with leaf photosynthetic rate and hence final yield. A positive correlation between A and dry matter production and yield is also reported for wheat (Condon et al 1987).

Effect of canopy conductance on CGR during the late reproductive period

Matsuura et al (2000) and Horie (2001) showed that the genotypic difference in CGR in the 1999 field experiment in Kyoto was highly correlated (r = 0.834, P <0.001) with the reciprocal of canopy (r_c) + aerodynamic (r_a) resistances ($1/(r_c + r_a)$) obtained by the remote-sensing method described earlier, under PAR flux density above 1,200 pmol m^{-2} s^{-1}. The generality of this relationship was examined for three seasons of rice crops shown in Table 1, plus two japonica cultivars, Kamenoo and Ginbouzu, grown in 1999. A high correlation coefficient (r = 0.75, P <0.01) existed between the overall conductance ($1(r_c + r_a)$) and CGR during the late reproductive period over

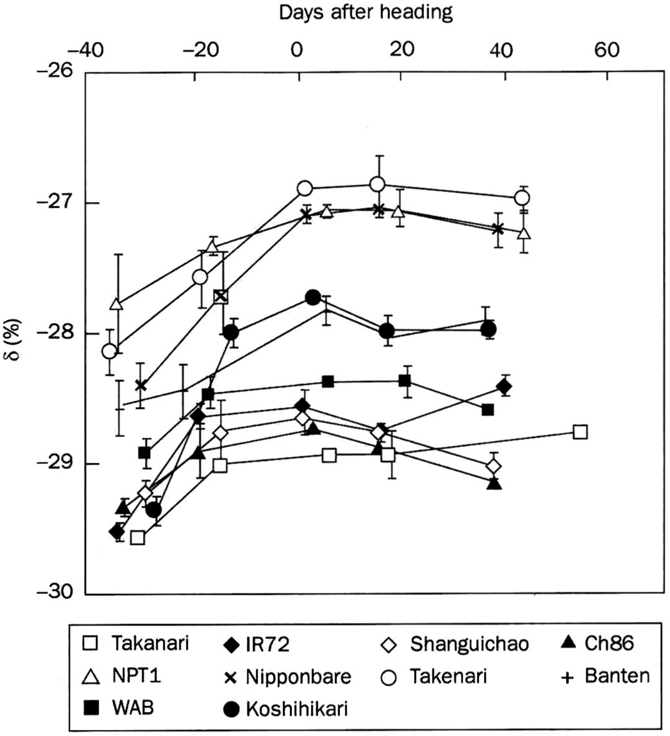


Fig. 10. Changes with time in carbon isotope composition (δ) for 10 different rice cultivars grown in Kyoto, Japan, in 2001. (Unpublished data of Ohsumi and Nil et al.)

15 cultivars grown in different years (Fig. 12). Since $1/(r_c + r_a)_a$ was highly correlated ($r = 0.90$, $P < 0.01$) with air-leaf temperature difference ($T_a - T_c$) measured in the afternoon for rice genotypes grown in 2001, $T_a - T_c$ also had a close relation ($r = 0.78$, $P < 0.01$) with CGR during the late reproductive period (Fig. 13).

Since there was a negligibly small difference in the aerodynamic resistance (r_a) among the genotypes, the genotypic difference in $r_c + r_a$ is due to that in r_c. As already described, the genotypic difference in leaf P_n during the late reproductive period was more closely related to stomatal conductance (g_s) than to leaf N percentage. The close relation between the overall canopy conductance ($1/(r_c + r_a)$) and CGR may reflect the leaf P_n and g_s relationship. Also, the fact that rice genotypes having a higher canopy conductance had a cooler leaf temperature leads to reduced canopy respiration rate. This may be another reason that the rice genotype that had a higher canopy conductance had a larger CGR during the late reproductive period. These results suggest that higher stomatal conductance and air-leaf temperature difference

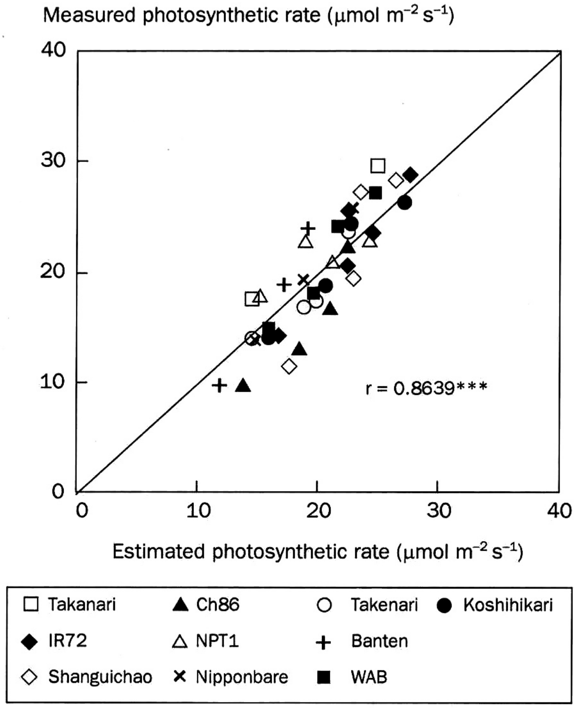


Fig. 11. Relationship between leaf photosynthetic rate measured and that estimated from carbon Isotope discrimination and leaf N percentage by equation 6 for 10 rice cultivars at different stages. * indicates significance at 0.1%.**

in the afternoon are important physiological traits for higher CGR and final yield. Such evidence was also reported for wheat (Fischer et al 1998).

A noticeable point in Figures 12 and 13 is that the new plant type (NPTI) had a relatively low canopy conductance and high leaf temperature in comparison with other genotypes. This is consistent with its relatively low stomatal conductance (Fig. 8). The low stomatal and canopy conductances of the NPT seem to limit its yield potential, despite its excellent plant type.

Other factors involved in genotypic difference in COR during the late reproductive period

In addition to the abovementioned factors, respiration rate and canopy architecture are likely to be involved in the genotypic difference in CGR during the late reproductive period. Synthesis and maintenance costs for NSC (starch and sugars) are much lower than for other compounds such as proteins and fats (Penning de

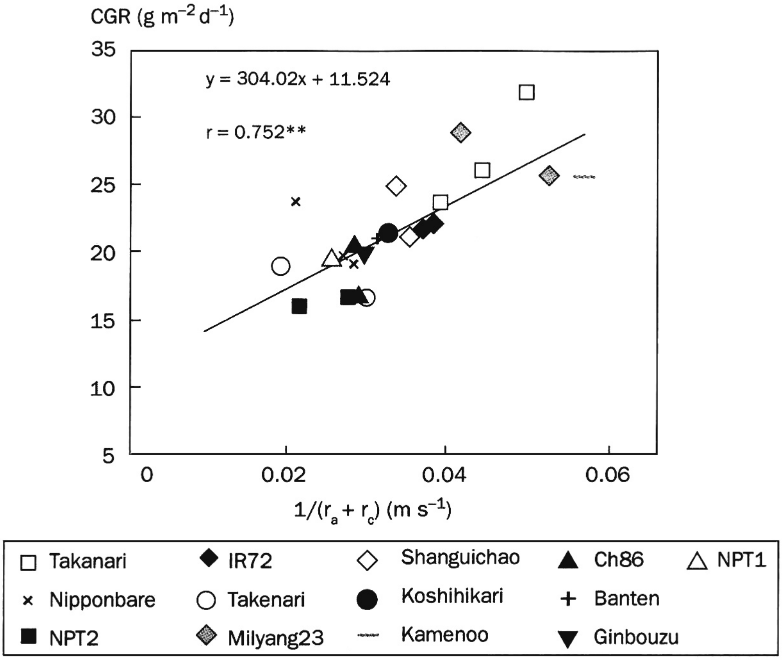


Fig. 12. Relationship between overall canopy conductance ($1/r_a + r_c$)) measured at midday by remote-sensing method and crop growth rate (COR) during the 2-wk period preceding full heading for different rice cultivars grown in three dlfferent years (Kuwasaki et al 2002).

Vries 1975, Amthor 1994). Therefore, a larger accumulation of NSC in high-yielding genotypes is not only a result of their higher CGR but is also a cause for the higher CGR. Unfortunately, no information is available to show that this occurred in high-yielding genotypes in rice, and further research is necessary. The high-yielding cultivars Takanari and Milyang23 had smaller radiation extinction coefficients than others, which might well be a cause for their higher CGR and yield.

Conclusions

Increasing rice yield potential is necessary because the gap between yield potential and farmers' yield is narrowing, despite the strong need for increased rice production under increasing world population. A brief review of previous work on rice yield determination processes and associated traits that were improved during the Green Revolution revealed the following three points. First, the past yield improvements were made based mainly on plant type or morphological features. Second, the past yield increase was achieved only through increasing postflowering biomass production and the fraction of preflowering biomass production translocated to the

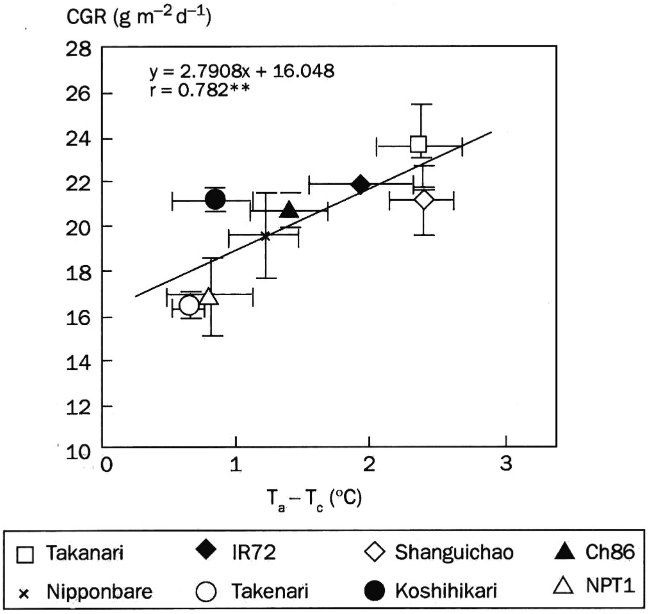


Fig. 13. Relationship between leaf-air temperature difference (T_a - T_c) and crop growth rate (CGR) during the late reproductive period for different rice cultivars grown in 2001 in Kyoto (Kuwasaki et al 2002).

grain after anthesis, whereas the preflowering biomass itself remained unchanged. Third, so long as these remain as the only ways to improve yield, room for a further increase in rice yield potential would be limited. To further increase yield potential, therefore, new insights are needed into yield determination processes of rice and associated traits, in addition to the traditional plant type concept. With this view, we conducted field experiments using widely different genotypes for three years in Kyoto, Japan. With the results of the experiments and a review of previous studies, we derived the following conclusions.

1. Rice yield potential is substantially determined by crop growth rate during the late reproductive period (the 2-wk period preceding full heading). The CGR at this stage has critical effects on final spikelet number by regulating spikelet degeneration and potential single-grain weight by determining husk size. It also has strong effects on grain filling through the formation of active sinks by way of pollen grain and husk development and by determining endosperm cell number by way of reserve substrate supply in initial grain filling.
2. A quite large genotypic difference existed in the CGR during the late reproductive period and hence in final yield. Genotypes with a higher CGR accumulated more nonstructural carbohydrates in culms and leaf sheaths. The genotypic difference in CGR was associated with radiation-use efficiency,

but not with radiation interception rate. It was also related to canopy diffusive conductance and air-leaf temperature difference. Genotypes having a higher CGR during this period had a higher maximum leaf photosynthetic rate (P_n)

3. The genotypic difference in P_n at the late reproductive period was closely related to leaf stomatal conductance (g_s) and moderately to leaf N percentage in g g^{-1} rather than in g m^{-2}. Leaf P_n of different genotypes at different development stages was proportional to the product of g, and N percentage. It was also proportional to the product of carbon isotope discrimination (A) and N percentage.
4. The major limiting processes in CGR during the late reproductive period and hence in final yield are leaf P_n and NSC accumulation. The traits associated with higher P_n are higher stomatal conductance, higher carbon discrimination, higher leaf N percentage, and a larger air-leaf temperature difference under field conditions. A considerably large genotypic difference in these processes and traits was observed in our experiments and reported in the previous studies on rice genotypes, their wild relatives, and progenies of their hybrids. This suggests that there is still much scope for breeding new rice genotypes that surpass current yield potential by accumulating genes that control these processes and traits, together with the traditional concept of ideal plant type.

References

Akita S. 1989. Improving yield potential in tropical rice. In: Progress in irrigated rice research. Manila (Philippines): International Rice Research Institute. p 41-73.

Amthor JS. 1994. Respiration and carbon assimilate use. In: Boote KJ et al, editors. Physiology and determination of crop yield. Madison, Wis. (USA): American Society of Agronomy. p 221-250.

Cock JH, Yoshida S, 1973. Accumulation of ^{14}C labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. Proc. Crop Sci. Soc. Jpn. 41:226-234.

Condon AG, Richards RA, Farquhar GD. 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field grown wheat. Crop Sci. 27:996-1001.

Cook MG, Evans LT. 1983. Some physiological aspects of the domestication and improvement of rice (*Oryza* spp.). Field Crops Res. 6:219-238.

Evans LT. 1993. Crop evolution, adaptation and yield. Cambridge (UK): Cambridge University Press. 500 p.

Evans LT, Fischer RA. 1999. Yield potential: its definition, measurement, and significance. Crop Sci. 39:1544-1551.

Farquhar GD, O'Leary MH, Berry J. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9:121-127.

Fischer RA, Ress D, Sayre KD, Lu Z-M, Gordon AG, Larque Saavedra A. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopy. Crop Sci. 38:1467-1475.

Hasegawa T, Koroda Y, Seligman NG, Horie T. 1994. Response of spikelet number to plant nitrogen concentration and dry weight in paddy rice. Agron. J. 86:673-676.

Hayami K. 1982. Studies on the physiological and ecological characteristics of high-yielding rice varieties with a high fertilization response. 1. The effect of a nitrogen supply on the photosynthetic characteristic of high-yielding varieties with a high fertilizer response. Bull. Tohoku Natl. Agric. Exp. Stn. 67:43-75. (In Japanese with English summary.)

Hiraoka H, Terashima K, Nishiyama I. 1986. Physiological and ecological characteristics of high-yielding varieties of rice plant. 9. Breeding criteria of high-yielding rice varieties from viewpoint of carbohydrate behavior. Jpn. J. Crop Sci. 55(extra issue 2):17-18. (In Japanese without English summary.)

Holliday RH. 1976. The efficiency of solar energy conversion by the whole crop. In: Duckam AN, Jones JGW, Roberts EH, editors. Food production and consumption: the efficiency of human food chains and nutrient cycles. North Holland, Amsterdam. p 127-145.

Horie T, Ohnishi M, Angus JF, Lewin LG, Tsukaguchi T, Matano T. 1997. Physiological characteristics of high-yielding rice inferred from cross-location experiments. Field Crops Res. 52:55-67.

Horie T. 2001. Increasing yield potential in irrigated rice: breaking the yield barrier. In: Peng S, Hardy B, editors. Rice research for food security and poverty alleviation. Proceedings of the International Rice Research Conference, 31 March-3 April 2000, Los Baños, Philippines. Los Baños (Philippines): International Rice Research Institute. p 3-25.

Hoshikawa K. 1967. Studies on the development of endosperm in rice. 3. Observation on the cell division. Proc. Crop Sci. Jpn. 36:210-215. (In Japanese with English summary.)

Hossain M. 1999. Long-term perspective for the demand supply balance for rice in Asia: implications for technological challenges. In: Horie T et al, editors. Proceedings of the International Symposium on World Food Security and Crop Production Technologies for Tomorrow, Kyoto University, Kyoto, Japan. p 31-39.

Ishihara K, Ishida Y, Ogura T. 1971. The relationship between environmental factors and behavior of stomata in the rice plant. 2. On the diurnal movement of the stomata. Proc. Crop Sci. Soc. Jpn. 40:497-504. (In Japanese with English summary.)

Ishihara K, Hirasawa T, Iida O, Kumura M. 1981. Diurnal course of transpiration rate, stomatal conductance, xylem water potential and leaf water potential in the rice plants under the different growth conditions. Jpn. J. Crop Sci. 50:25-37. (In Japanese with English summary.)

Ishihara K, Takigawa Y. 1981. Comparison between Japanese rice cultivar Nipponbare and Indica-Japonica crossbred cultivar Milyang23 in canopy structure and dry matter production. Jpn. J. Crop Sci. 50(extra issue 2):121-122. (In Japanese without English summary.)

Katsura K, Lubis I, Takai T, Horie T, Nii A, Yoshida H, Shiraiwa T. 2002. Identification and evaluation of major traits determining yield potential of rice under field conditions. 4. The genotypic difference in the yielding ability and associated growth characteristics. Jpn. J. Crop Sci. 7l(extra issue 2):12-13. (In Japanese without English summary.)

Keeling CD, Mook WG, Tans PP. 1979. Recent trends in the $^{13}C/^{12}C$ ratio of atmospheric carbon dioxide. Nature 277:121-123.

Khush GS, Peng S. 1996. Breaking the yield frontier of rice. In: Reynolds MP et al, editors. Increasing yield potential in wheat: breaking the barriers. Proceedings of a workshop held on 26-28 March 1996 in Ciudad Obregón, Sonora. Mexico: International Maize and Wheat Improvement Center.

Kobayashi K, Horie T. 1994. The effect of plant nitrogen condition during reproductive stage on the differentiation of spikelets and rachis-branches in rice. Jpn. J. Crop Sci. 63:193-199. (In Japanese with English summary.)

Kropff MJ, Cassman KG, Peng S, Matthews RB, Setter TL. 1994. Quantitative understanding of yield potential. In: Cassman KG, editor. Breaking the yield barrier. Los Baños (Philippines): International Rice Research Institute. p 21-38.

Ku SB, Agarie S, Nomura M, Fukuyama HT, Tsuchida H, Ono K, Hirose S, Toki S, Miyao M, Matsuoka M. 1999. High-level expression of maize phosphoenolpyruvate carboxylase in transgenic rice plants. Nat. Biotechnol. 17:76-80.

Kuroda E, Kumura A. 1990a. Difference in single-leaf photosynthesis between old and new rice varieties. I. Single-leaf photosynthesis and its dependence on stomatal conductance. Jpn. J. Crop Sci. 59:283-292. (In Japanese with English summary.)

Kuroda E, Kumura A. 1990b. Difference in single-leaf photosynthesis between old and new rice varieties. II. Physiological basis for the difference in stomatal conductance between varieties. Jpn. J. Crop Sci. 59:293-297. (In Japanese with English summary.)

Kuroda E, Kumura A. 1990c. Difference in single-leaf photosynthesis between old and new varieties. III. Physiological basis of varietal difference in single-leaf photosynthesis between varieties viewed from nitrogen content and nitrogen-photosynthesis relationship. Jpn. J. Crop Sci. 59:298-302. (In Japanese with English summary.)

Kuwasaki K, Horie T, Takai T, Ohsumi A. 2002. Identification and evaluation of major traits determining yield potential of rice under field conditions. 6. Genotypic difference in the remote-sensed canopy conductance and its relationship with crop growth rate. Jpn. J. Crop Sci. 71(extra issue 2): 16-17. (In Japanese without English summary.)

Matsushima M. 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice. Bull. Natl. Inst. Agric. Sci. Ser. A5:l-271. (In Japanese with English summary.)

Matsushima S. 1976. High-yielding rice cultivation. Tokyo (Japan): University of Tokyo Press. 367 p.

Matsuura S, Horie T, Takai T, Nishio T. 2000. Identification and evaluation of major traits determining yield potential of rice under field conditions. 3. Genotypic difference in the canopy diffusive conductance at later half of reproductive period as measured by remote sensing technology. Jpn. J. Crop Sci. 69(extra issue 2):38-39. (In Japanese without English summary.)

Moriwaki T. 1999. On the ideal culm elongation in rice plants (3). Nogyogijyutu 54:133-138. (In Japanese without English summary.)

Murata Y. 1961. Studies on the photosynthesis of rice plants and its cultural significance. Bull. Natl. Inst. Agric. Sci. D 9:1-169. (In Japanese with English summary.)

Murayama N. 1969. Nitrogen nutrition of rice plant. JARQ 3:1-4.

Nakamura T, Matsunaga D, Hoshikawa K. 1992. Relationship between initial growth of spikelet, and fertility and number of endosperm cells in rice. Jpn J. Crop Sci. 61(extra issue 2):129-130. (In Japanese without English summary.)

Nishio T, Matsuura T, Takai T, Horie T. 2000. Identification and evaluation of major traits determining yield potential of rice under field conditions. 1. Genotypic difference in the grain filling and associated plant factors. Jpn. J. Crop Sci. 69(extra issue)2:34-35. (In Japanese without English summary.)

Ohnishi M. 1999. Modeling the yield formation processes of rice in relation to the environments and analysis of high-yielding rice. PhD thesis submitted for Graduate School of Agriculture, Kyoto University, Kyoto (Japan). p 1-113. (In Japanese with English summary.)

Ohno Y. 1976. Varietal differences of photosynthetic efficiency and dry matter production in indica rice. Tech. Bull. Tropic. Agric. Res. Centre 91-72.

Ohsumi A, Lubis I, Horie T, Ohnishi M. 2002. Identification and evaluation of major traits determining yield potential of rice under field conditions. 5. Genotypic difference in leaf photosynthetic rate and associated plant factors. Jpn. J. Crop Sci. 71(extra issue 2):14-15. (In Japanese without English summary.)

Peng S, Khush GS, Cassman KG. 1994. Evolution of the new plant type ideotype for increased yield potential. In: Cassman KG, editor. Breaking the yield barrier. Proceedings of a Workshop on Rice Yield Potential in Favorable Environments. Los Baños (Philippines): International Rice Research Institute. p 5-20.

Peng S, Laza RC, Khush GS, Sanico AL, Visperas RM, Garcia FV. 1998. Transpiration efficiency of indica and improved tropical japonica rice grown under irrigated conditions. Euphytica 103:103-108.

Peng S, Cassman KG, Virmani SS, Sheehy J, Khush GS. 1999. Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. Crop Sci. 39:1552-1559.

Penning de Vries FWT. 1975. Use of assimilates in higher plants. In: Cooper J, editor. Photosynthesis and productivity in different environments. Cambridge (UK): Cambridge University Press. p 459-480.

Saito K, Tamai H, Ishihara K. 1981. Comparison between Japanese rice cultivar Nipponbare and Indica-Japonica crossbred cultivar Milyang23 in the photosynthetic rate and stomatal aperture. Jpn. J. Crop Sci. 50(extra issue 2):123-124. (In Japanese without English summary.)

Saito K, Shimoda H, Ishihara K. 1993. Characteristics of dry matter production process in high-yielding rice varieties. VI. Comparisons between new and old rice varieties. Jpn. J. Crop. Sci. 62:509-517. (In Japanese with English summary.)

Sasaki H, Ishii R. 1992. Cultivar differences in leaf photosynthesis of rice bed in Japan. Photosyn. Res. 32:139-146.

Seo SW, Ota Y. 1983. Role of the hull in the ripening of rice plant. Bull. Natl. Inst. Agric. Sci. Ser. D 35:33-102.

Shiga H, Sekiya S. 1976. Effect of the nitrogen supplying method for getting high yield in rice plants in cool regions. Res. Bull. Hokkaido Natl. Exp. Stn. p 116-138. (In Japanese with English summary.)

Sinclair TR, Horie T. 1989. Leaf nitrogen, photosynthesis and crop radiation use efficiency: a review. Crop Sci. 29:90-98.

Son H, Ito T, Maruyama S, Koyama K, Tanaka T. 1979. Dry matter production characteristics in japonica-indica crossbred cultivars. Jpn. J. Crop Sci. 48(extra issue 1):75-76. (In Japanese without English summary.)

Song XF, Agata W, Kawamitsu Y. 1990a. Studies on dry matter and grain production of F_1 hybrid rice in China. I. Characteristic of dry matter production. Jpn. J. Crop Sci. 59: 19-28. (In Japanese with English summary.)

Song XF, Agata W, Kawamitsu Y. 1990b. Studies on dry matter and grain production of F_1 hybrid rice in China. II. Characteristic of grain. Jpn. J. Crop Sci. 59:29-33. (In Japanese with English summary.)

Sumi A, Hakoyama S, Weng JH, Agata W, Takeda, T. 1996. Analysis of plant characteristics determing ear weight increase during the ripening period in rice (*Oryza sativa* L.). II. The role of the reserved carbohydrate at heading stage upon the receptive efficiency of assimilation products in spikelets. Jpn. J. Crop Sci. 65:214-221. (In Japanese with English summary.)

Takano Y, Tsunoda S. 1971. Curvilinear regression of the leaf photosynthetic rate on leaf nitrogen content among strains of *Oryza* species. Jpn. J. Breed. 21:69-76.

Takeda T, Weng JH, Agata W. 1980. The role of reserved carbohydrate at heading in ear weight increase during the grain-filling of rice. Jpn. J. Crop Sci. 49(extra issue):75-76. (In Japanese without English summary.)

Takeda T, Oka M, Agata W. 1983. Characteristic of dry matter and grain production of rice cultivars in the warmer part of Japan. I. Comparison of dry matter production between old and new types of rice cultivars. Jpn. J. Crop Sci. 52(3):299-306. (In Japanese with English summary.)

Takeda T, Oka M, Agata W. 1984. Characteristic of dry matter and grain production of rice cultivars in the warmer part of Japan. II. Comparison of grain production between old and new types of rice cultivars. Jpn. J. Crop Sci. 53(extra issue 1):12-21. (In Japanese without English summary.)

Tsukaguchi T, Horie T, Ohnishi M. 1996. Filling percentage of rice spikelets as affected by availability of non-structural carbohydrates at the initial phase of grain filling. Jpn. J. Crop Sci. 63(3):445-452. (In Japanese with English summary.)

Tsunoda S. 1959. A developmental analysis of yielding ability in varieties of field crops. II. The assimilation system of plants as affected by the form, direction and arrangement of single leaves. Jpn. J. Breed. 9:237-244.

Uchida N, Matsumoto C, Ishii T. 2002. Genes from wild rice enhance rice photosynthesis. Jpn. J. Crop Sci. 71(extra issue)1:294-295. (In Japanese without English summary.)

Wada G. 1969. The effect of nitrogenous nutrition on the yield-determining process of rice plant. Bull. Natl. Inst. Agric. Sci. Ser. A 16: 167. (In Japanese with English summary.)

Yamada N. 1972. Studies on the developmental physiology in rice pollen. I. The metabolic patterns connected with the structural changes in developing pollen. Proc. Crop Sci. Soc. Jpn. 41:320-334. (In Japanese with English summary.)

Yoshida S. 1972. Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23:437-464.

Yuan LP. 1994. Increasing yield potential in rice by exploitation of heterosis. In: Virmani SS, editor. Hybrid rice technology: new developments and future prospects. Los Baños (Philippines): International Rice Research Institute. p 1-6.

Yuan L. 2000. Breeding of super hybrid rice. In: Peng S, Hardy B, editors. Rice research for food security and poverty alleviation. Proceedings of the International Rice Research Conference, 31 March-3 April 2000, Los Baños, Philippines. Los Baños (Philippines): International Rice Research Institute. p 143-149.

Notes

Authors' address: Laboratory of Crop Science, Graduate School of Agriculture, Kyoto University, Sakyo-ku, Kyoto 606-8502, Japan.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Genomics

Complete and accurate sequencing of the entire rice genome of *Oryza sativa* japonica Nipponbare by the IRGSP

T. Sasaki

Rice is an indispensable staple food for half of the world's population, especially in Asia, Africa, and Latin America. With the rapidly increasing population in these areas and the limited land available for rice cultivation, there is an urgent need to improve the rice plant by increasing its tolerance for biotic and abiotic stresses or modifying its genetic composition by introducing alien genes. To attain these goals in a promising and logical manner, the most fundamental information on inheritance must be obtained and decoded at the molecular level. Recent progress in tools and strategies of genome analysis has made the realization of this task possible even if it is very laborious and expensive. In 1998, the International Rice Genome Sequencing Project (IRGSP) started to read the 400-Mb rice genome with 99.99% accuracy and to release the analyzed sequence to the public domain immediately. Initially organized by five countries, 11 countries now participate in this consortium and share the sequencing of the entire region or specific regions of the 12 chromosomes using the clone-by-clone method. Although this approach is quite tedious and requires the construction of a sequence-ready physical map of the genome, it allows accurate positioning of the sequence because each BAC/PAC clone is allocated to its correct genomic position using genetic or related markers and fingerprint data of each clone. The IRGSP expects to obtain a phase 2 high-quality draft sequence of the entire genome by December 2002. This sequence information will be of immense value in many aspects of rice research, such as gene isolation by genetic and reverse-genetic methods, comparative genome analysis of many rice cultivars and *Oryza* species, and control of recombination and gene transfer. The success of the IRGSP in providing highly accurate sequence data and allowing unrestricted access to the information by the public and private sectors indicates the significant role of collaboration among publicly funded laboratories in approaching the challenges of modern science. Still, many aspects of rice genomics remain that must be investigated by an international collaborative system. Considering the intellectual property issues as well, we must clarify the mechanism of inheritance of rice and improve this plant to achieve food security.

Rice has a very long history of cultivation, which started in South Asia and diverged for adaptation and selection in various cultivation environments. As a result, rice has become one of the most important cereal crops in the world. We have sufficient knowledge on how to grow rice plants from sowing seeds to harvesting as well as storing seeds and cooking. However, our understanding of rice as a plant in itself seems far behind that of other species, such as *Arabidopsis thaliana* and maize. The reasons are as follows: (1) rice is used worldwide only as a main staple and not as an industrial resource so that, ironically, this makes rice a local plant; (2) rice is mainly cultivated in economically limited countries and the main efforts to improve rice production have focused on farming; and (3) rice is a politically strategic plant and perhaps the science community is not so comfortable with this situation.

However, this is now the time to fully develop rice science because improvement in rice plants is urgently required to feed the burgeoning population in the near future (Khush 1999). Extensive efforts in traditional and empirical breeding have shown that problems that remain unsolved for a long time are difficult to overcome. Fortunately, during the past decade, we have made great progress in thinking and technology for genome analysis (Lander and Weinberg 2000). Genome analysis has been applied to rice plants and many successful results have been produced, such as restriction fragment length polymorphism (RFLP) or simple sequence repeat (SSR) markers (http://rgp.dna.affrc.go.jp/publicdata/geneticmap2000/index.html, www.gramene.org/microsat/RM-primers.html), the expressed sequence tag (EST) catalogue (Yamamoto and Sasaki 1997), and physical maps (Wu et al 2002, Chen et al 2002). These tools have been used for various types of application, such as marker-assisted selection of desirable progenies (McCouch et al 1997), gene identification by map-based cloning (Tanksley et al 1995), and the identification of disrupted genes by insertion mutagenesis (Hirochika 2001).

Under these circumstances, we strongly believe in the need for a complete set of rice genome sequence information to accelerate application (Sasaki 1998). The genome size of rice is 430 Mb and, within this genome, many repetitive sequences and guanine-cytosine (GC)-rich cores are expected. However, recent advances in the high-throughput sequencing apparatus and high-speed data processor should overcome these difficulties. In addition, since the rice genome was revealed as a reference cereal crop, rice genome information is not only for rice research but also for that of maize and wheat (Moore et al 1995). These factors make it possible and indispensable to sequence the rice genome through international collaboration. In this article, progress in the collaboration is reported, along with our strategy for physical mapping and data analysis.

History of the IRGSP

The first international workshop to discuss the mechanism of collaboration in rice genome sequencing was held at the 5th International Congress of Plant Molecular Biology in Singapore, in September 1997. At this workshop, participants from five countries—Japan United States, the United Kingdom, China, and Korea-agreed to form an international consortium, now known as the International Rice Genome Sequencing Project, or IRGSP, to accelerate the sequencing of the rice genome. The rice cultivar Nipponbare, which belongs to subspecies japonica of *Oryza sativa,* was chosen as the template for sequencing. The primary reasons for choosing this cultivar are that more than 10,000 EST sequences from the strain have been released to the DDBJ and that a physical map based on yeast artificial chromosomes (YACs) that covers more than 50% of the genome has been published. Also crucial to this collaboration was the agreement to share materials, including libraries, and to timely release physical mapping information and annotated DNA sequences to public databases (http://demeter.bio.bnl.gov/rice.html).

At the first working group meeting held in Tsukuba, Japan, in February 1998, the most urgent concerns of the IRGSP were discussed, such as the sharing of chromosomes, sequencing strategy, sequence accuracy to be attained, data release policy, and time schedule for completion. Although more than half of the 12 chromosomes were not yet assigned to any country during that time and financial support was not guaranteed yet for some members, the participating members were optimistic to perform the job (http://demeter.bio.bnl.gov/rice.html).

In 1999, several more countries or regions, as well as Taiwan Province of China, Thailand, India, and France, joined the IRGSP. These countries were assigned to particular chromosomes or chromosomal regions that they were interested in. The U.S. also started extensive rice genome sequencing that year (http://demeter.bio.bnl.gov/tsukuba99.html).

In April 2000, a private company, Monsanto, announced the completion of a rough draft sequence data of cultivar Nipponbare. At the same time, it agreed to share the sequence data and accompanying bacterial artificial chromosome (BAC) clones with the IRGSP. Although the Monsanto physical map had many gaps and the sequence quality was not of the same level as the IRGSP sequence data, the transferred data and materials have been extremely useful in accelerating the sequencing efforts of the IRGSP (http://demeter.bio.bnl.gov/clemson.html).

In February 2001, another private company, Syngenta, announced the completion of the Nipponbare genome sequence by the whole-genome shotgun method, though more than 30,000 sequence contigs existed. However, Syngenta declined to transfer its sequence data to the IRGSP at that time. The IRGSP announced a target date, December 2002, to obtain the rice genome sequence at the phase 2 level, of a much higher quality than the Syngenta sequence (http://rgp.dna.affrc.go.jp/rgp/press_conference.html).

Chromosome sharing was finalized in February 2002 and Japan was assigned to sequence half of the 12 chromosomes. Although some groups backed out of the collaboration, a total of nine countries either remain as active members or have contributed to the efforts of the IRGSP: Japan, U.S., China, France, India, Korea, Brazil, UK, and Thailand (Fig. 1). In April, Syngenta and the Beijing Genome Institute published the draft genome sequence of japonica and indica rice, respectively, in *Science* (Yu et al 2002, Goff et al 2002). Subsequently, Syngenta agreed to transfer its data to the IRGSP. Its data will be used to fill gaps in the physical map and sequence data of the IRGSP.

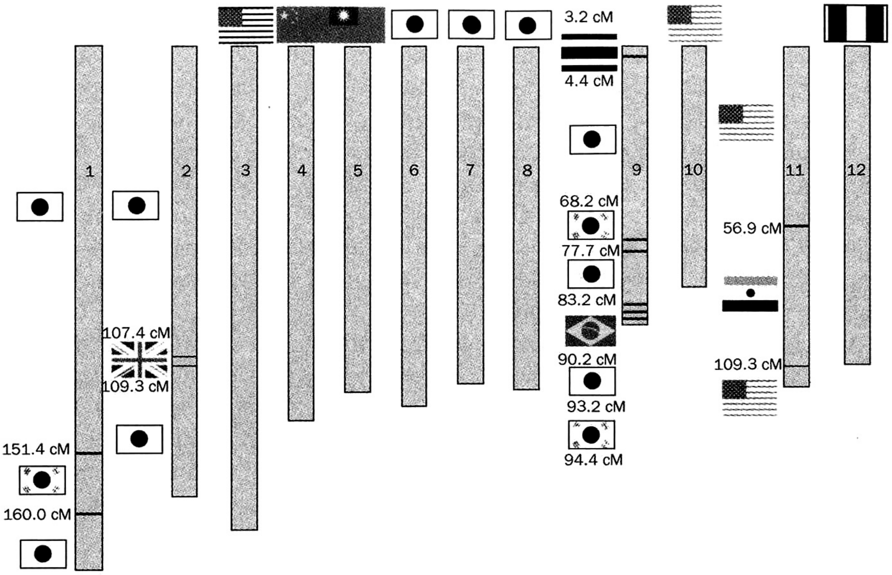


Fig. 1. Chromosomal sharing of the 12 rice chromosomes by 10 participating countries in the IRGSP (as of February 2002).

All the discussion results, progress reports from each working group meeting, and important announcements from the IRGSP can be accessed through our Web site at http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/seqcollab.pl/.

Sequencing strategy of the IRGSP

Basically, a clone-by-clone strategy has been adopted by the IRGSP to pursue the sequencing of accurately assigned clones to specific chromosomal positions. This strategy takes time because physical mapping of BACPAC (P1 artificial chromosome) clones using fingerprint data or polymerase chain reaction (PCR) screening using primers designed by genetically mapped marker sequences is laborious. In the IRGSP, three BAC libraries constructed after digestion with *Hin*dIII, *Eco*RI, and *Mbo*1 and one PAC library after digestion with *Sau*3A1 are used for the construction of a sequence-ready physical map. The total coverage by these libraries is about 60 times that of the rice genome. In addition, Monsanto provided 3,400 BAC clones from a *Hin*dIII library selected among 76,000 clones and assigned to specific chromosomal positions.

The Clemson University Genomics Institute (CUGI) has fingerprinted *Hin*dIII and *Eco*Rl BAC clones and made contigs by FPC analysis (www.genome.clemson.edu/projects/rice/fpc/). Contig assignment to chromosomal position was performed with genetic markers produced by the Rice Genome Research Program

(RGP) (http://rgp.dna.affrc.go.jp/publicdata/geneticmap2000/index.html). In addition to fingerprint data, both end sequences of all the BAC clones were analyzed and summarized (www.genome.clemson.edu/projects/rice/rice-bac-end/). These end sequences have been used to select the minimally overlapped BAC clones within a contig once a key BAC clone of the contig was sequenced. The cut-off score and tolerance in the fpc program are the most important factors in the fingerprinting method to obtain the correct overlaps (www.genome.clemson.edu/fc/). It is therefore important to establish these factors to ensure an accurate overlap among clones in a contig.

For PAC/BAC screening, the RGP primarily relies on genetically mapped markers and EST markers mapped on the skeleton YAC physical map, which was also constructed using genetically mapped markers (Wu 2002, Saji et al 2001). Genetic analysis using about 200 individual F_2 rice plants can differentiate a genetic distance of 0.25 cM, which corresponds to 66 kb of the rice genome, considering a total genetic distance of 1,500 cM and a genome size of 400 Mb. This number agrees with the results obtained using our strategy to identify the correct PAC/BAC clones corresponding to the chromosomal position. These markers have also been used for reconfirmation of Monsanto BAC contig assignment and overlapping. PAC/BAC clones screened by markers are fingerprinted and minimally overlapped clones are selected (http://rgp.dna.affrc.go.jp/genomicdata/seqstrategy/newstrategy.html). The gaps between contigs are filled by PCR screening using gap-flanking sequences.

Genome sequencing has been performed by the shotgun method for selected PAC/BAC clones in the contig to make 2-5-kb insert-length subclones. Templates of sequencing are not PCR products but plasmids to overcome biased amplification because of high GC contents. To attain 99.99% accuracy of the sequence, usually 10X sequence coverage is obtained and the resulting sequences are edited by phred/phrap/consed programs (http://rgp.dna.affrc.go.jp/genomicdata/seqatrategy/Seq-strategy.html). The edited sequence data are released immediately to public databases, such as DDBJ, GenBank, or EMBL.

Current sequencing results

As of 15 July 2002, a total of 360 Mb nucleotide sequence has been released to the public domain and, among these sequence data, 228 Mb and 122 Mb are in phase 2 and phase 3 sequences, respectively (Fig. 2) (http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/seqcollab.pl). Based on the NCBI (National Center for Biotechnology Information) definition, phase 2 sequences are unfinished but ordered sequences with one or more gaps, whereas phase 3 sequences correspond to high-quality finished sequences without gaps. Recently, the genome size of rice was reevaluated from 430 Mb to 400 Mb (Chen et al 2002). Based on this estimate, the IRGSP has now already published 85% of the rice genome. In particular, chromosome 1 by the RGP, chromosome 4 by the NCGR of China, and chromosome 10 by the U.S. groups are almost completely sequenced. By the end of 2002, the IRGSP will release all of the rice genome sequences with a quality of at least phase 2. Upon completion of this

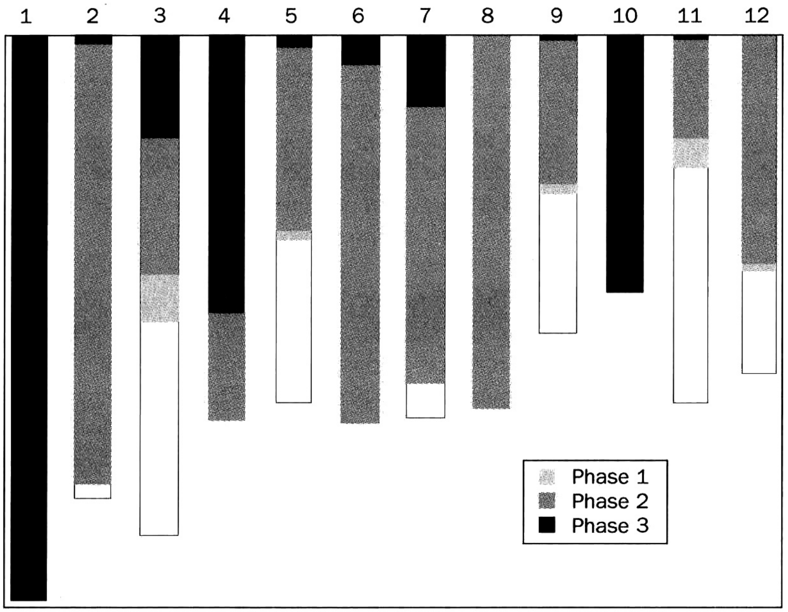


Fig. 2. The current status of genome sequencing in the IRGSP (as of 22 July 2002). The solid, 50%-shaded, and 25%-shaded regions represent the sequenced genomic regions in phase 3, phase 2, and phase 1, respectively. The white regions corresponds to regions with no published sequences yet. Each region represents the total corresponding sequenced region within each chromosome.

goal, the IRGSP will continue to obtain a fully contiguous physical map of the entire rice genome and finished nucleotide sequences at the phase 3 level.

Database

The sequence data are annotated using several gene prediction programs and homology search tools. In the IRGSP, the RGP and TIGR (The Institute for Genomic Research) are independently annotating the sequence data using their own systems with the same annotation standards. The RGP uses a coding region prediction system called RiceGAAS (Rice Genome Automated Annotation System) (http://RiceGAAS.dna.affrc.go.jp/), which is mainly composed of gene prediction programs (Genscan, RiceHMM, FGENESH, MZEF), a splice site prediction program (SplicePredictor), and homology search analysis programs (BLAST, HMMER, Profilescan, MOTIF). The manual inspection of the results by RiceGAAS is performed to finally curate the coding region(s) of each gene. The annotated sequences are shown using a graphical view tool, INE (INtegrated rice genome Explorer) (http://rgp.dna.affrc.go.jp/INE.html), which works by Java applet. The information shown on INE primarily depends on a molecular genetic map that can guarantee the accuracy of the physical map used for sequencing. On the other hand, TIGR uses similar prediction programs and database search programs to annotate the genome sequence (www.tigr.org/tdb/e2k1/osal/annotation.shtml). TIGR informatics aims to compare rice annotated data with those of a broader range of plant species.

Experimental data on rice gene function will be added to INE. For example, the position where the rice endogenous retrotransposon *Tos17* is transposed during cell culture should be shown with the information on resultant phenotype indicated by a regenerated rice plant (Hirochika 2001). This information is very important for understanding the relationship between gene and phenotype. On the other hand, comparison of sequences among rice cultivars and rice subspecies must be pursued to implement INE because a thorough knowledge of the allelic variation among these rice plants is indispensable for understanding phenotypic variation, especially the interaction of genes for phenotypes controlled by multigenes (Yano 2001).

Conclusions

The IRGSP is a multinational and multi-institutional organization that successfully functions to sequence a common-template rice variety to achieve a high quality and reliable data. Despite some political problems associated with the position of rice as an important staple in different countries, the members agreed to publicly release the sequence data immediately. This agreement makes it possible to keep the status of the IRGSP invaluably high to support the development of rice functional genomics and bioinformatics. This is the reason why two large private companies, Monsanto and Syngenta, decided to offer their data to the IRGSP to partly devote their data for public use. In addition, the sequencing strategy adopted by the IRGSP has proven to be the only way to obtain accurate and reliable data that can be used as a "gold standard" for many research fields.

It will take a few more years to complete the sequence of Nipponbare with no gaps in the physical map and sequence because sequencing such highly repetitive regions as the centromere and telomere remains a bottleneck. In the case of rice, the size of the core of the centromere varies from 1.4 Mb to 100 kb depending on the chromosome (J. Jiang, personal communication, 2002). We can possibly sequence the smallest segment and its information can be used to elucidate the structure and function of the centromere at the molecular level.

At present, the IRGSP members do not have a concrete idea on how to maintain the organization after completion of the Nipponbare genome sequence, As in the case of *Arabidopsis,* after the completion of the sequence, each member might be engaged in rice functional genomics. In such a scenario, intellectual property will be the main concern of each member and this must be taken into consideration. Therefore, a collaborative style of organization as in the present IRGSP setup may not be agreeable to the members. However, the rice genome resource contains a large number of accessions and the sequencing of Nipponbare is only a first step in decoding the genetic code. We need much more genome sequence information to understand the relationship between allelic variation and its effects on phenotype. Once we get the "gold standard" of the genome sequence, a different type of collaboration should be organized to facilitate whole-genome comparisons and more rapid discovery of gene functions.

Rice will remain as an important staple for human beings forever. Therefore, we must have much more interest in this plant and continuously sustain the challenge to develop rice cultivars with high yield potential under any environment.

References

Chen M, Presting G, Barbazuk WB, Goicoechea JL, Blackmon B, Fang G, Kim H, Frisch D, Yu Y, Sun S, Higingbottom S, Phimphilai J, Phimphilai D, Thurmond S, Gaudette B, Li P, Liu J, Hatfield J, Main D, Farrar K, Henderson C, Barnett L, Costa R, Williams B, Walser S, Atkins M, Hall C, Budiman MA, Tomkins JP, Luo M, Bancroft I, Sake J, Regad F, Mohapatra T, Singh NK, Tyagi AK, Soderlund C, Dean RA, Wing RA. 2002. An integrated physical and genetic map of the rice genome. Plant Cell 14:537-545.

Goff S, Ricke D, Lan TH, Presting G., Wang R, Dunn M, Glazebrook J, Sessions A, Oeller P, Varma H, Hadley D, Hutchison D, Martin C, Katagiri F, Lange BM, Moughamer T, Xia Y, Budworth P, Zhong J, Miguel T, Pasxkowski U, Zhang S, Colbert M, Sun WL, Chen L, Cooper B, Park S, Wood TC, Mao L, Quail P, Wing R, Dean R. Yu Y, Zharkikh A, Shen R, Sahasrabudhe S, Thomas A, Cannings R, Gutin A, Pruss D, Reid J, Tavtigian S, Mitchell J, Eldredge G., Scholl T, Miller RM, Bhatnagar S, Adey N, Rubano T, Tusneem N, Robinson R, Feldhaus J, Macalm T, Oliphant A, Briggs S. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Hirochika H. 2001. Contribution of the *Tos17* retrotransposon to rice functional genomics. Curr. Opin. Plant Biol. 4: 118-122.

http://rgp.dna.affrc.go.jp/publicdata/geneticmap2000/index.html

http://www.gramene.org/microsat/RM_primers.html

http://demeter.bio.bnl.gov/rice.html

http://demeter.bio.bnl.gov/tsukuba99.html

http://demeter.bio.bnl.gov/clemson.html

http://rgp.dna.affrc.go.jp/rgp/press_conference.html

http://www.genome.clemson.edu/projects/rice/fpc/

http://www.genome.clemson.edu/projects/rice/rice_bac_end/

http://www.genome.clemson.edu/fpc/

http://rgp.dna.affrc.go.jp/genomicdata/seqstrategy/newstrategy.html

http://rgp.dna.affrc.go.jp/genomicdata/seqstrategy/Seq-strategy.html

http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/seqcollab.pl

http://RiceGAAS.dna.affrc.go.jp/

http://rgp.dna.affrc.go.jp/INE.html

http://www.tigr.org/tdb/e2kl/osal/annotation.shtml

Khush GS. 1999. Green revolution: preparing for the 21st century. Genome 42:646-655.

Lander ES, Weinberg RA. 2000. Journey to the center of biology. Science 287:1777-1782.

McCouch SR, Chen X, Panaud O, Temnykh S, Xu Y, Cho YG. Huang N, Ishii T, Blair M. 1997. Microsatellite marker development, mapping and applications in rice genetics and breeding. Plant Mol. Biol. 35:89-99.

Moore G, Devos KM, Wang 2, Gale MD. 1995. Cereal genome evolution: grasses, line up and form a circle. Curr. Biol. 5:737-739.

Saji S, Umehara Y, Antonio BA, Yamane H, Tanoue H, Baba T, Aoki H, Ishige N, Wu J, Koike K, Matsumoto T, Sasaki T. 2001. A physical map with yeast artificial chromosome (YAC) clones covering 63% of the 12 rice chromosomes. Genome 44:32-37.

Sasaki T. 1998. The rice genome project in Japan. Proc. Natl. Acad. Sci. USA 95:2027-2028.

Tanksley SD, Ganal MW, Martin GB. 1995. Chromosomal landing: a paradigm for map-based gene cloning in plants with large genomes. Trends Genet. 11:63-68.

Wu J, Maehara T, Shimokawa T, Yamamoto S, Harada C, Takazaki Y, Ono N, Mukai Y, Koike K, Yazaki J, Fujii F, Shomura A, Ando T, Kono I, Waki K, Yamamoto K, Yano M, Matsumoto T, Sasaki T. 2002. A comprehensive rice transcript map containing 6591 expressed sequence tag sites. Plant Cell 14:525-535

Yano M. 2001. Genetic and molecular dissection of naturally occurring variation. Curr. Opin. Plant Biol. 4:130-135.

Yamamoto K, Sasaki T. 1997. Large-scale EST sequencing in rice. Plant Mol. Biol. 35:135-144.

Yu J, Hu S, Wang J, Wong GK, Li S, Kiu B, Deng Y, Dai L, Zhou Y, Zhang X, Cao M, Liu J, Sun J, Tang J, Chen Y, Huang X, Lin W, Ye C, Tong W, Cong L, Geng J, Han Y, Li L, Li W, Hu G, Huang X, Li W, Ki J, Liu Z, Li L, Liu J, Qi Q, Liu J, Li L, Li T, Wang X, Lu H, Wu T, Zhu M, Ni P, Han H, Dong W, Ren X, Feng X, Cui P, Li X, Wang H, Xu X, Xhai W, Xu Z, Zhang J, He S, Zhang J, Xu J, Zhang K, Zheng X, Dong J, Zeng W, Tao L, Ye J, Tan J, Ren X, Chen X, He J, Liu D, Tian W, Tian C, Xia H, Bao Q, Li G, Gao H, Cao T, Wang J, Zhao W, Li P, Chen W, Wang X, Zhang Y, Hu J, Wang J, Liu S, Yang J, Xhang G, Xiong Y, Li Z, Mao L, Zhou C, Zhu Z, Chen R, Hao B, Zheng W, Chen S, Guo W, Li G, Liu S, Tao M, Wang J, Zhu L, Yuan L, Yang H. 2002. A draft sequence of the rice genome (Oryza sativa L. ssp. indica). Science 296:79-92.

Notes

Author's address: National Institute of Agrobiological Sciences, 1-2, Kannondai 2-chome, Tsukuba, Ibaraki 305-8602, Japan.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The Chinese Sup0erhybrid Rice Genome Project (SRGP) has entered its next phase

Jun Yu, Songnian Hu, Jun Wang, Gane K.-S. Wong, Xingwang Deng, Lihuang Zhu, Mengliang Cao, Longping Yuan, Jian Wang, and Huanming Yang

As an ongoing genome project, the Chinese Superhybrid Rice Genome Project (SRGP) is designed to accelerate rice genomics research by providing immediately applicable information and resources, such as sequence databases and microarrays, that are desirable for furthering biological studies and crop improvement. The SRGP produced a “working draft” sequence as one of its major goals, from the paternal cultivar 9311, early in 2002 and released the data unconditionally to the public. Based on the draft sequence assembly, we have developed a high-density rice microarray system for gene expression studies. The finesequence map of this indica rice variety with greater than 99% gene coverage, high nucleotide accuracy, and community-acceptable contiguity will be produced, accompanied by a draft sequence of the maternal variety of the superhybrid rice LYPS, PA645 which is a rice cultivar of complex genetic background. The project will eventually provide basic information and tools for rice biology, together with international efforts on a finished sequence map from the japonica variety.

The Chinese Superhybrid Rice Genome Project (SRGP) has entered its second phase after we reported the draft assembly in *Science* early in 2002 (Yu et al 2002). We have been focusing on building up more sequence coverage and a new assembly of the draft sequence now has more than 6X genome coverage. The new assembly is freely accessible from our Web site (genomics.org.cn) and genome-wide analysis of this assembly is expected to yield further knowledge about the rice genome. Microarray systems are also being developed, which contain nearly 60,000 cDNA-verified and predicted genes. We are establishing collaborations with rice biologists worldwide and hoping to expand information and knowledge from genomic basics to cellular and molecular applications. We report our plan to build a fine genome map of indica rice and some of our recent progress in the project.

Building a fine map for indica rice from *93-11* and defining a fine-sequence map

In the second phase of the SRGP, we have added 2X coverage to the genome sequence assembly of the paternal strain of *LYPY, 93-11* (*Oryza sativa* L. subsp. *indica*), and achieved nearly 2X sequence coverage over the genome of the maternal strain, *PA64S.* Combined with a rigorous finishing strategy, the current assembly with more than 6X coverage of the *93-11* genome is projected to have a much lower number of contigs than our early assembly as parameters for repeat identification and assembly are optimized. Our current 6X assembly has fewer than 40,000 sequence contigs. Experimental data and physical map information will be added to aid the new scaffolding process. These contigs and scaffolds will be positioned onto physically mapped bacterial artificial chromosome clones (BACs) using new STSs (sequence-tagged sites) designed from unmapped contig and scaffold sequences. Smaller sequence gaps between contigs are to be closed by polymerase chain reaction (PCR)-based methods. Closure of larger gaps and long-range scaffolding will rely on new data from the end sequences of large insert clones, cosmids/fosmids, or mini-BACs, with insert sizes ranging from 15 to 30 kb.

To optimize our finishing strategy, we analyzed the distribution of gene islands and repeat clusters over the genome, based on our draft assembly. We took 102 BACs from the public database and aligned their sequences to our shotgun assembly annotated with mathematically defined 20-mer repeats (Jun Wang et al 2002). "Gene islands" are defined as the sequences that are mostly unique sequences between repeat clusters. To estimate the size of the gene islands, we systematically merged the 20-mer repeats by eliminating gaps from 1 to 100 20-mer repeat units. Such a process allowed us to join the repeats into larger clusters until two adjacent gene islands were merged together (Fig. 1). This gave us a maximal gap range of 100 to 150 bp. Using 150 bp as a fixed parameter, we estimated the minimal repeat cluster sizes to be from 1 to 10 kbp (Fig. 2). It appears that the average size of the gene islands is about 26.6 kbp, given a maximal gap of 150 bp between repeat units and a minimal repeat size of 1.5 kbp between repeat clusters. With a current estimate of the average rice gene size of 7 kbp, a typical gene island contains three or four genes. Since almost half of the rice genome is occupied by repetitive sequences, the repeat clusters are most likely distributed as if they resembled the inverse picture of the gene islands. The implications of the analysis are multifold. First, it indicates that any gap-closing procedure will be challenged by the size of the repeat clusters; a majority of them are tens of kilobase pairs in length. PCR-based gap closing is useful only when the gaps are within genes. It is more difficult to fill gaps between genes and contigs that are separated by repeat clusters that are large with high copy numbers. Second, for scaffold building, the most useful size range for cloned inserts is from a few kbp to tens of kbp in length. Small insert clones for shotgun sequencing are not useful at all for scaffolding other than for fulfilling basic coverage. Third, serious doubts are unavoidable as to how complete the sequence map could be and what the arguments are to assemble the last gap that is full of repeats and is kilobase pairs in length. Thus, it is extremely difficult to validate the assembly. Collectively,

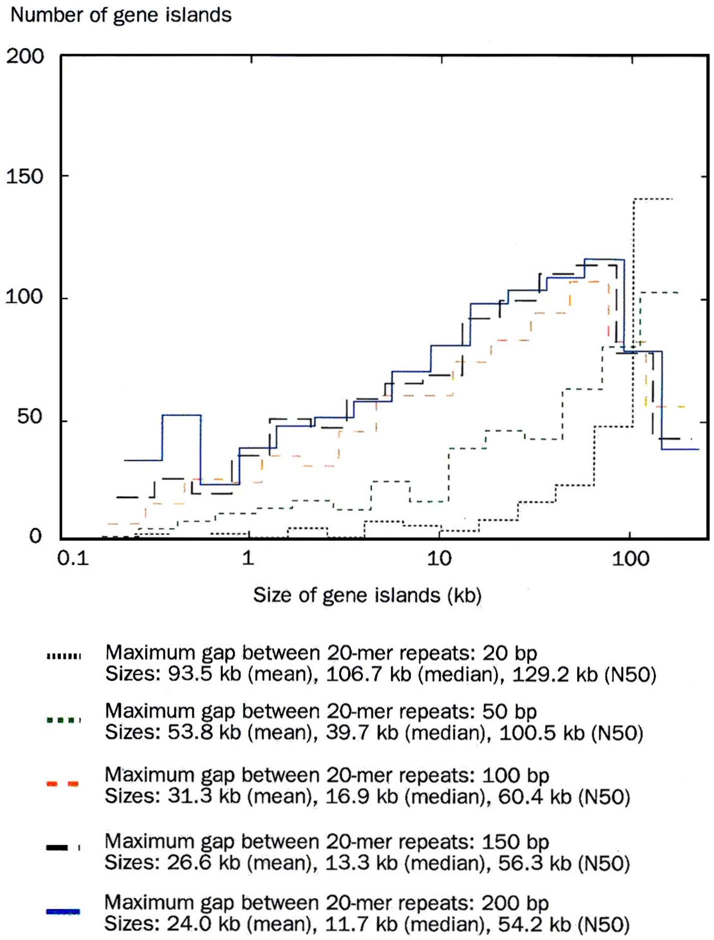


Fig. 1. Distribution of "gene Island" in *O. sativa.* Based on finished sequences from 102 rice bacterial artificial chromosomes, we aligned 20-mer repeats from the 4X whole-genome shotgun data and merged any repeats separated by less than the maximal gap sizes ranging from 20 to 200 bp (color-coded lines). The minimal repeat cluster size set for the plot is 1.5 kbp, which includes most of the miniature inverted transposable elements but excludes larger repeat units. Gene islands are defined as the sequences that are mostly, but not all, unique sequences between these repeat clusters. The mean, median, and N50 sizes are also indicated.

our results suggest that certain unique structural features of the rice genome should be considered when criteria for constructing a fine-sequence map and later an integrated physical-genetic map are discussed. The basic strategy for the rice genome map is very useful for sequencing other larger cereal crop genomes, such as those of wheat, maize, and barley.

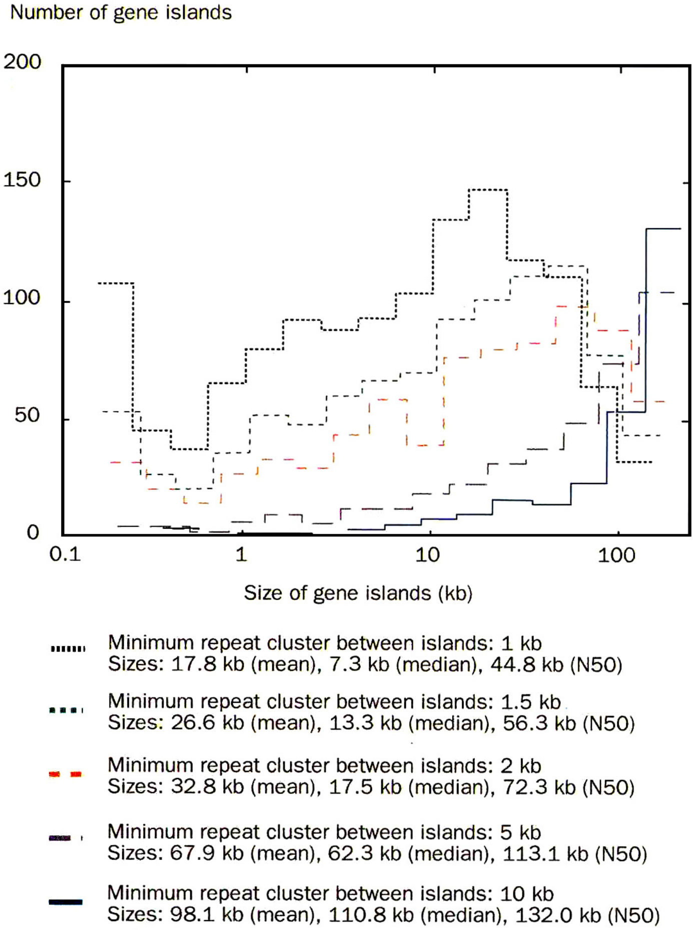


Fig. 2. Distribution of "gene island" size in *O. sativa.* The 20-mer repeats from our 4X whole-genome shotgun data were aligned to finished sequences of 102 rice bacterial artificial chromosomes from the public databases. Gaps were merged between repeats in lengths less than 150 bp. The distribution of gene islands is plotted when the minimal sizes of these repeat clusters range from 1 to 10 kbp (color-coded lines). Gene islands are defined as the sequences between the repeat dusters. The mean, median, and N50 sizes are indicated.

Our analysis of the distribution of high-copy repeats published earlier (Yu et al 2002) showed that most of the transposons in the rice genome are located in the intergenic regions between genes and are clustered together, forming "blocks" of repetitive sequences. Such a distribution is in sharp contrast with that of human repetitive sequences, which are mostly contained by genes, or are within introns. One of the criteria for a fine-sequence map is to join the sequence gaps within rice genes when they are split into different contigs or scaffolds. Another subject related to sequence contiguity is how to decide if one contig should and could be joined to the next. We have decided to fill any gaps and finish any contig ends that contain repeated sequences in a redundancy of 10 or fewer copies within the rice genome. We will also place such contigs onto chromosomes by STS mapping. If every contig in the draft assembly containing genes is ordered and oriented, we should be able to complete the project in constructing a fine-sequence map. It is unnecessary to sequence the very last base pair comparable to the proposed finishing standard for the human genome, where the error rate is constrained to less than 1 base pair per 10,000 bases. This standard was based on the polymorphism rate of 1 in 1,000 found in humans, which is almost 10 times lower than that of many other species, including rice. A base-pair quality standard for finishing the rice genome should be in the range of 1/10,000 to 1/2,000. Finishing reads should be added only if the sequence is of low copy number as measured by genome-wide repeat content, less than or equal to 10.

In the meantime, we are developing software tools to integrate various data sets, assemble the repetitive sequences (biologically defined repeats or BDRs), and further annotate the genes that include the genes homologous to the *Arabidopsis* genome and the nonhomologous genes unique to the rice genome. We are developing gene-identification software using alternative approaches other than the current common practice. A comparative analysis is under way to compare the draft assemblies of the indica and japonica rice released by Syngenta Company.

The major undertaking of the SRGP's second phase is to construct fine, integrated, and biology user-oriented rice genome maps that are, though mosaic in nature, incorporated with genomic sequences from different cultivars, and that include ordered sequence contigs and relevant genomic resources, such as BACs, cDNAs, and physical markers with a density that exceeds the number of sequence-derived contigs. The physical (sequence) maps will be integrated with a genetic map that provides an adequate framework for gene and marker ordering. The sequence-derived contigs (>2 kbp in length) will be finished to the adjacent high-copy repeats (equal to or greater than 50 copies per genome) of the LTR (long terminal repeat) type, such as repeats of *copia* and *gypsy* families. Gaps smaller than 1 kbp between contigs will also be closed regardless of the repeat content. Contigs ending with low-copy repeats (less than 50 copies per genome) or that are extendable will be analyzed to the nearest high-copy repeats. Putative genes or exons will be extended to have their flanking sequences greater than 100 bp or equal to a typical sequencing read length toward both directions. Another major product of our phase II effort is a collection of validated genetic markers, preferably single nucleotide polymorphisms, or SNPs. This is being done in two steps: *in silico* identification of putative SNPs from sequence comparison and experimental validation on a mapping panel of genetically related but diverged rice cultivars representing the three major subspecies. Gene-coding SNPs will be given high priority in the mapping endeavor.

Building microarrays for rice genes and the rice gene expression map

The last, but not the least, product is a set of rice genes that are verified to be informative for expression profiling. The collection has started from the genes identified *in silico* with various software tools. No consensus sequences were built from these putative genes but experimental procedures were designed to verify them.

The sequenced clones containing more than 60,000 putative genes were picked, PCR-amplified, and gridded onto microarrays for cDNA-based hybridization experiments. Informative sequences (limited by the diversity of cDNA sources) are rearrayed on a new set of grids for intensive validation and study. The process will be repeated several times to include as many informative representative gene sequences as possible since novel genes will be identified in cDNA-based experiments by using more diversified materials from different tissues and developmental stages. The short-term goal of this initiative is to define gene sequences that are useful for expression profiling and suitable for *de novo* synthesis as oligonucleotides in an unlimited amount as we have envisaged that these “gene chips” are “portable tools” for rice molecular biologists.

A super-computational environment is also being built in our genome center to handle and analyze all the rice genomic data produced by other public or private efforts, and our own. It includes biologist-friendly databases and data sets, general tools for genome landscape elucidation and gene annotation, as well as pipelines for the genomic and cDNA data processing.

Our long-term goals are not only to have the genome of indica rice fully “cooked” (complete), but also to have genomes of all three rice subspecies sequenced. We will use genetic markers mapped across rice cultivars and ample genomic information to examine experimentally many biological questions, including characteristics and mechanisms of segmental gene duplication, the molecular behavior of heterosis, and the nature of environment-sensitive and fast-evolving genes in the rice genome.

Concluding remarks

The completeness of a genome project, such as the SRGP, is not going to be benchmarked by local sequence contiguity, even more unlikely for larger crop plant genomes such as wheat or maize, but by the usefulness of the genomic data collectively produced by scientific teams, virtual or real, that are undoubtedly multidisciplinary and international. Constructive discussions and suggestions are of essence to encourage the working teams to achieve their goals. Although complaints about the incomplete products of genome projects at various stages are often voiced, we believe that biologists as a whole will always cheer their successes when any of the competitive teams accomplish their goals, even when these are sometimes stepwise achievements.

References

Jun Wang, Gane Ka-Shu Wong, Jian Wang, Peixiang Ni, Yujun Han, Xiangang Huang, Jianguo Zhang, Chen Ye, Yong Zhang, Jianfei Hu, Kunlin Zhang, Xin Xu, Lijuan Cong, Hong Lu, Xide Ren, Xiaoyu Ren, Dan Dai, Jun He, Lin Tao, Douglas A. Passey, Huanming Yang, Jun Yu, Songgang Li. 2002. RePS: a sequence assembler that masks exact 20-mer repeats identified from the shotgun dataset. Genome Res. 12:817-823.

Yu J and 99 others. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science 296:79-93.

Notes

Authors' address: Beijing Genomics Institute, Chinese Academy of Sciences, Beijing, People's Republic of China. E-mail: junyu@genomics.org.cn.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Public rice sequence database: structure and applications

T. Matsumoto, Y. Katayose, J. Wu, N. Namiki, K. Yamamoto, K. Sakata, and T. Sasaki

The Rice Genome Research Program (RGP) has accumulated various kinds of information on rice genomics since it started in 1991. This information is freely available from public databases, including our Web site. In 1998, the RGP started a new project on sequencing the whole rice genome in cooperation with researchers from an international consortium. The sequence data produced by a map-based clone-by-clone sequencing strategy as well as the sequence annotation have been deposited in the DDBJ (DNA Data Bank of Japan). These data are also presented in a more user-friendly manner in our rice genome database, known as INE, which integrates the genetic linkage map with the genome sequence. This enables rice researchers to traverse the world of genetics and that of molecular biology. These genomic data also facilitate the isolation of genes controlling phenotypic traits, finding the underlying mechanisms, and engineering biological functions.

Rice (*Oryza sativa* L.) is one of the most important crops in the world. It is a staple food for more than half of the world's population. Rice is not only seen as an economically important plant for food production but is also recognized as a model monocotyledonous plant, in the same manner that *Arabidopsis* is considered as a model dicotyledonous plant (NPGI progress report, 2001). The syntenic relationship among grass genomes means that the colinearity in the order of genes over large blocks in the chromosomes is now widely accepted (Ahn and Tanksley 1993, Devos and Gale 1997, Bennetzen et al 1998, Gale and Devos 1998). Rice has the estimated size of 430 Mb (Arumuganathan and Earle 1991), which is the smallest among the major cereals. A recent size estimation based on the physical length of bacterial artificial chromosome (BAC) fingerprint contigs shows that the actual size is about 400 Mb (Chen et al 2002, Burr 2002). Since a complete sequence of *Arabidopsis thaliana* was published in 2000 (The Arabidopsis Genome Initiative 2000), sequence information has become basic knowledge for both plant genomics and plant biology.

As a model plant of monocots and the best-studied crop plant with a large effect on food production, the complete rice genome sequence will be extremely valuable. Thus, an international consortium, the International Rice Genome Sequencing Project (IRGSP), was established in 1998 to accelerate rice genome sequence analysis (Sasaki and Burr 2000).

The consortium members use one japonica variety, Nipponbare, as a standard for sequence analysis. This standardization is essential for constructing a cross-referable database, The Rice Genome Research Program (RGP) has continuously used this single variety for rice genome analysis since 199 1 and thus much information is already available, including more than 29,000 cDNA clones from various organs and cultured cells under stress conditions (Yamamoto and Sasaki 1997), a high-density genetic linkage map (Harushima et al 1998, Yano 2000), a yeast artificial chromosome (YAC)-based physical map (Saji et al 2001), and a rice transcript map with 6,591 expressed sequence tag (EST) sites (Wu et al 2002). There are many efforts to construct rice genome databases, both public and private. In this paper, we would like to describe some public and private databases and explain how both plant biology and crop breeding could benefit from a genome sequence database.

Rice genome sequence production

As a member of the IRGSP, the RGP is assigned to sequence six chromosomes (1,2, 6,7,8, and 9), with a total length of 208 Mb. The PAC (P1 artificial chromosome) or BAC clones (typically 100–150 kb in size) were selected from the Nipponbare libraries (Baba et al 2000, Wing 1996) and mapped on the chromosome using polymerase chain reaction (PCR) screening with the mapped ESTs. As of July 2002, a total of 1,453 PAC or BAC clones have been aligned along these chromosomes by RGP. These clones cover 183 Mb, which correspond to 88% of the assigned physical length. The selected clones were cultured in liquid media and PAC/BAC DNA was purified. Then, the PAC/BAC DNA was fragmented by sonication and shotgun plasmid (pUC18) clone libraries of two average insert sizes (2 and 5 kb) were constructed. Sequence reactions were done with the Dye Terminator method (PE Biosystems). Sequence products from both ends of 2- and 5-kb clones (a total of 1,000 clones from each library) were analyzed by the capillary sequencers (PE 3700). The typical read length from each reaction was 500 bases. This analysis yielded a 10X or more coverage sequence, which has 99.99% accuracy in most of the region, and it was verified to be sufficient for HTG (high-throughput genomic sequence: www.ncbi.nlm.nih.gov/HTGS/) phase 2 assembly. Monsanto Co. announced the completion of the Nipponbare draft sequence, with a total of 399 Mb from 3,391 BAC clones (www.monsanto.com/monsanto/media/00/00apr4 rice.html). At the same time, Monsanto decided to share this sequence information and other materials with the IRGSP to accelerate the completion of rice genome sequencing (Bany 2001). In conjunction with this development, the RGP has modified the sequencing pipeline, including physical map construction, to maximize the production of sequence with already available sequence from Monsanto (Fig. 1, http://rgp.dna.affrc.go.jp/

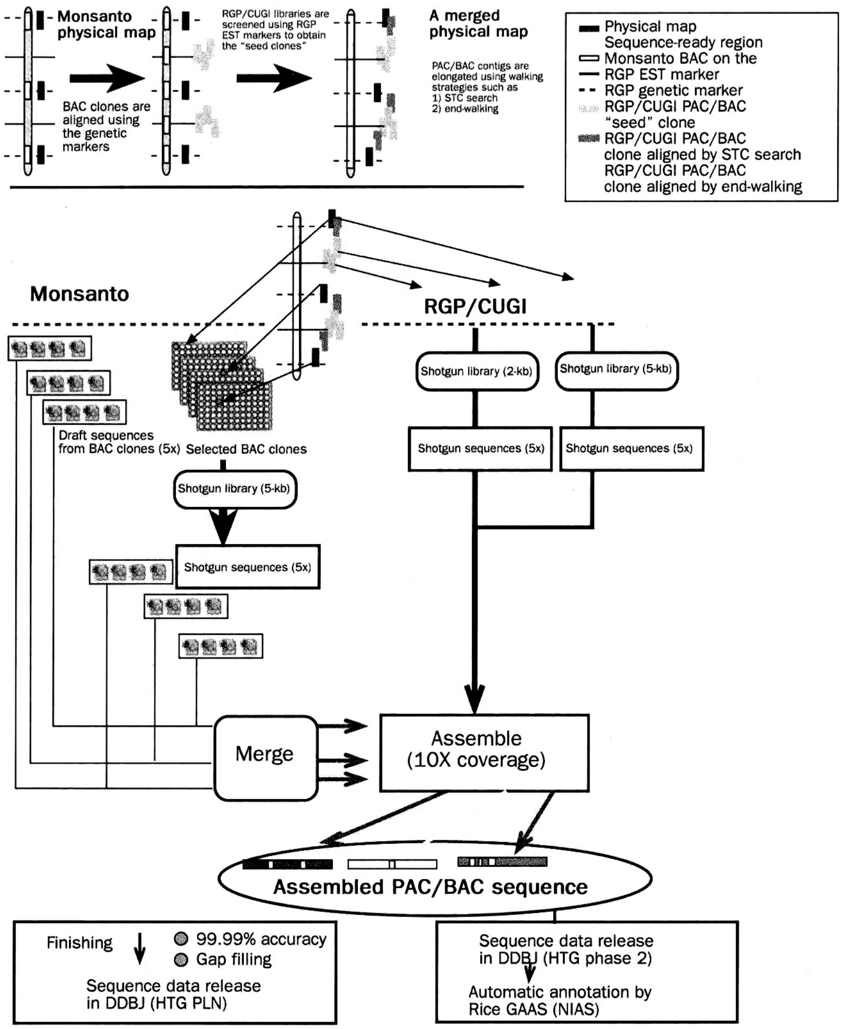


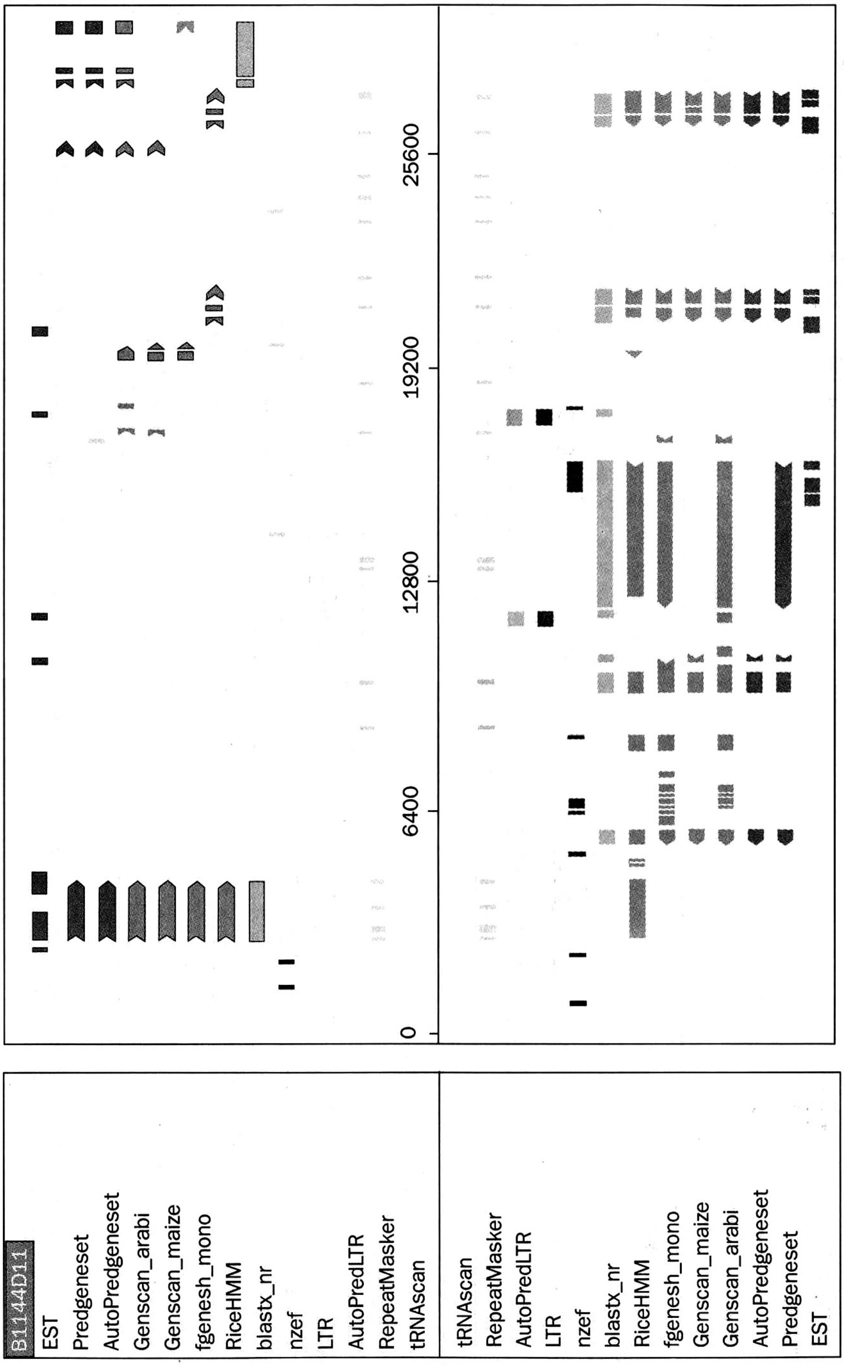
Fig. 1. A new strategy for the accelerated release of the rice genomic sequence.

genomicdata/seqstrategy/newstrategy.html). In this strategy, we have remapped Monsanto BAC clones with high-density EST markers to avoid redundancy and misassignment of BAC clones. This has facilitated the construction of BAC minimum-tiling contigs in a short period of time. For these BAC clones, 5-kb shotgun libraries were constructed and 1,000 shotgun clones from each library were sequenced from both ends. Since draft sequences were already available for these clones, 2-kb insert libraries were unnecessary. Finally, our sequence data and the Monsanto draft sequence data were merged for Phrap-based sequence assembly (www.phrap.org/).

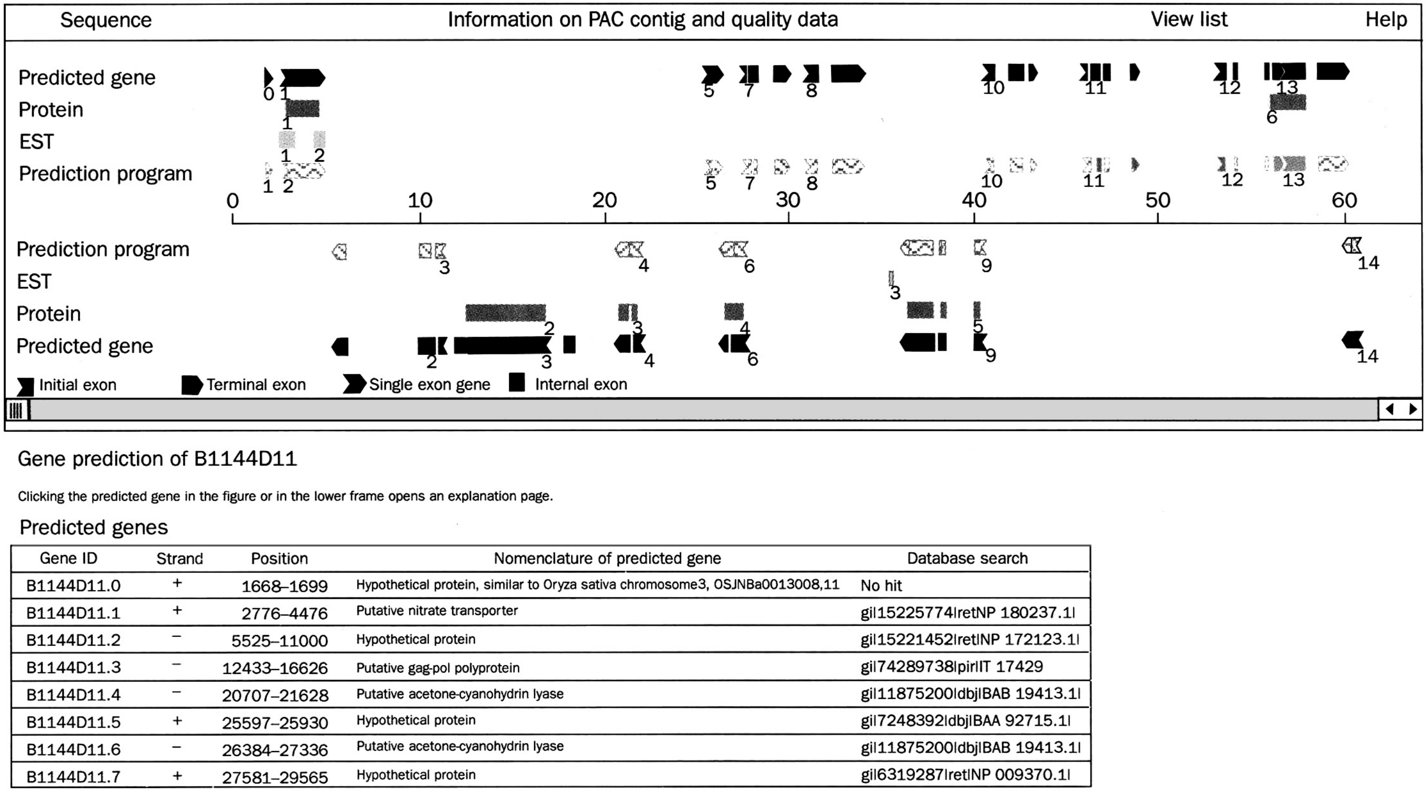
For the gap regions where Monsanto BAC clones could not be assigned, other libraries (RGP PAC and BAC libraries, CUGI BAC libraries) were used for screening with EST markers to construct the minimum tiling path. These clones underwent 10X shotgun sequencing. With this strategy, we could accelerate sequence production, and so far we have succeeded in producing more than 100 Mb phase 2 sequences in a year. As of 22 July 2002, the RGP had already submitted about 206 Mb of genome sequence to the DDBJ (DNA Data Bank of Japan) from the six chromosomes. However, this figure may be somewhat overestimated because it does not take into consideration the overlaps between clones. When the average overlapped length (typically 15%) is considered, the net sequence submission may be around 170 Mb, 84% of the total length of the six chromosomes and 95% of the regions where physical contigs have been constructed. Simultaneously, the RGP has been finishing the sequences, filling the remaining sequence gaps within the phase 2 PAC/BAC clones, and improving the low-quality regions to complete the sequence. So far, we have already completed 95% of the entire rice chromosome 1, the longest chromosome, as phase 3. These regions do not include the centromere and seven gaps where walking efforts using six kinds of PAC/BAC libraries and clones, which are shared with the IRGSP, are still under way. Currently, we have shifted our sequencing efforts to chromosome 7 and, so far, 82 clones have been completed as phase 3.

A step-by-step publication of rice genome sequence

A phase 3 sequence that corresponds to a completely finished sequence with no gaps is most desirable for rice researchers. But, since the 10X sequences produce relatively accurate shotgun sequence assembly, the IRGSP has recognized to a certain extent that it is valuable to publish phase 2 sequences in the public domain prior to phase 3 completion. Thus, PAC or BAC sequences of phase 2 are immediately submitted to the DDBJ according to the IRGSP data publication guidelines (demeter.bio.bnl.gov/Guidelines.html). After the finishing process, these sequences are updated to phase 3 and, upon resubmission to the DDBJ, the data files with the complete sequence are revised without changing the accession numbers. At the same time, the sequences also undergo the annotation step in the RGP. We have adopted a two-phase annotation system in our annotation procedure. First, in an automatic annotation process, a system called RiceGAAS (Rice Genome Automated Annotation System, Sakata et al 2002) performs parallel analyses of the sequence with 14 analysis programs, including the similarity search analysis by BLASTX (www.ncbi.nlm.nih.gov/BLAST, against the nonredundant protein database of NCBI) and BLASTN (to our Nipponbare rice EST database), gene prediction software such as GENSCAN (Burge and Karlin 1997) for *Arabidopsis,* GENSCAN for maize, RiceHMM, which has been tuned for rice genes (www.rgp.dna.affrc.go.jp/RiceHMM/index.html, Sakata et al 2000a), and FGENESH (www.softberry.com/berry.phtml, Salamov and Solovyev 2000) for monocots. The results are integrated and presented as the "autopredicted genes" (an example of an annotation map of an RGP BAC clone is shown in Fig. 2, upper frame). RiceGAAS also executes automatic characterization of all autopredicted



continued on next page



Gene prediction of B1144D11

Clicking the predicted gene in the figure or in the lower frame opens an explanation page.

Predicted genes

Gene ID	Strand	Position	Nomenclature of predicted gene	Database search
B1144D11.0	+	1668–1699	Hypothetical protein, similar to Oryza sativa chromosome3, OSJNBa0013008,11	No hit
B1144D11.1	+	2776–4476	Putative nitrate transporter	gil15225774lretNP 180237.1l
B1144D11.2	–	5525–11000	Hypothetical protein	gil15221452lretlNP 172123.1l
B1144D11.3	–	12433–16626	Putative gag-pol polyprotein	gil74289738lpirlIT 17429
B1144D11.4	–	20707–21628	Putative acetone-cyanohydrin lyase	gil11875200ldbjlBAB 19413.1l
B1144D11.5	+	25597–25930	Hypothetical protein	gil7248392ldbjlBAA 92715.1l
B1144D11.6	–	26384–27336	Putative acetone-cyanohydrin lyase	gil11875200ldbjlBAB 19413.1l
B1144D11.7	+	27581–29565	Hypothetical protein	gil6319287lretlNP 009370.1l

Fig. 2. Annotation map view. Previous page: results of the auto-annotation by RiceGAAS. This page: results of the manual curation of the RiceGAAS output and functional characterization of the predicted genes.

genes, showing the results of BLASTP, and domain searches by HMMER. These results could be viewed at the RiceGAAS site for the respective clone. These autopredicted gene sets are edited by human curation, the second stage in annotation. Based on the results of BLAST (BLASTN, BLASTX) analysis and its alignment, the exon-intron constitution in the gene models is corrected. This process also includes the functional characterization of the predicted genes by human interpretation. BLASTP analysis indicates proteins with structural similarities with an E-value (expectation value). Proteins that have an E-value less than 10^{-20} are classified as the "same protein," "putative protein," "similar to the protein," "unknown protein," and "hypothetical protein," according to the degree of similarity to known proteins. Examples of the final annotation map of the same BAC clone as shown in the automatic annotation are presented in the lower frame in Figure 2. The manually annotated PACs/BACs are submitted to the DDBJ together with the predicted protein CDSs (coding sequences) and also to our database INE (http://rgp.dna.affrc.go.jp/giot/INE.html, Sakata et al 2000b).

Rice database (as of 28 June 2002)

Many databases collect useful rice data and sequences. Some of these database sites are briefly surveyed. (Please note that this is not a detailed comparison of the databases, but the description of each database from the standpoint of a database user.)

In NCBI (National Center for Biotechnology Information), the Plant Genome Central (www.ncbi.nlm.nih.gov/PMGifs/Genomes/PlantLIST.html) section collects results from the plant genome project featuring genome sequences and ESTs deposited in GenBank®. In the section of large-scale sequencing projects, the comparative map information of *Oryza sativa* and the status of the RGP and other IRGSP members are linked. It also has a map of *Arabidopsis thaliana* on which rice ESTs and rice UniGenes are identified by BLAST analysis.

The Expressed Sequence Tags database (dbEST) of NCBI (www.ncbi.nlm.nih.gov/dbEST/dbEST-summary.html) shows the accumulation of EST entries by organism. Almost 104,973 entries of ESTs are currently available. GenBank has 15,249 clusters of UniGene entries, 350,795 genomic sequences, and 2,400 HTG sequences from PACBAC clones.

The TIGR (The Institute for Genomic Research) rice genome database (http://tigr.org.tdb/e2kl/osal/) displays data from TIGR's rice genome project. It contains *in silico* mapping of rice genetic markers to rice sequences, the status of the project in collaboration with the ACCW (Arizona Genomics Institute, Clemson University, Cold Spring Harbor Laboratory, and Washington University) rice sequence consortium, the automated annotation pipeline, and a collection of rice gene data (TIGR Rice Gene Index:OSGI), which have 117,222 sequence entries as of 1 June 2002. It also graphically presents the sequencing progress of the IRGSP.

The Gramene database (www.gramene.org, Ware 2002) is based on the Oracle database-Ensemble (www.ensemble.org) object-oriented layer. It is financially supported by the United States Department of Agriculture (USDA) and aims to construct the comparative genome mapping database for grasses and the cumulative database for the rice community. It has a browser that shows the marker positions, EST positions, and annotation. It has integrated the IRGSP material such as information on PACBAC clones and the FPC (fingerprinted contigs; www.genome.arizona.edu/software/fpc) physical map.

The AGI (Arizona Genomics Institute, www.genome.arizona.edu) database consists of data from STC (sequence-tagged connectors) sequencing projects of various plants, rice genomic sequence data, and physical maps. AGI has also constructed 80 BAC libraries from agricultural plants and bacteria. As an IRGSP member, it supplied BAC clones from two kinds of Nipponbare libraries to other members and also provided the end-sequence data of the individual BAC clone together with the FPC contig information.

The Oryzabase (www.shigen.nig.ac.jp/rice/oryzabase/) is a comprehensive rice database maintained by the National Institute of Genetics in Japan. Currently, it gathers information on classical genetics such as genetic resources, strain descriptions (10,746), descriptions of phenotypic mutants, and gene characterization and chromosomal location to provide a wide range of information to rice researchers.

The NIAS (National Institute of Agrobiological Sciences) DNA bank (www.dna.affrc.go.jp/) preserves and distributes all cDNA clones and YAC clones that the RGP has analyzed. It is also responsible for the distribution of restriction fragment length polymorphism (RFLP) markers (part of the markers coincide with cDNAs) and Nipponbare YAC filters for global physical map construction. It also supplies some informatics services, including various homology searches (FASTA, BLAST), RiceGAAS, and PLACE (PLAnt Cis-acting regulatory DNA Elements, Higo et al 1999) Signal Scan search.

The Monsanto Web site (www.rice-research.org/) provides access to the Monsanto Rice Genome Sequence Database. Upon registration, academic and nonprofit researchers could use the BLAST systems to search homologous sequences against their queries.

Recently, Syngenta (TMRI, Torrey Mesa Research Institute, www.tmri.org/index.html) has published the results from the gene analysis of the assembled sequences of the whole-genome shotgun draft sequences from the Nipponbare genome (Goff et al 2002). However, the sequence data were not accessible to the public. Instead, Syngenta has proposed collaboration for nonprofit purposes by making part or all of the sequences of the Syngenta rice genome sequence (Syd) accessible. Nevertheless, in a recent announcement, Syngenta has agreed to share Syd draft data with the IRGSP to accelerate completion of the finished rice genome sequencing (www.nias.affrc.go.jp/pressrelease/2002/20020523/announcement.html).

The BGI (Beijing Genomics Institute, China) has also reported the publication of the draft sequence of an indica-type cultivar, 93-11, using a whole-genome shotgun sequencing method (Yu et al 2002). The contig sequences have been deposited in public databases and could also be downloaded from their database (RiceGD, http://btn.genomics.org.cn/rice/). The database also includes the results of analysis of 77,150 ESTs from super-hybrid rice cultivar LYP9 and its parental cultivars.

Structure of the RGP database

The rice genome database of the RGP (http://rgp.dna.affrc.go.jp/) is presented through a Web-browser interface, which facilitates easy access to researchers. The database has several sections, such as the important data repository from the RGP, the current status presentation of RGP and IRGSP genome sequencing, and an integrated rice genome database, INE (INtegrated rice genome Explorer). The RGP has been accumulating sequence data and map information on the rice genome, including the full list of the cDNA clones deposited in NIAS DNAbank, a YAC physical map with 80% coverage, a high-density genetic linkage map with 3,267 markers, and a YAC-based rice transcript map with 6,591 EST sites. Although these data do not include genome sequence data, they have played crucial roles for rice genome sequencing. For example, high-density EST markers could help to align PACBAC clones throughout the chromosomes. The marker data and mapping data here also greatly facilitate trait mapping, map-based cloning of genes for important traits, and marker-aided breeding in rice. The RGP has been regularly updating the present status of rice genome sequencing for each chromosome and each sequencing step. Figure 3 shows the part of the clone status table of chromosome 6. This table indicates each PAC/BAC clone name for its corresponding genetic markers and positions, its neighboring clone names, and status in the sequencing pipeline. Thus, researchers could easily obtain the genome sequence information of a particular clone or region that they are interested in. Another purpose of this status table is to keep the public (both scientific and nonscientific) informed about the status of this publicly funded project. The accession number directly links to the DDBJ entry through which the data are submitted to GenBank and the EMBL database. The RGP Web site also supplies the IRGSP database. Rice genomic sequence data produced by IRGSP members are automatically retrieved from Genbank entries daily, and the present status table from the respective institute and chromosome is updated daily. Therefore, our database also acts as the IRGSP homepage and database. As of 22 June 2002, the cumulative sequence length was 360,909,961 nucleotide base pairs.

The database INE was constructed in 1999 to integrate the genomic information of the RGP and to correlate this information with the rice genome sequence. The graphical user-interface can be viewed by the Web-based browser on desktop PCs so that researchers can easily get information on the rice genome, from genetic to molecular biology scope. On the opening page of INE, upon choosing a specific chromosome, a JAVA-based applet GIOT (Genome Information display Orderly Tool) will open and a specific region in the chromosome can be viewed using sliding windows, which can also be magnified to show the details. The integrated map view of chromosome 1, about 41-45 cM, is shown in Figure 4. From the left as shown here, a linkage map with the genetic markers, a YAC physical map with genetic or EST markers, EST marker positions, and PACBAC alignment for sequencing are displayed. These different types of rice maps are correlated with the corresponding markers. When putting a mouse pointer on a DNA marker, a line that connects the same DNA markers in the different maps appears. Referring to the positions of the

cM	Marker name	Clone name	Status	North clone	South clone	Accession
0-0.9	–	B1162F03	Shotgun	–	P0681G01	–
0.9	C1003B	P0681G01	Finishing	B1162F03	OSJNBa0075G19	–
0.9	C1003B	OSJNBa0075G19	Annotation	P0681G01	P0644B06	AP002842
1.4	S924	P0644B06	Completed	OSJNBa0075G19	P0514G12	AP001129
1.7	G8018	P0514G12	Completed	P0644B06	OSJNBa0004I20	AP000616
1.7–3.1	–	OSJNBa0004I20	Annotation	P0514G12	P0029D06	AP002805
3.1	R2869	P0029D06	Completed	OSJNBa0004I20	P0541H01	AP001522
3.6	S1515	P0541H01	Completed	P0029D06	OSJNBa0019F11	AP001389
3.6	–	OSJNBa0019F11	Annotation	P0541H01	OSJNBa0062J13	AP002837
3.6	E213S	OSJNBa0062J13	Finishing	OSJNBa0019F11	P0660D08	AP003564
3.6–5.1	–	P0660D08	Finishing	OSJNBa0062J13	P0542E10	AP003457
5.1	S2107	P0542E10	Finishing	P0660D08	P0425F02	AP003456
6.0	R3139	P0425F02	Completed	P0542E10	OSJNBa0038F22	AP001168
6.0–6.3	–	OSJNBa0038F22	Annotation	P0425F02	P0538C01	AP002838
6.3	G8010	P0538C01	Completed	OSJNBa0038F22	P0493C11	AP000391
6.9	C425A	P0493C11	Completed	P0538C01	P0679C08	AP000559
7.4	C402	P0679C08	Completed	P0493C11	P0001H02	AP002542
8.2	C76A	P0001H02	Finishing	P0679C08	P0548D03	AP004234
9.0	C52026	P0548D03	Finishing	P0001H02	OSJNBa0041F13	AP003526
9.8	C1084	OSJNBa0041F13	Annotation	P0548D03	P0535G04	AP003708
10.4	R1952	P0535G04	Completed	OSJNBa0041F13	OSJNBa0007020	AP000399
10.4	G8008	OSJNBa0007020	Annotation	P0535G04	P0036F10	AP003487

Fig. 3. Rice chromosome 6 sequencing. Clone status table in the Rice Genome Research Program (RGP) database. Phase 2 clones have the accession numbers for the public database. P = RGP PAC clone; B = RGP BAC clone; OSJNB = CUGI BAC clone.

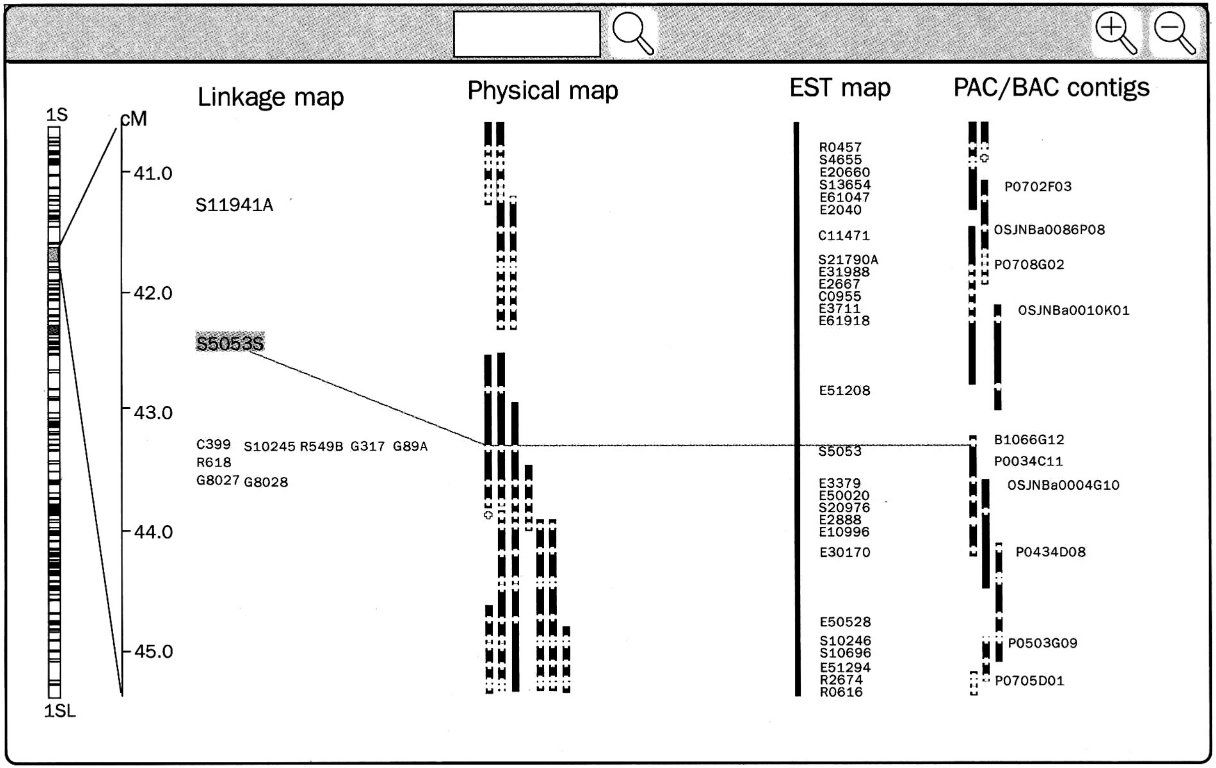


Fig. 4. Integrated map view in INE. From the left, linkage map with the genetic markers, YAC physical map, EST map position, and PAC/BAC contigs for genome sequencing.

same markers, it is feasible to refer to the same region on the different maps. On clicking on the DNA markers, another JAVA applet opens, showing the marker information, which contains the RFLP hybridization images and sequence information from the NIAS DNA bank. On the other hand, clicking on the PAC/BAC clones completed by the RGP will open another applet, which shows the detailed annotation on the clone sequences. The scope of the database in INE is not limited to the completed clones, or six chromosomes, that have been assigned to the RGP. Using IRGSP data retrieved from updated GenBank entries, the PAC/BAC clones from the members other than the RGP are located based on the BLAST hit results against the DNA markers nearby. As these clones, most of which are published in phase 2, were not annotated manually, results from RiceGAAS auto-annotation are linked. In this way, INE could be the only detailed physical map-based annotation browser of the entire genome.

RiceGAAS is a system for an automated annotation and browsing of rice genomic sequence. It automatically analyzes all the rice genomic sequence stored in the database. As of 22 July 2002, the RiceGAAS database had a total entry of 2,797 PAC/BAC clones, 384,460,383 nucleotides, and 72,946 predicted genes. Although some of these sequences may be revised in the future, so far it is a genome-wide annotation database based on all the public sequence. This will help us for the comprehensive survey in terms of gene annotation for the rice genome with the most-updated sequences and databases. We are now incorporating a keyword search service for this database.

Use of the rice genome sequence database in comparative genomics

Since *Arabidopsis* is the only plant genome that is fully sequenced, many endeavors to investigate the relationships between genomes of *Arabidopsis* and crop plants have been made (Devos et al 1999, Mayer et al 2001, Brendel et al 2002), but all failed to find any global colinearity. Rice genome sequencing at phase 2 will be completed within 2002. Since the grass family is categorized as a single genetic system (Freeling 2001), rice sequence information is not only of utmost importance to rice, but also to other grass genomes, including wheat, maize, barley, etc., which are also agronomically important. It may not be easy and practical to sequence the whole genome of these crops because their genomes are large and contain abundant repeats and transposons. The hypothesis of "gene space," which claims that, in Gramineae, the genes in the genome are not evenly distributed (Barakat et al 1997), is an idea of selective analysis of "gene-rich'' regions in maize (Bennetzen et al 2001). Detailed comparison of maize and sorghum sequences indicated good colinearity between segments around orthologous *adh* genes (Tikhonov et al 1999) although there were some gene deletions or severe retrotransposon insertions in the maize genome. Therefore, we could expect a microsyntenic relationship in the closely related species and this would be essential for the characterization of the complex genomes, which are not fully sequenced.

Gene and trait cloning (functional genomics)

The RGP has effectively used our genome resources for gene cloning in collaboration with NIAS and the STAFF-Institute. Using the map-based cloning method, *Xa1* (Yoshimura et al 1998), *Pib* (Wang et al 1999), *d1* (Ashikari et al 1999), *Hd1* (Yano 2000), *Hd6* (Takahashi et al 2001), and *Sp17* (Yamanouchi et al 2002) have been cloned and characterized. Map data and sequence data from the RGP have been accelerating the molecular cloning of the genes for various enzymes and traits.

Comparative studies among cereals will also be helpful in isolating genes for traits. The gene responsible for dwarfism in wheat (*Rht*) was one of the key factors that increased grain yield in the Green Revolution in the 1960s. Using the syntenic relationship among wheat, rice, and maize, and information on *Arabidopsis Gibberellin Insensitive* (GAI) mutant (Koornneef et al 1985), *Rht* and maize *D8* genes for dwarfism have been proven to encode gibberellin-responsive regulators (Peng et al 1999). This wheat-maize synteny was not directly revealed but was revealed using rice ESTs and the rice genetic map as a comparative intermediate. Rice has no gene locus for dwarfism in this syntenic region. However, the rice *slender* gene for rapid growth was mapped to the corresponding region. This gene has been proven to encode SLR (slender rice) protein, an ortholog of GAI (Ikeda et al 2001). The syntenic gene cloning will facilitate isolating agronomically important genes for traits.

Recently, many plant cDNAs and ESTs have been submitted to the public database (263,737 soybean, 225,515 barley, 189,791 wheat, 174,624 *Arabidopsis,* 166,757 maize, 162,741 *Medicago,* and 104,973 rice in database EST entries, as of 12 July 2002). Also, the whole-genome annotation of *Arabidopsis* produced about 25,000 predicted proteins. Comparing these sequences will reveal the similarities and differences in gene structure and functions. Published results indicate that most of the *Arabidopsis* genes have orthologs in rice, but half of the rice genes have no counterparts in *Arabidopsis.* Part of this apparent discrepancy could be caused by an inaccurate prediction of the computer programs, but some of these genes may also correspond to genes unique to monocots. In any case, plants may be more gene-rich than all the genomes that have been sequenced so far. This can be attributed to a lot of factors unique to plants, including the fact that plants must protect themselves without moving into dangerous circumstances. The National Plant Genome Initiative (NPGI) established the *Arabidopsis* 2010 program (Ausubel 2002), which aims to identify the functions of all the genes in *Arabidopsis.* The genome database will be crucial for integrating all the information on genes, traits, proteins, metabolites, and genetic maps to investigate the gene functions of plants, including rice.

DNA marker establishment for crop improvement

DNA markers are most important for marker-assisted breeding. From the era of phenotypic markers, researchers have developed RFLP, microsatellite, randomized amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and CAPS (cleaved amplified polymorphic sequences) for markers. The target of modern breeding, especially in Japan, has been the introgression of segments of the genomes of useful varieties into a closely related variety. In most cases, the low frequency of polymorphism for these markers between the varieties hampered the selection of progenies that have the minimal substituted regions. The single nucleotide polymorphism (SNP) between closely related varieties, recombinant lines, or naturally occurring mutants could identify some candidates for mutations responsible for phenotypic traits using either linkage analysis or association studies. Since rice has a value for application, many competing projects for genome sequencing were carried out from public and private domains. This could make rice a good material for the study of SNPs. Polymorphism (SNPs and In-Dels, insertions-deletions) found in the whole-genome shotgun assembly is 0.67%. Comparison among these rice sequences by either clone-by-clone sequences or whole-genome shotgun sequences will detect these SNPs in either a specific region or overall genome.

A public versus private database

The importance of the rice genome sequence has been well recognized by both the public domain and private sector. Monsanto has sequenced 3,391 rice BACs from Nipponbare, but with only a lower coverage. Syngenta also has sequences from the whole-genome shotgun sequencing from the Nipponbare library. The sequencing efforts of these two companies produced two rice sequence databases that have genome-wide information on rice. Apart from the contribution to the IRGSP, these databases are open to researchers at the company Web sites and are freely available because these companies desire to contribute information to or exchange information with the rice community. However, this does not mean that the information is available unlimitedly to any researcher or breeder. In contrast, the purpose of the public database is free access to the public rice genome data for any researcher.

For this purpose, the IRGSP has an agreement that it improve the draft sequences to IRGSP standards before these sequences are published. This rule also applies to the sequence data that Monsanto and Syngenta have shared with the IRGSP. Through this process, a new relationship between the public and private sector has been established in the rice genome sequencing effort. Compared with the human genome sequencing project, competition has given way to cooperation. The RGP has disclosed both the process for and information on all the sequences.

A recent report on the Proteome Databases of *Caenorhabditis elegans, Saccharo: myces cerevisiae,* and *S. pombe* owned by a company would become a subscription service, which alerts us to the recent tendency that too much dependence is placed upon the private databases (from an editorial in *Nature Genetics,* 31:223-224,2002). The case of the three model proteome databases has made clear the roles from each standpoint, public and private. Public database development and use for researchers, including ones from the private sector, will be the common source of scientific information.

Conclusions

As a publicly funded cooperative project, the IRGSP is scheduled to publish all the phase 2 rice genome sequences and related information in the public database by the end of 2002. The IRGSP will continue efforts to finish (to the phase 3 level) the genome to accomplish the "golden standard" for monocotyledonous plants, especially crop plants. Rice functional genomics, through several methodologies such as proteomics, transcriptomics, and informatics, based on rice genome sequences and various technologies, has become very important. Public databases, together with the private subdatabases, should be the major information sources on rice and plant genome-wide biology for all.

References

Ahn S, Tanksley SD. 1993. Comparative linkage maps of rice and maize genomes. Proc. Natl. Acad. Sci. USA 90:7980-7984.

Arumuganathan K, Earle ED. 1991. Nuclear DNA content of some important species. Plant Mol. Biol. Rep. 9:208-218.

Ashikari M, Wu J, Yano M, Sasaki T, Yoshimura A. 1999. Rice gibberellin-insensitive dwarf mutant gene *dwarf1* encodes the a-subunit of GTP-binding protein. Proc. Natl. Acad. Sci. USA 96:10284-10289.

Ausubel FM. 2002. Summaries of National Science Foundation-sponsored *Arabidopsis* 2010 projects and National Science Foundation-sponsored plant genome projects that are generating *Arabidopsis* resources for the community. Plant Physiol. 129:394-437.

Baba et al. 2000. Construction and characterization of rice genomic libraries: PAC library of Japonica variety Nipponbare and BAC library of Indica variety Kasalath. Bull. Natl. Inst. Agrobiol. Res. 14:41-52.

Barakat A, Carels N, Bernardi G. 1997. The distribution of genes in the genomes of Gramineae. Proc. Natl. Acad. Sci. USA 94:6857-6861.

Barry GF. 2001. The use of the Monsanto draft rice genome sequence in research. Plant Physiol. 125: 1164-1165.

Bennetzen JL, SanMiguel P, Chen MS, Tikhonov A, Francki M, Avramova Z. 1998. Grass genomics. Proc. Natl. Acad. Sci. USA 95:1975-1978.

Bennetzen JL, Chandler VL, Schnable P. 2001. National Science Foundation-sponsored report: maize genome sequencing project. Plant Physiol. 127:1572-1578.

Brendel V, Kurtz S, Walbot V. 2002. Comparative genomics of *Arabidopsis* and maize: prospects and limitations. Genome Biol. 3:1-6.

Burge C, Karlin S. 1997. Prediction of complete gene structures in human genomic DNA. J. Mol. Biol. 268:78-94.

Burr B. 2002. Mapping and sequencing the rice genome. Plant Cell 14:521-523.

Chen M et al. 2002. An integrated physical and genetic map of the rice genome. Plant Cell 14:537-545.

Devos KM, Gale MD. 1997. Comparative genetics in the grasses. Plant Mol. Biol. 35:3-15.

Devos KM, Beales J, Nagamura Y, Sasaki T. 1999. *Arabidopsis*-rice: Will colinearity allow gene prediction across the eudicot-monocot divide? Genome Res. 9:825-829.

Freeling M. 2001. Grasses as a single genetic system: reassessment 2001. Plant Physiol. 125:1191-1197.

Gale MD, Devos KM. 1998. Plant comparative genetics after 10 years. Science 282:656-659.

Goff SA et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Harushima Y et al. 1998. A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics 148:479-494.

Higo K, Ugawa Y, Iwamoto M, Korenaga T. 1999. Plant cis-acting regulatory DNA elements (PLACE) database. Nucleic Acids Res. 27:297-300.

Ikeda A, Sonoda Y, Vernieri P, Perata P, Hirochika H, Yamaguchi J. 2001. *Slender* rice, a constitutive gibberellin response mutant, is caused by a null mutation of the *SLR1* gene, an ortholog of the height-regulating gene *GAI/RGA/RHT/D8.* Plant Cell 13:999-1010.

Koornneef M et al. 1985. A gibberellin insensitive mutant of *Arabidopsis thaliana.* Physiol. Plant. 65:33-39.

Mayer K et al. 2001. Conservation of microstructure between a sequenced region of the genome of rice and multiple segments of the genome of *Arabidopsis thaliana.* Genome Res. 11:1167-1174.

NSTC (The National Science and Technology Council). 2001. Progress report for National Plant Genome Initiative 2001. Washington, D.C. (USA): NSTC. 1 p.

Peng J et al. 1999. "Green revolution " genes encode mutant gibberellin response modulators. Nature 400:256-261.

Saji S et al. 2001. A physical map with yeast artificial chromosome (YAC) clones covering 63% of the 12 rice chromosomes. Genome 44:32-37.

Sakata K et al. 2000a. RiceHMM: gene domain prediction program for rice genome sequence. Abstracts of 4th annual conference on computational genomics. p 31.

Sakata K, Antonio BA, Mukai Y, Nagasaki H, Sakai Y, Makino K, Sasaki T. 2000b. INE: a rice genome database with an integrated map view. Nucleic Acids Res. 28:97-101.

Sakata K, Nagamura Y, Numa H, Antonio BA, Nagasaki H, Idonuma A, Watanabe W, Shimizu Y, Horiuchi I, Matsumoto T, Sasaki T, Higo K. 2002. RiceGAAS: an automated annotation system and database for rice genome sequence. Nucleic Acids Res. 30:98-102.

Salamov A, Solovyev V. 2000. Ab initio gene finding in *Drosophila* genomic DNA. Genome Res. 10:516-522.

Sasaki T, Burr B. 2000. International Rice Genome Sequencing Project: the effort to completely sequence the rice genome. Curr. Opin. Plant Biol. 3:138-141.

Takahashi Y, Shomura A, Sasaki T, Yano M. 2001. *Hd6,* a rice quantitative trait locus involved in photoperiod sensitivity, encodes the a-subunit of protein kinase CK2. Proc. Natl. Acad. Sci. USA 98:7922-7927.

The Arabidopsis Genome Initiative. 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana.* Nature 408:796-815.

Tikhonov AP et al. 1999. Colinearity and its exceptions in orthologous *adh* regions of maize and sorghum. Proc. Natl. Acad. Sci. USA 96:7409-7414.

Wang A-X, Yano M, Yamanouchi U, Iwamoto M, Monna L, Hayasaka H, Katayose Y, Sasaki T. 1999. The *Pib* gene for rice blast resistance belongs to the nucleotide binding and leucine-rich repeat class of plant disease resistance genes. Plant J. 19:55-64.

Ware D. 2002. Gramene: a resource for comparative grass genomics. Nucleic Acids Res. 30:103-105.

Wing R. 1996. www.genome.clemson.edu/where/nippon bac/index.html.

Wu J et al. 2002. A comprehensive rice transcript map containing 6591 expressed sequence tag sites. Plant Cell 14:525-535.

Yano M. 2000. *Hd1,* a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the *Arabidopsis* flowering time gene *CONSTANS.* Plant Cell 12:2473-2484.

Yamamoto K, Sasaki T. 1997. Large-scale EST sequencing in rice. Plant Mol. Biol. 35:135-144.

Yamanouchi U, Yano M, Hongxuian L, Ashikari M, Yamada K. 2002. A rice leaf gene, *Spl7,* encodes a heat stress transcription factor. Proc. Natl. Acad. Sci. USA 99:7530-7535.

Yano M. 2000. The latest high-density rice genetic map, including 3267 markers. http://rgp.dna.affrc.go.jp.publicdata/genetic map2000/index.html (Web site presentation).

Yoshimura S et al. 1998. Expression of *Xa1,* a bacterial blight–resistance gene in rice, is induced by bacterial inoculation. Proc. Natl. Acad. Sci. USA 95:1663-1668.

Yu J et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science 296:79-92.

Notes

Authors' addresses: T. Matsumoto, Y. Katayose, K. Yamamoto, K. Sakata, and T. Sasaki, Rice Genome Research Program, National Institute of Agrobiological Sciences, 2-1-2, Kannondai, Tsukuba, Ibaraki 305-8602, Japan; J. Wu, N. Namiki, Rice Genome Research Program, STAFF Institute, Ippaizuka, Kamiyokoba, Tsukuba, Ibaraki 305-0854, Japan.

Acknowledgments: The authors wish to thank our many colleagues in the RGP for collaborating in this study. This work was supported by the MAFF Rice Genome Project grants (GS-1101, 1103, 1201, 1302).

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Annotation of the rice genome: producing relevant information for plant biologists

C.R. Buell

Rice is the most important food staple in the world and is a tractable model for understanding plant biology in monocots, especially grass species. The rice genome has been sequenced by several entities, both public and private. With access to the complete rice genome, it will be possible to answer questions at a genome level rather than the previous “one gene at a time.” However, although the sequence of the rice genome is available, the utility of the genome sequence for the general plant community is limited without the annotation of the underlying nucleotide sequence. Annotation involves the identification of genes, regulatory sequences, the assignment of putative function, the assignment of gene ontologies, expression patterns, and the identification of paralogs and orthologs. At The Institute for Genomic Research (TIGR), we have developed a robust annotation database for rice that enables users to develop physical maps of local regions of the rice genome, search the publicly available rice sequence for genes of interest, identify related orthologs and paralogs, and identify domains within the rice proteome. This collective set of tools provides an entry point for biologists into the rice genome.

The rice genome is estimated to be 430 Mb in size (Arumuganathan and Earle 1991). In addition to recent reports on the production of the rice genome sequence, several resources have been constructed to facilitate the understanding and dissection of the rice genome. These include construction of a dense genetic map, generation of expressed sequence tags (ESTs), and construction of yeast artificial chromosome (YAC), bacterial artificial chromosome (BAC), and P1 artificial chromosome (PAC) libraries and physical maps. These resources, coupled with a complete genome sequence, will allow for rice to be fully developed into a robust model organism for monocotyledonous plants.

A dense genetic map for rice with 2,275 markers covering 1,521 cM was developed using an F_2 population derived from a cross between *O. sativa* subsp. *japonica* var.

Nipponbare and subsp. *indica* var. Kasalath (Harushima et al 1998). In addition, high-density YAC and BAC physical maps are available for rice (Chen et al 2002, Kurata et al 1997). The initial YAC map was constructed using YACs made from *O. sativa* subsp. *japonica* var. Nipponbare and spanned an estimated 52% of the rice genome (Kurata et al 1997). The current YAC map has been anchored with 6,591 ESTs and provides an estimated 80% coverage of the rice genome (Wu et al 2002). BACs from two Nipponbare libraries have been fingerprinted and clustered into contigs based on fingerprint similarity using the FPC program (Chen et al 2002). The BAC physical map of the rice genome covers 90% of the genome (Chen et al 2002). BAC end sequences have been produced from these two Nipponbare libraries and a total of 88,054 BAC end sequences representing 54.7 Mb have been submitted to Genbank (www.genome.clemson.edu/ews.html).

The genetic and physical maps described above provide a resource for further genomic efforts such as EST sequencing, transcript mapping, and whole-genome sequencing. For ESTs, a wide range of rice tissues have been sampled. As of 7 June 2002, there are 106,134 rice ESTs in the EST section of Genbank (dbEST release 060702; www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html). A majority of the rice ESTs in Genbank are from the subspecies japonica and recently the Beijing Genomics Institute (BGI) released 86,623 ESTs from the indica subspecies (http://210.83.138.53/rice/download.php). The number of unique sequences represented in these ESTs can be determined through clustering and assembly processes such as the TIGR gene indices (Quackenbush et al 2000,2001). In the current release of the TIGR Rice Gene Index (Release 9.0; www.tigr.org/tdb/tgi/ogi/release_notes.html), 117,222 rice ESTs and expressed transcripts (ETs) could be reduced to 38,032 unique sequences with 13,745 tentative consensus (TC) sequences, 5,831 singleton ETs, and 18,456 singleton ESTs.

The rice genome has been (is being) sequenced four times. The first report of a draft of the rice genome was made by the Monsanto corporation and the sequence was done using draft sequencing of BAC clones from *O. sativa* subsp. *japonica* var. Nipponbare (Barry 2001). The Monsanto draft provides about 60% coverage (259 Mb) of the rice genome and access to these data is available to academic entities through a licensing agreement (Barry 2001; www.rice-research.org). The second report of a draft of the rice genome was that of the Syngenta corporation. As with Monsanto, Syngenta sequenced the Nipponbare cultivar; however, instead of a BAC-by-BAC approach, Syngenta used a whole-genome draft approach (Goff et al 2002). As with the Monsanto draft, the Syngenta sequence can be accessed by academic laboratories through a licensing agreement. In 2002, there was a third report of a draft version of the rice genome. However, this sequencing was done using cultivar 93-11 of the indica subspecies by the BGI (Yu et al 2002). The 5X draft sequence of 93-11 is available from the BGI Web site. The fourth and most complete draft sequence of the rice genome is being determined by the International Rice Genome Sequencing Project (IRGSP), which is a consortium of laboratories focused on producing a high-quality sequence of the rice genome (Sasaki and Burr 2000). The approach of the IRGSP is that of a BAC-by-BAC approach using the Nipponbare cultivar of *japonica.*

The estimated completion date for a high-quality draft (10X) by the IRGSP is December 2002. As of 18 June 2002, the IRGSP had completed an estimated 84% of the rice genome (www.tigr.org/tdb/e2kl/osal/BACmapping/description.shtml). All of the IRGSP sequence is available through public databases such as Genbank, DDBJ (DNA Data Bank of Japan), and EMBL (European Molecular Biology Laboratory).

What is annotation?

Annotation is simply the addition of notes or descriptive features. In genome annotation, this typically means the identification of genes, coding regions, promoters, domains, regulatory regions, functions, orthologs, paralogs, and anything else of biological relevance. Annotation can involve solely computational approaches and or be manually curated by experts in bioinformatics and biological processes. Annotation is not delved into lightly and any consideration of the extent of manual annotation must involve the quality of the sequence, the robustness of the computational applications, and the availability of other biological data to attach to the genome sequence. The shear volume of sequence data for an organism such as rice, coupled with the draft nature of the current public rice genome sequence, warrants an initial automated annotation of the whole genome followed by manual curation where the sequence quality is high, that is, finished.

TIGR rice genome annotation

At TIGR, we have developed extensive resources for the annotation of the rice genome, all of which are built on the availability of publicly generated sequences from the IRGSP. Our annotation methods and our underlying database are the results of our experience from annotation of other eukaryotic genomes, including the human and *Arabidopsis*. As a consequence, we have robust protocols and methodologies for annotating a genome such as rice.

Locating the BAC within the genome

The first level of rice annotation is the assignment of a BACPAC sequence to a chromosome and a map position either using an anchored genetic marker or by identifying overlapping rice BAC clones that are also anchored. At TIGR, we routinely download all new rice BACPAC sequences from Genbank, search them against the available genetic markers, and, using high-stringency cutoff criteria, anchor them to one of the 12 rice chromosomes (www.tigr.org/tdb/e2kl/osal/BACmapping/description.shtml). We provide multiple levels of output for these data, including a graphic depiction of the progress of the IRGSP, a graphic display of the anchoring of the rice BACs to the 12 rice chromosomes, and tables and search tools for users to readily identify a BAC of interest using known genetic markers (www.tigr.org/tdb/e2kl/osa1/BACmapping/description.shtml). As of 18 June 2002, we have been able to anchor 2,347 BACsPACs representing 327 Mb (76% of the genome) to 10,675 markers in the rice genome.

Construction of gene models

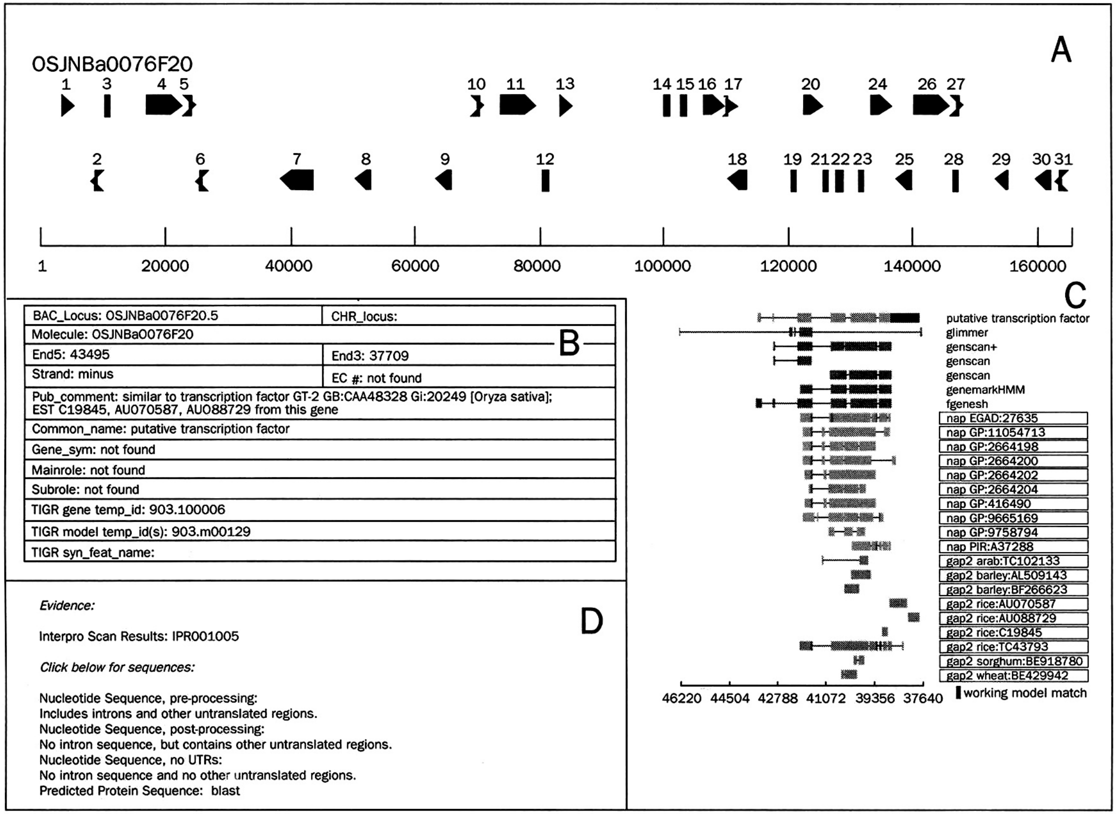
The second level of annotation is the development of gene models within a nucleotide sequence. Two distinct types of computational output are used to produce a gene model. The first is *ab initio* gene prediction programs that rely solely on computational methods to identify a gene. In rice, several gene prediction programs are available: FGENESH (www.softbeny.com), Genemark.hmm (rice matrix; http://opal.biology.gatech.edu/GeneMark/eukhmm.cgi), Genscan (maize matrix; http://genes.mit.edu/GENSCAN.html), Genscan+ (*Arabidopsis* matrix; http://genes.mit.edu/GENSCAN.html), and GlimmerM (rice matrix; www.tigr.org/tdb/glimmerm/glm_form.html). In addition to the output from these computational programs, the sequence is searched against DNA and protein sequence databases to identify genes with sequence similarity. The sequence is processed through two other computational programs—tRNAscan-SE (Lowe and Eddy 1997) and RepeatMasker2 (Smith AFA and Green P, unpublished; http://ftp.genome.washington.edu/RM/RepeatMasker.html)—to identify tRNAs and simple repeats, respectively. These programs provide additional information on structural RNAs and distribution of repetitive sequences.

To provide the plant community with a uniform level of annotation for the rice genome, we have developed an automated annotation pipeline for rice. In our current rice annotation database (11 June 2002), we have annotation data for 1,768 BACs representing 242 Mb of rice genomic DNA sequence. In our current whole-genome annotation database, we have identified a total of 39,509 genes with an average gene length of 2.51 kb. We have been able to assign a putative function to 70% of the genes, leaving 0.6% as unknown (EST match only) and 29.4% as hypothetical. On average, we were able to identify a gene every 6.1 kbp in the rice genome, suggesting that in total there are 63,442 genes in the rice genome based on the assumption of a 430-Mb genome with about 10% of the genome encoding large tracts of noncoding repetitive sequences such as within the centromere and telomere.

We manually curate BACs that have been finished and are free of sequencing gaps and other errors. Figure 1 shows an example of a manually curated BAC. BACs that are still unfinished (as defined by the sequencing center and the division of Genbank/DDBJ/EMBL in which it is placed) are annotated using only our automated annotation pipeline. Our automated annotation pipeline is rather robust in the identification of the genes as shown by a comparison of annotation results from manually curated versus automated annotation (Table 1).

Construction of motif and domain catalogs for the rice proteome

Putative functions can be assigned to some proteins on the basis of the presence of specific domains or motifs such as transmembrane domains or catalytic sites. We have identified motifs and domains in the rice proteome using algorithms such as SignalP (Nielsen et al 1997) and TMHMM V2.0 (Krogh et al 2001) and by searching the rice proteome against the Pfam (Bateman et al 2002) and ProSite databases (Falquet et al 2002). The precomputed results are available through multiple search tools on the TIGR Rice Genome Web pages, thereby allowing researchers to readily



BAC_Locus: OSJNBa0076F20.5	CHR_locus:
Molecule: OSJNBa0076F20	
End5: 43495	End3: 37709
Strand: minus	EC #: not found
Pub_comment: similar to transcription factor GT-2 GB:CAA48328 Gi:20249 [Oryza sativa]; EST C19845, AU070587, AU088729 from this gene	
Common_name: putative transcription factor	
Gene_sym: not found	
Mainrole: not found	
Subrole: not found	
TIGR gene temp_id: 903.100006	
TIGR model temp_id(s): 903.m00129	
TIGR syn_feat_name:	

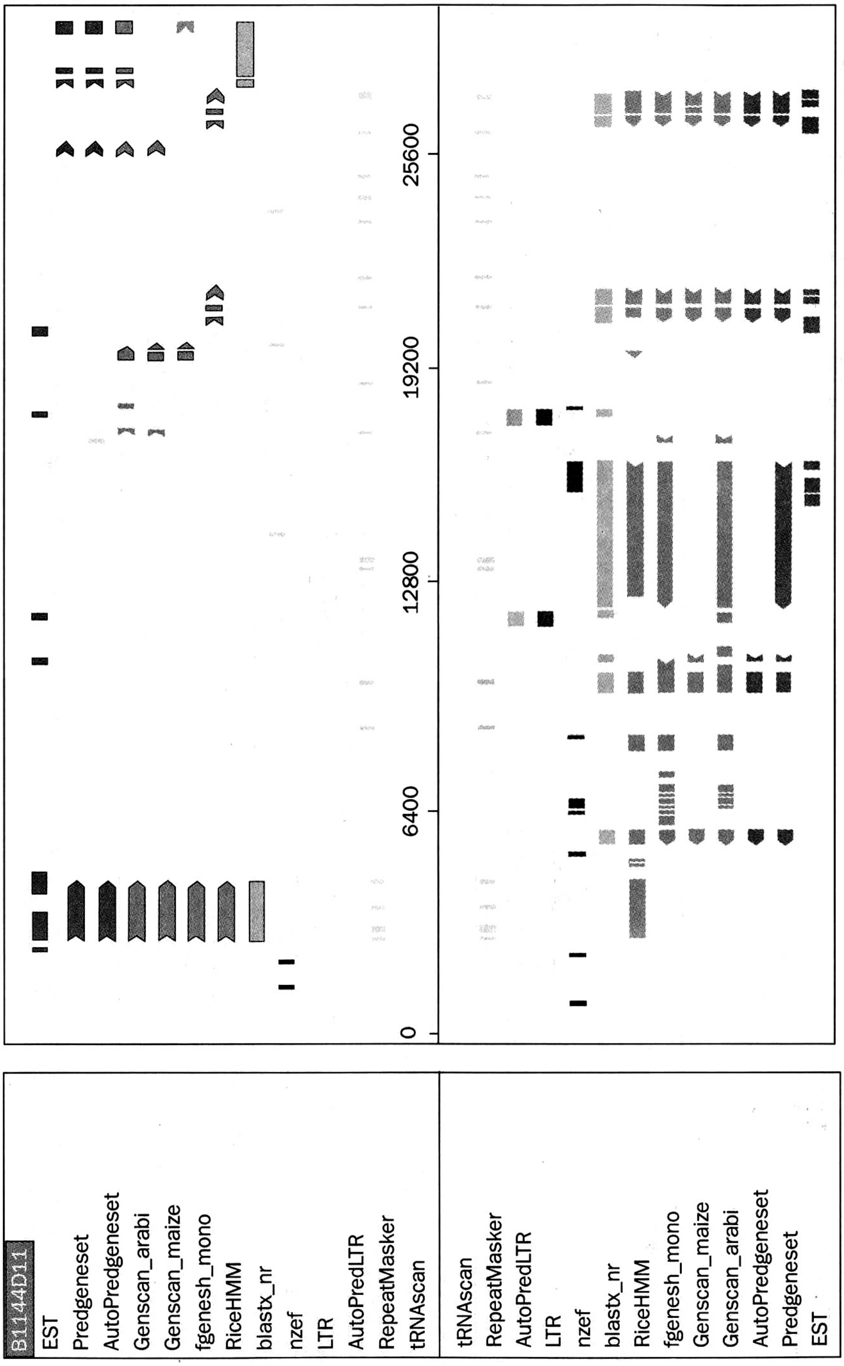
Evidence:

Interpro Scan Results: IPR001005

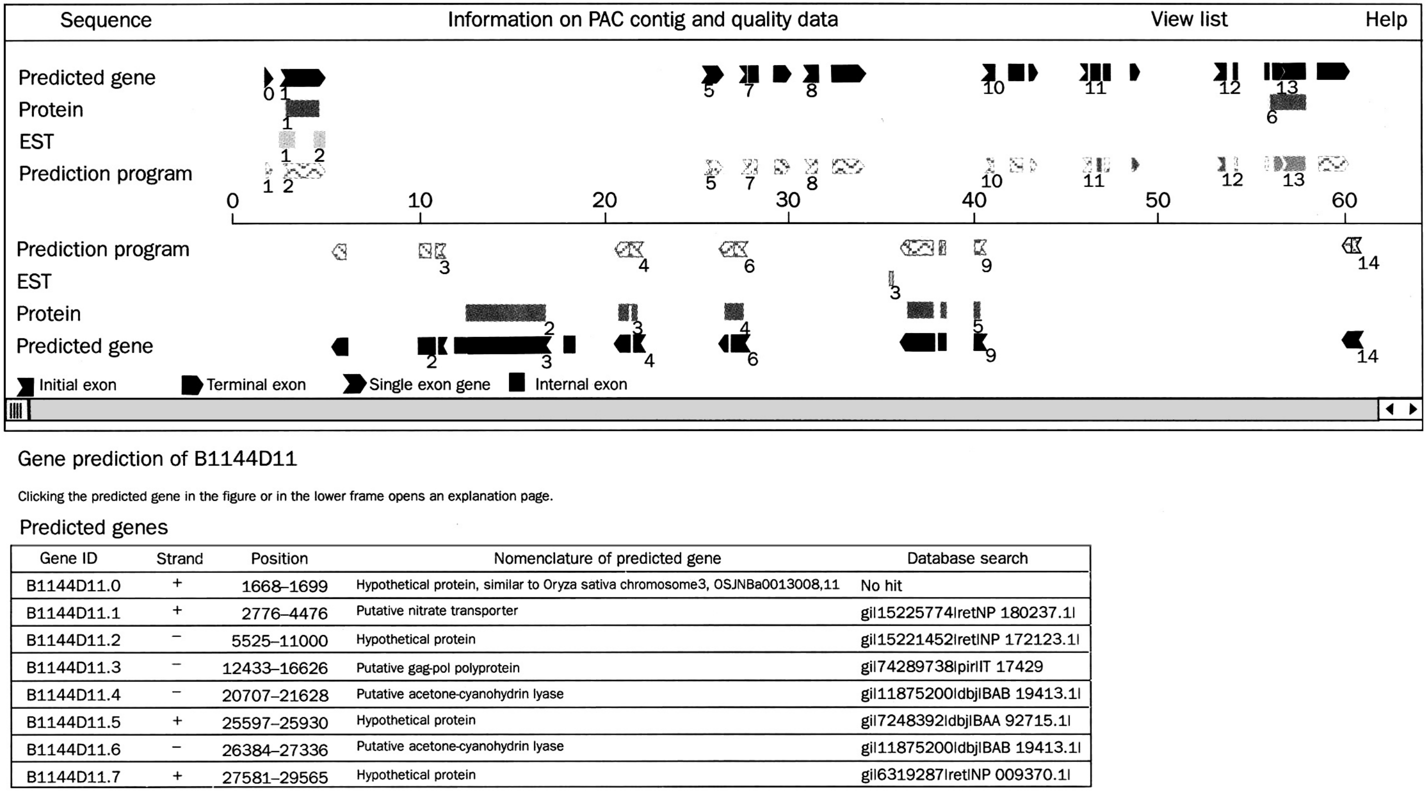
Click below for sequences:

Nucleotide Sequence, pre-processing:
Includes introns and other untranslated regions.
Nucleotide Sequence, post-processing:
No intron sequence, but contains other untranslated regions.
Nucleotide Sequence, no UTRs:
No intron sequence and no other untranslated regions.
Predicted Protein Sequence: blast

Fig. 1. Depiction of the annotation of a manually curated rice bacterial artificial chromosome (BAC). The BAC is OSJNBa0076F20 and can be viewed online at www.tigr.ork/tigr-scripts/e2k1/nbac_dispiay.spl?db=osa1&name=OSJNBa0076F20&asmbi_id=903. Panel A: Graphic view of all the gene models located on the BAC. Panel B: Annotation notes associated with model OSJNBa0076F20.5. Panel C: Gene model, gene prediction output, and database search results for OSJNBa0076F20.5. The working (final) model is drawn on top with the output from the five gene prediction programs below, followed by the output from the database searches. Similarity to entries in the nonredundant amino acid database is prefixed with nap and similarity to ESTs is prefixed with gap2. Panel D: Links to domain information and sequence of the gene and predicted protein.



continued on next page



Gene prediction of B1144D11

Clicking the predicted gene in the figure or in the lower frame opens an explanation page.

Predicted genes

Gene ID	Strand	Position	Nomenclature of predicted gene	Database search
B1144D11.0	+	1668–1699	Hypothetical protein, similar to Oryza sativa chromosome3, OSJNBa0013008,11	No hit
B1144D11.1	+	2776–4476	Putative nitrate transporter	gi|15225774|retNP 180237.1|
B1144D11.2	–	5525–11000	Hypothetical protein	gi|15221452|ret|NP 172123.1|
B1144D11.3	–	12433–16626	Putative gag-pol polyprotein	gi|74289738|pir|IT 17429
B1144D11.4	–	20707–21628	Putative acetone-cyanohydrin lyase	gi|11875200|dbj|BAB 19413.1|
B1144D11.5	+	25597–25930	Hypothetical protein	gi|7248392|dbj|BAA 92715.1|
B1144D11.6	–	26384–27336	Putative acetone-cyanohydrin lyase	gi|11875200|dbj|BAB 19413.1|
B1144D11.7	+	27581–29565	Hypothetical protein	gi|6319287|ret|NP 009370.1|

Fig. 2. Annotation map view. Previous page: results of the auto-annotation by RiceGAAS. This page: results of the manual curation of the RiceGAAS output and functional characterization of the predicted genes.

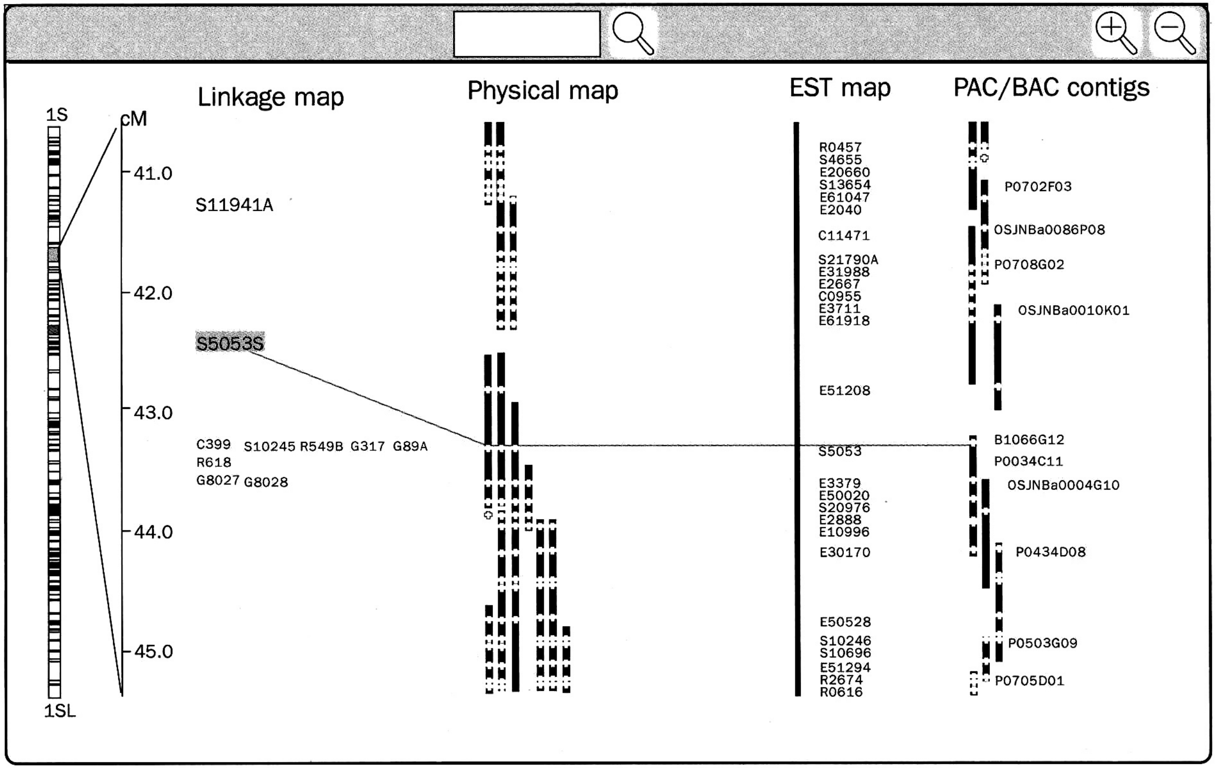
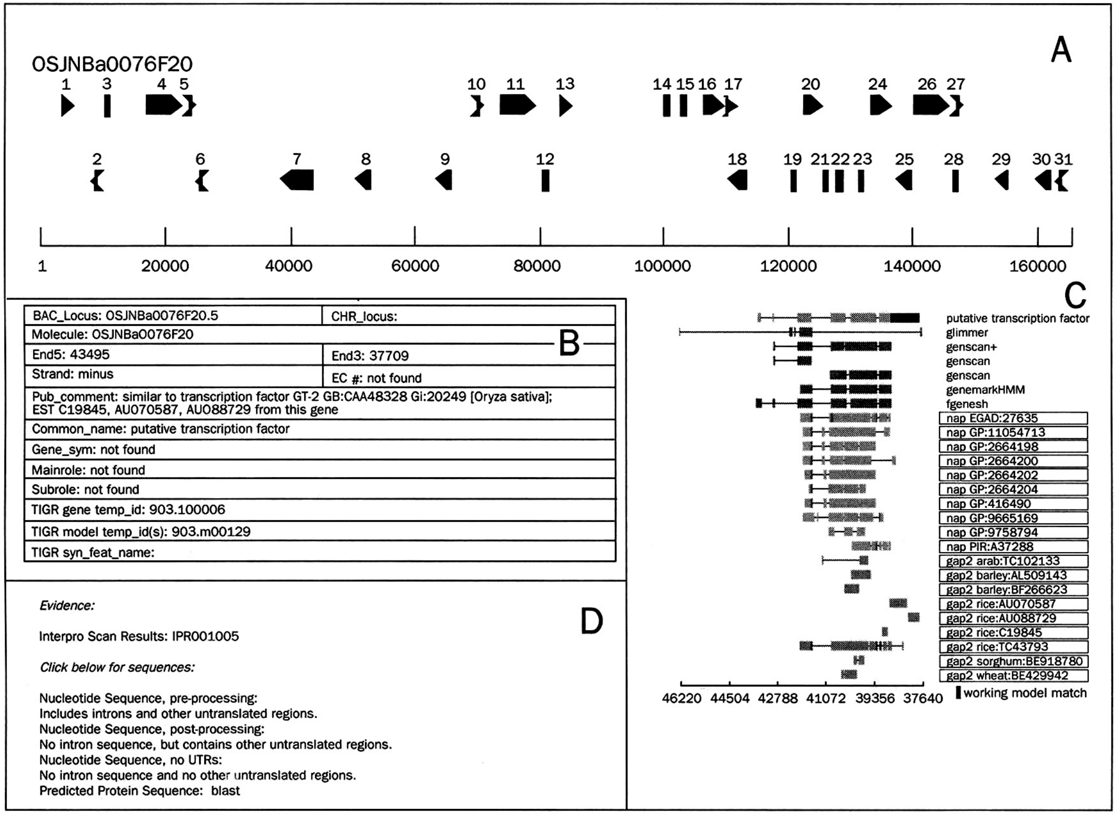


Fig. 4. Integrated map view in INE. From the left, linkage map with the genetic markers, YAC physical map, EST map position, and PAC/BAC contigs for genome sequencing.



BAC_Locus: OSJNBa0076F20.5
CHR_locus:
Molecule: OSJNBa0076F20
End5: 43495
End3: 37709
Strand: minus
EC #: not found
Pub_comment: similar to transcription factor GT-2 GB:CAA48328 Gi:20249 [Oryza sativa]; EST C19845, AU070587, AU088729 from this gene
Common_name: putative transcription factor
Gene_sym: not found
Mainrole: not found
Subrole: not found
TIGR gene temp_id: 903.100006
TIGR model temp_id(s): 903.m00129
TIGR syn_feat_name:

Evidence:

Interpro Scan Results: IPR001005

Click below for sequences:

Nucleotide Sequence, pre-processing:
Includes introns and other untranslated regions.
Nucleotide Sequence, post-processing:
No intron sequence, but contains other untranslated regions.
Nucleotide Sequence, no UTRs:
No intron sequence and no other untranslated regions.
Predicted Protein Sequence: blast

Fig. 1. Depiction of the annotation of a manually curated rice bacterial artificial chromosome (BAC). The BAC is OSJNBa0076F20 and can be viewed online at www.tigr.ork/tigr-scripts/e2k1/nbac_dispiay.spl?db=osa1&name=OSJNBa0076F20&asmbi_id=903. Panel A: Graphic view of all the gene models located on the BAC. Panel B: Annotation notes associated with model OSJNBa0076F20.5. Panel C: Gene model, gene prediction output, and database search results for OSJNBa0076F20.5. The working (final) model is drawn on top with the output from the five gene prediction programs below, followed by the output from the database searches. Similarity to entries in the nonredundant amino acid database is prefixed with nap and similarity to ESTs is prefixed with gap2. Panel D: Links to domain information and sequence of the gene and predicted protein.

Table 1. Summary of TIGR rice genome annotation.

Features[a]	Manually curated	Automated	Total
Number of BACs	89	1,679	1,768
Total BAC length (bp)	12,264,076	229,293,936	241,558,012
Total number of genes	2,113	37,396	39,509
Average BAC GC content (%)	43.4	43.4	43.4
Average gene GC content (%)	46.8	46.4	46.5
Average intergenic region GC content (%)	40.9	41.3	41.3
Average exon GC content (%)	55.0	53.6	53.6
Average intron GC content (%)	38.7	38.7	38.7
Average gene size (bp)	2,471	2.510	2,508
Gene density (bp per gene)	5,804	6,131	6,113
Total number of known genes	1,078 (51%)	26.449 (70.8%)	27,527 (69.7%)
Average known gene size (bp)	3,158	3,019	3,025
Total number of unknown genes	170 (8%)	57 (0.2%)	227 (0.6%)
Average unknown gene size (bp)	2,429	2,528	2,453
Total number of hypothetical genes	865 (41%)	10,890 (29%)	11,755 (29.7%)
Average hypothetical gene size (bp)	1,622	1,272	1,298
Average exon size (bp)	284	305	303
Average intron size (bp)	376	365	366

[a] BAC = bacterial artificial chromosome, GC = guanine-cytosine.

identify genes of interest within the rice proteome based solely on motif/domain information (www.tigr.org/tigr-scripts/e2kl/irgsp.spl).

Construction of a rice repeat database

In genome annotation, the identification of repetitive sequences can be important because repetitive sequences complicate database searches. To meet this need, we constructed the TIGR Rice Repeat Database, which contains a comprehensive set of known repetitive elements in the rice genome and includes transposable elements, centromeric repeats, telomeric repeats, and rDNA sequences. To construct this database, known repetitive sequences from rice and closely related monocot species were downloaded from public databases and were categorized into superclasses, classes, and subclasses depending on sequence identity and structure. Using this set of grass repetitive sequences as the query, we searched about 190 Mb of rice genomic DNA and were able to expand the database by identifying orthologs and paralogs within the rice genome. We were able to identify rice orthologs for all of the superclasses of repetitive elements, with the transposable element class being the largest in terms of number and size within the rice genome. The final TIGR Rice Repeat Database, which contains only rice repetitive sequences, contains 19,087 entries representing 7.7 Mb. This database is available for BLAST searches and can be downloaded through FTP (File Transfer Protocol) (www.tigr.org/tdb/e2k1/osal/blastsearch.shtml).

Table 2. Representation of orthologs of rice genes in the EGO (Eukaryotic Gene Orthologs) Database.

EGOpair	Number of pairs	Percent identity
Rice-maize	2,907	78.6
Rice-wheat	2,378	79.5
Rice-sorghum	2,592	78.4
Rice-barley	2,194	78.3
Rice-rye	683	80.1
Rice-*Arabidopsis*	2,070	69.9

Identification of related sequences in other plant species, including orthologs and paralogs

To maximally leverage the rice genome to that of other plant species, we provide a low level of annotation for the rice genome by searching all of the rice BACs against the available TIGR plant gene indices, which are clustered and assembled sequences from 12 publicly available plant EST projects. The alignments are displayed graphically, providing a global alignment of rice BACs with those of other plant genomes (www.tigr.org/tdb/ogi/alignTC.html). As we are aware that there is a reduced degree of sequence identity among the monocots and dicots, we use lower stringencies than used in our annotation pipeline, thereby providing as much information as possible to users.

To provide a more stringent set of alignments between genomes, TIGR has developed the Eukaryotic Gene Orthologs (EGO) Database using a reciprocal top-hit method in which the TIGR plant gene indices are used to identify candidate orthologs and paralogs (Lee et al 2002; www.tigr.org/tdb/tgi/ego/index.shtml). As a large number of rice and other cereal ESTs are represented in the TIGR gene indices, we have been able to identify a large number of candidate orthologs (Table 2). In total, we have been able to identify 10,754 candidate orthologs of rice in five cereal species (maize, wheat, barley, rye, and sorghum) and 2,070 candidate orthologs in *Arabidopsis.*

Development of syntenic maps

The genomes of the major cereal species are highly collinear and the availability of the rice genome sequence provides a foundation for comparative genomics among the cereals (Gale and Devos 1998, Freeling 2001). In addition, the production of syntenic maps between the cereals is critical as the genome size of most cereal species is prohibitive for full genome sequencing. To produce syntenic maps between rice and maize, we aligned all available rice BACsPACs to the rice genetic map and to publicly available maize genetic markers. Using 1,259 maize genetic marker sequences from the Missouri MaizeDB database (www.agron.missouri.edu/focused.html) and following trimming of polyA/polyT or N sequences from the ends of the maize markers, we identified a total of 331 marker sequences in maize that align with the rice genome. As shown in Figure 2, rice chromosome 1 is highly syntenic with maize chromosomes 3 and 8. In total, we estimate that about 60% of the maize markers are syntenic with their homologous chromosome in rice.

Construction of a distributed annotation system for rice

Currently, our annotation data are available primarily through the TIGR Rice Genome Web site although annotation data for finished BACs are deposited in Genbank. We do provide an FTP site at which users can download sequences (DNA and peptide). To expand access to our annotation, we have developed a Distributed Annotation System (DAS; www.tigr.org/tigr-scripts/nhgi_scripts/dasView/dasview_rice_chrl). Through the DAS, annotation of the rice BACs, along with alignments of the rice BACs with genetic markers, and alignments of the BACs with the TIGR plant gene indices are provided.

Prospects for improvements in rice genome annotation

As with other genome projects, the production of high-quality annotation requires substantial funding and efforts that are typically outside the scope of a genome sequencing project. The assumption that, once the nucleotide sequence is unveiled, the annotation should be readily available is widely held in the scientific community. Thus, the delay in availability of high-quality annotation for a genome of interest such as rice is always troubling for the general scientific community. The current reality is that annotation requires the development of computational processes and the availability of a comprehensive set of experimental data such as ESTs, full-length cDNAs, mutagenesis data, gene expression data, etc. These are just now being developed for rice on a whole-genome level and, with continued funding and access to more experimental evidence, the rice genome can be annotated to a high level and consequently become the robust model organism for monocotyledonous plants that it should be.

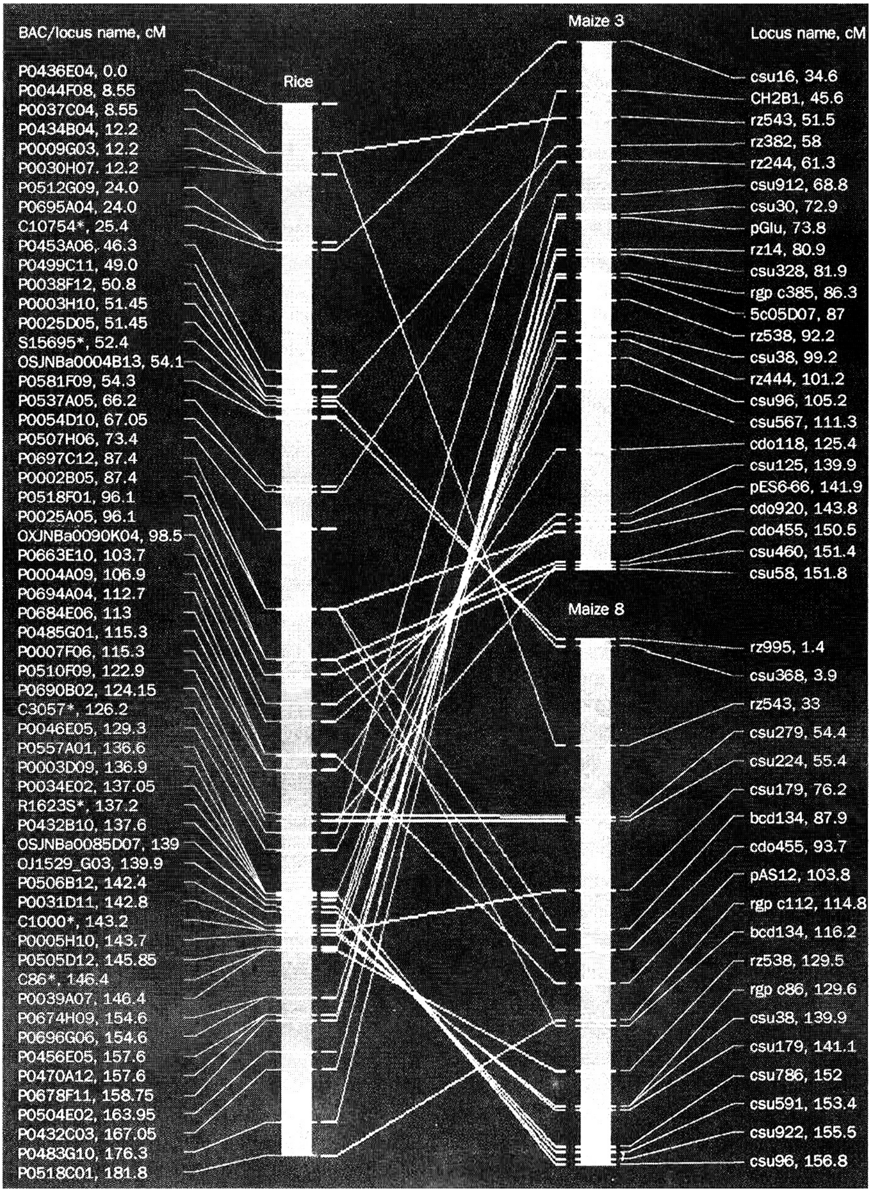


Fig. 2. Syntenic mapping of maize genetic markers to rice genomic sequences on rice chromosome 1. Maize map and sequence information for 1,259 markers were obtained from Missouri MaizeDB database or Genbank. The position of the rice bacterial artificial chromosome/P1 artificial chromosome (BAC/PAC) clones was determined by alignment of the rice genetic markers obtained from the Japanese Rice Genome Program and Cornell RiceGenes Database. Significant homology between rice and maize sequences is depicted by a line connecting rice and maize chromosome regions. The position of rice BACs/PACs and maize genetic markers is indicated by cM.

References

Arumuganathan K, Earle ED. 1991. Nuclear DNA content of some important plant species. Plant Mol. Biol. Rep. 9:208-219.

Barry GF. 2001 The use of the Monsanto draft rice genome sequence in research. Plant Physiol. 125:1164-1165.

Bateman A, Birney E, Cerruti L, Durbin R, Etwiller L, Eddy SR, Griffiths-Jones S, Howe KL, Marshall M, Sonnhammer ELL. 2002. The Pfam protein families database. Nucl. Acids Res. 30:276-280.

Chen M, Presting G, Barbazuk B, and 37 other authors. 2002. An integrated physical and genetic map of the rice genome. Plant Cell 14:537-545.

Falquet L, Pagni M, Bucher P, Hulo N, Sigrist CJ, Hofmann K, Bairoch A. 2002. The PROSITE database, its status in 2002. Nucl. Acids Res. 30:235-238.

Freeling M. 2001. Grasses as a single genetic system. Plant Physiol. 125:1191-1197.

Gale MD, Devos KM. 1998. Comparative genetics in the grasses. Proc. Natl. Acad. Sci. USA 95:1971-1974.

Goff SA, Ricke D, Lan TH, Presting G, Wang R, Dunn M, Glazebrook J, Sessions A, Oeller P, Varma H, Hadley D, Hutchison D, Martin C, Katagiri F, Lange BM, Moughamer T, Xia Y, Budworth P, Zhong J, Miguel T, Paszkowski U, Zhang S, Colbert M, Sun WL, Chen L, Cooper B, Park S, Wood TC, Mao L, Quail P, Wing R, Dean R, Yu Y, Zharkikh A, Shen R, Sahasrabudhe S, Thomas A, Cannings R, Gutin A, Pruss D, Reid J, Tavtigian S, Mitchell J, Eldredge G, Scholl T, Miller RM, Bhatnagar S, Adey N, Rubano T, Tusneem N, Robinson R, Feldhaus J, Macalma T, Oliphant A, Briggs S. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush GS, Sasaki T. 1998. A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics 148:479-494.

Krogh A, Larsson B, von Heijne G, Sonnhammer ELL. 2001. Predicting transmembrane protein topology with a hidden Markov model: application to complete genomes. J. Mol. Biol. 305:567-580.

Kurata N, Umehara Y, Tanoue H, Sasaki T. 1997. Physical mapping of the rice genome with YAC clones. Plant Mol. Biol. 35:101-113.

Lee Y, Sultana R, Pertea G, Cho J, Karamycheva S, Tsai J, Parvizi B, Cheung F, Antonescu V, White J, Holt I, Liang F, Quackenbush J. 2002. Cross-referencing eukaryotic genomes: TIGR Orthologous Gene Alignments (TOGA). Genome Res. 12:493-502.

Lowe TM, Eddy SR .1997. tRNAscan-SE: a program for improved detection of transfer RNA genes in genomic sequence. Nucl. Acids Res. 25:955-964.

Nielsen H, Engelbrecht J, Brunak S, von Heijne G. 1997. Identification of prokaryotic and eukaryotic signal peptides and prediction of their cleavage sites. Protein Eng. 10: 1-6.

Quackenbush J, Liang F, Holt I, Pertea G, Upton J. 2000. The TIGR gene indices: reconstruction and representation of expressed gene sequences. Nucl. Acids Res. 28:141-145.

Quackenbush J, Cho J, Lee D, Liang F, Holt I, Karamycheva S, Parvizi B, Pertea G, Sultana R, White J. 2001. The TIGR Gene Indices: analysis of gene transcript sequences in highly sampled eukaryotic species. Nucl. Acids Res. 29: 159-164.

Sasaki T, Burr B. 2000. International Rice Genome Sequencing Project: the effort to completely sequence the rice genome. Curr. Opin. Plant Biol. 3: 138-141.

Wu J, Maehara T, Shimokawa T, and 16 other authors. 2002. A comprehensive rice transcript map containing 6591 expressed sequence tag sites. Plant Cell 14:525-535.

Yu J, Hu S, Wang J, Wong GK, Li S, Liu B, Deng Y, Dai L, Zhou Y, Zhang X, Cao M, Liu J, Sun J, Tang J, Chen Y, Huang X, Lin W, Ye C, Tong W, Cong L, Geng J, Han Y, Li L, Li W, Hu G, Huang X, Li W, Li J, Liu Z, Li L, Liu J, Qi Q, Liu J, Li L, Li T, Wang X, Lu H, Wu T, Zhu M, Ni P, Han H, Dong W, Ren X, Feng X, Cui P, Li X, Wang H, Xu X, Zhai W, Xu Z, Zhang J, He S, Zhang J, Xu J, Zhang K, Zheng X, Dong J, Zeng W, Tao L, Ye J, Tan J, Ren X, Chen X, He J, Liu D, Tian W, Tian C, Xia H, Bao Q, Li G, Gao H, Cao T, Wang J, Zhao W, Li P, Chen W, Wang X, Zhang Y, Hu J, Wang J, Liu S, Yang J, Zhang G, Xiong Y, Li Z, Mao L, Zhou C, Zhu Z, Chen R, Hao B, Zheng W, Chen S, Guo W, Li G, Liu S, Tao M, Wang J, Zhu L, Yuan L, Yang H. 2002: A draft sequence of the rice genome (*Oryza* sativa L. ssp. *indica*). Science 296:79-92.

Notes

Author's address: The Institute for Genomic Research, 9712 Medical Center Dr., Rockville, MD 20850, USA; phone: (301) 838-3558; fax: (301) 838-0208; Email: rbuell@tigr.org.

Acknowledgments: Funding for this work was provided by a grant to the author from the U.S. Department of Agriculture (99-35317-8275), the National Science Foundation (DBI998282), and the U.S. Department of Energy (DE-FG02-99ER20357). The author wishes to thank Qiaoping Yuan, Shu Ouyang, Jia Liu, John Quackenbush, Dan Lee, Foo Cheung, Razvan Sultana, Lowell Umayan, Jeremy Peterson, Qi Yang, Brian Haas, Sam Angiouli, Owen White, Michael Heaney, Susan Lo, Vadim Sapiro, Billy Lee, Jeff Shao, Corey Irwin, Rajeev Kramchedu, Jacqueline Neubrech, Mark Sengamalay, and Eddy Arnold for their bioinformatic and information technology support.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Activation tagged mutants to discover novel rice genes

Gynheung An, Dong-Hoon Jeong, Suyoung An, Hong-Gyu Kang, Sunok Moon,
Jongjin Han, Sunhee Park, Hyun Sook Lee, and Kyungsook An

An activation T-DNA tagging vector, pGA2715, was developed to identify novel rice genes. The binary vector contains the promoterless *glucuronidase (GUS)* reporter gene next to the right border. In addition, the multimerized transcriptional enhancers from the cauliflower mosaic virus (CaMV) 355 promoter are located next to the left border. Therefore, the vector can be used for both gene trapping and activation tagging. A total of 13,450 T-DNA insertional lines have been produced using pGA2715. The histochemical GUS assay has revealed that the GUS-staining frequency from those lines is about twice as high as that from lines transformed with binary vector pGA2707, which lacks the enhancer element. This result suggests that the enhancer sequence present in the T-DNA improves GUS-tagging efficiency. Reverse transcriptase-polymerase chain reaction analysis of a subset of randomly selected pGA2715 lines has shown that expression of the genes immediately adjacent to the inserted enhancer increases significantly. The large population of T-DNA-tagged lines transformed with pGA2715 could be used for trapping a gene using the *gus* reporter, as well as for isolating gain-of-function mutants.

Recent completion of the draft sequence for the rice genome has resulted in an explosion of sequence information on rice genes (Goff et al 2002, Yu et al 2002). The challenge for the postsequencing era is to identify the biological functions for these sequenced genes. Of all the approaches used to discover gene function, the most direct is to disrupt the genes and analyze the consequences. Various methods have been developed in plants for this purpose. These include using ethyl methanesulfonate (EMS) or fast neutrons, or insertion of an element, such as a transposable element or T-DNA (Koornneef et al 1982, Sundaresan 1996, Krysan et al 1999). Because the inserted element acts as a tag of the mutant gene, this technique of insertional mutagenesis has an advantage over other isolation methods. However, the approach also has some limitations. Because it relies on the presence of recognizable phenotypes when a particular gene is mutated, it is difficult to identify the function of redundant genes. Other drawbacks include problems with elucidating the functions of genes required in early embryogenesis or gametophyte development.

The activation-tagging system is one of the methods for complementing conventional insertional mutagenesis. This system uses T-DNA or a transposable element containing multimerized CaMV 35S enhancers (Hayashi et al 1992, Suzuki et al 2001). Because enhancers can function in either orientation and at a considerable distance from the coding regions, they can cause transcriptional activation of nearby genes, resulting in dominant gain-of-function mutations. Through genetic screening for those mutations, activation-tagging can be used for analyzing the function of important genes that either are redundant members of a gene family or are essential for survival. In this way, the tagging system has been used for cloning several genes in *Arabidopsis* (Borevitz et al 2000, Huang et al 2001, Ito and Meyerowitz 2000, van der Graaff et al 2000), *Petunia* (Zubko et al 2002), and Madagascar periwinkle (*Vinca;* van der Fits and Memelink 2000).

Although the activation-tagging system has been widely used in *Arabidopsis,* its usefulness has not been demonstrated in monocot plants. In this study, we investigated the possibility of using multimerized 35S enhancer elements to carry out activation-tagging with rice genes.

Results

The 35S enhancer element is functional in rice

To examine whether the CaMV 35S enhancer elements function in rice, we placed the enhancer sequence upstream of the minimal promoter- *gus* fusion molecules. This was followed by assays for GUS activity. In the transgenic plants transformed with the minimal promoters of *nos* or CaMV, we observed only mild GUS-staining from the calli and no significant GUS-staining from the leaves or flowers. However, placing the tetramerized 35S enhancers upstream of the CaMV 35S minimal promoter or minimal *nos* promoter enhanced expression, not only in the calli but also in the leaves and flowers. To further evaluate the enhancing activity of the 35S enhancers, we placed the enhancer upstream of the minimal 35S promoter in the reverse direction and the enhancer sequences downstream of the *nos* terminator. In plants transformed with either of those vectors, enhanced GUS activities were detected in the leaves and flowers of the transformants. This is consistent with the observations of Fang et al (1989), who reported that, in dicotyledonous plants, the 35S enhancer element functioned both upstream and downstream of a gene, in either orientation. Our results demonstrate that the CaMV 35S enhancer sequence can be used as an enhancer element for carrying out activation-tagging in rice.

Construction of an activation-tagging vector

Plasmid pGA2715 (Fig. 1) contained the promoterless *gus* reporter gene with an intron and multiple splicing donors and acceptors immediately next to the right border. Multimerized transcriptional enhancers from the CaMV 35S promoter were inserted

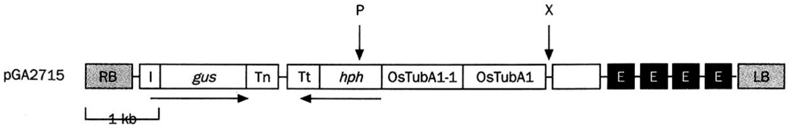


Fig. 1. Map of the T-DNA region of tagging vector pGA2715. RB and LB in the gray bar represent right and left borders of T-DNA, respectively. I = the *OsTubA1* intron 2 carrying three putative splicing acceptor and donor sites; gus = *ß-glucuronidase*; Tn = *nos* terminator; Tt = *OsTubA1* terminator; *hph* = hygromycin phosphotransferase gene; OsTubA1-1 = the first intron of *OsTubA1*; E = enhancer element of CaMV 35S promoter; P = *Pst*I site; X = *Xho*I site.

Table 1. Frequencies of GUS expression in transgenic rice seedlings. A total of 2,990 lines from pGA2707-tagged plants and 3,842 ilnes from pGA2715-tagged plants were examined at the T_2 seedling stage.

Vector organ	pGA2707				pGA2715			
	Stained lines		Preferential		Stained lines		Preferential	
	n	(%)	n	(%)	n	(%)	n	(%)
Mature seeds	158	(5.3)	45	(1.5)	359	(9.3)	91	(2.4)
Roots	85	(2.8)	6	(0.2)	241	(6.3)	14	(0.4)
Shoots	115	(3.8)	21	(0.7)	404	(10.5)	78	(2.0)
Total	194	(6.5)	72	(2.4)	514	(13.4)	183	(4.8)

next to the left border within the T-DNA. The hygromycin-resistant selectable marker gene, with the rice alpha tubulin (*OsTubA1-1*) promoter, was placed between the *gus* gene and the 35S enhancer. Because of that construction, this vector can aim at achieving both gene-trapping and activation-tagging. The other binary vector, pGA2707, resembles pGA2715 except for its lack of enhancer elements. Using *Agrobacrerium*-mediated rice transformation (Lee et al 1999), we have produced more than 20,000 fertile transgenic plants transformed with pGA2715 and 20,810 fertile transgenic plants with pGA2707.

Gene-trapping using the *gus* reporter

To assess the efficiency of gene-trapping, we examined GUS expression patterns in various organs of both the primary and progeny transgenic plants. Six-d-old seedlings of T_2 progenies underwent the GUS assay (Table 1). Out of 2,990 pGA2707 lines, 194 (6.5%) displayed GUS expression; among these, 158 lines (5.3%) were GUS-positive in the mature seeds (including endosperm, scutellum, and seed coat). Likewise, 85 lines (2.8%) were GUS-positive in the roots and 115 (3.8%) in the shoots (including the apical meristems, coleoptiles, leaf blades, and sheaths). The frequency of preferential expression to seeds, roots, and shoots was 1.5% (45 lines),

Table 2. Frequencies of GUS expression in mature flowers of transgenic rice plants. A total of 11,189 lines from pGA2707-tagged plants and 5,489 lines from pGA2715-tagged plants were examined at the flowering stage in the T_1 generation.

Vector organ	pGA2707				pGA2715			
	Stained lines		Preferential		Stained lines		Preferential	
	n	(%)	n	(%)	n	(%)	n	(%)
Rachilla	225	(2.0)	1	(0.01)	186	(3.4)	2	(0.04)
Pedicel	201	(1.8)	10	(0.09)	248	(4.5)	11	(0.20)
Palea/lemma	329	(2.9)	17	(0.15)	370	(6.7)	30	(0.55)
Lodicules	224	(2.0)	1	(0.01)	117	(2.1)	2	(0.04)
Stamen	322	(2.9)	58	(0.52)	211	(3.8)	32	(0.58)
Carpel	279	(2.5)	17	(0.15)	156	(2.8)	11	(0.20)
Total	526	(4.7)	104	(0.93)	515	(9.4)	88	(1.60)

0.2% (6 lines), and 0.7% (21 lines), respectively. In contrast, 2.3% (70 lines) expressed the *gus* gene in all organs at the seedling stage.

For the pGA2715-transformed lines, the frequency of GUS-positive lines was higher in all organs (Table 1). Of the 3,842 lines, 5 14 (13.4%) were GUS-positive. Among them, 359 lines (9.3%) were positive in the mature seeds, 241 (6.3%) in the roots, and 404 (10.5%) in the shoots. The frequency of preferential expression to seeds, roots, and shoots was 2.4% (91 lines), 0.4% (14 lines), and 2.0% (78 lines), respectively. A total of 173 lines (4.5%) expressed the reporter in the roots and shoots at the seedling stage. The frequency of GUS expression in the pGA2715 plants was about two times higher than that in the pGA2707 plants, not only overall and at the organ level but also at the levels for ubiquitous and preferential expression.

We also screened the mature flowers of primary transgenic plants to identify lines that were GUS-positive, and found expression in 4.7% of the pGA2707 lines (526/11,189) and 9.4% of the pGA2715 lines (515/5,489). The frequencies of GUS expression in various floral organs (e.g., rachillae, pedicels, paleae/lemmae, lodicules, stamens, and carpels) are summarized in Table 2. As with the seedlings, the GUS-positive frequency for floral organs in the pGA2715 lines was about twice as high as that in the pGA2707 lines. These results imply that the multimerized CaMV 35S enhancers elevate the expression levels of the gus reporter gene located in the same T-DNA, thereby increasing the efficiency of gene-trapping.

Enhancing gene expression by activation-tagging

To determine the action of the multimerized CaMV 35S enhancers at the molecular level, we analyzed expression of the genes adjacent to the inserted enhancer elements. Using inverse PCR on 100 lines, we isolated 71 sequences flanking the T-DNA. These isolated sequences were examined by comparing them with entries in publicly available DNA databases, and were then annotated for their identifying open reading frames (ORFs). Among them, 28 insertions (39.4%) occurred in the intragenic regions, whereas 43 (60.6%) were located in the intergenic regions. Insertions of enhancer elements within 4.5 kb upstream or downstream of the nearest ORF occurred in 12 and 9 lines, respectively. We regarded these 21 lines (29.6%) as candidates for activation-tagging.

Ten candidate lines were randomly selected and examined for the expression levels of genes near the enhancers. We planted 15 progenies per line and determined their genotypes by PCR analysis using a gene-specific primer and a T-DNA primer. The expression levels for candidate genes in the leaves of 10-d-old seedlings were then examined via reverse transcriptase (RT)-PCR using gene-specific primers. Although RT-PCR products were obtained from eight lines, the remaining two lines showed no expression in the leaves. We first hypothesized that our annotation may have been incorrect. However, among the eight lines examined, four showed that the levels of product from the gene near the enhancers increased significantly in heterozygote and homozygote plants compared with those in the wild-type tissue (Fig. 2). In those lines, the distance between the enhancers and the overexpressed gene ranged from 1.5 to 4.3 kb. Therefore, because the enhancer sequence was found both upstream and downstream of the target genes, we could confirm that the tetramerized 35S enhancer sequence acted as a true enhancer in rice (see also Fang et al 1989).

Discussion

We demonstrated that activation-tagging can be applied to a monocot species such as rice. Although one of the main prerequisites is a strong enhancer element, until now it had been difficult to isolate such a strong element from monocots because the regulatory elements for gene expression are often found in an intron rather than in the 5′-flanking region of the gene. For example, the promoter activity of the rice actin 1 gene, *Act1,* is dependent on the presence of an intact rice *Act1 5′* intron (McElroy et al 1990). The effect of the rice *Acr1* intron on gene expression is similar to the dependence on introns by maize *Adh1-S.* In addition, expression of *OsTubA1,* which is strong in actively dividing tissues, is regulated at the posttranscriptional level (Jeon et al 2000). In rice, the CaMV 35S promoter is widely used as a constitutive strong promoter (Terada and Shimamoto 1990). Likewise, the CaMV 35S enhancer can elevate gene expression in monocotyledonous plants, including maize (Omirulleh et al 1993) and rice (Mitsuhara et al 1996). We found in our rice study that the CaMV 35S enhancers were functional in both orientations, either upstream or downstream, of the nearby genes. Therefore, we developed an activation-tagging vector using the CaMV 35S enhancers and produced a large number of transgenic plants that were tagged by those enhancers.

GUS analysis from the activation-tagging lines has revealed a wide variety of expression patterns—some constitutive and others tissue-preferential. The frequency of gene-trapping using the *gus* reporter is 9.4% in flowers and 13.4% in mature seeds and seedlings. Chin et al (1999) reported finding 10.0% of their gene traps in *Ds*-tagged rice lines. Screening of the tagging lines after various environmental or

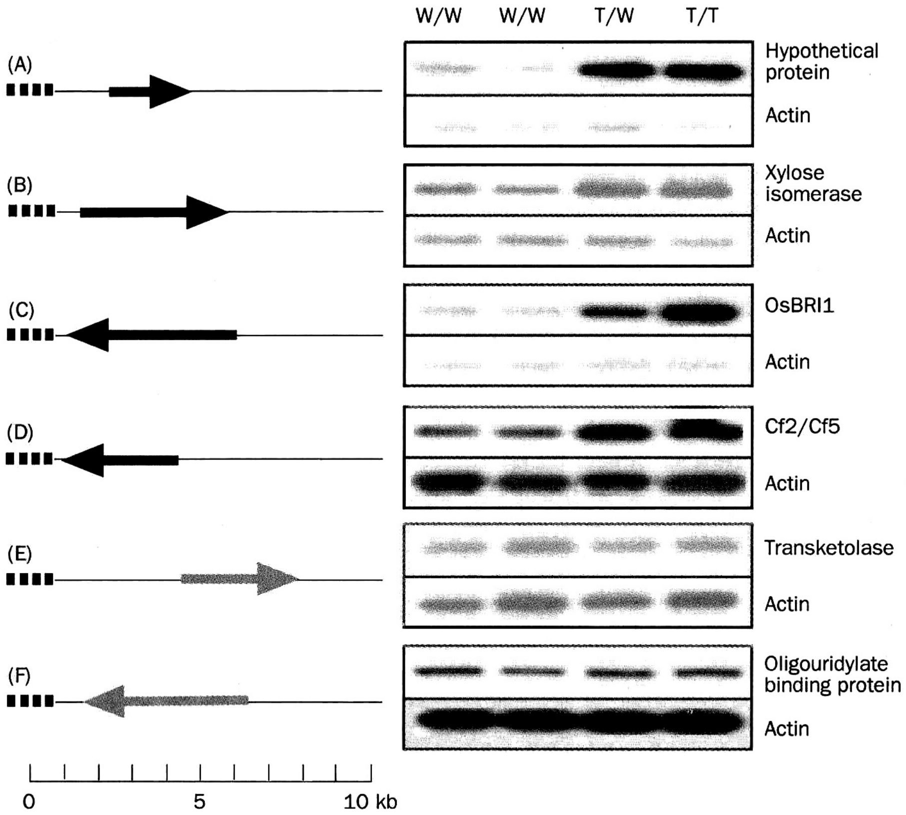


Fig. 2. Mapping the insertion position of the 35S enhancer element and RT-PCR analyses of the expression level of tagged genes. At left are the schematic representations of the 35S enhancer elements relative to nearby genes. Black bars indicate the CaMV 35s enhancers. The nearby gene is indicated with an arrow pointing in the direction of transcription. At right are the RT-PCR analyses of the expression pattern of genes near the CaMV 35S enhancers. RNAs were isolated from progeny leaves of the activation-tagging line. Rice *actin* transcript was amplified as a control. (A) Line 1B-002-24 was tagged 2.0 kb upstream of a hypothetical gene. (B) Line 1B-035.09 was tagged 0.7 kb upstream of a gene homologous to xylose isomerase. (C) Line 1B-001-07 was tagged 0.3 kb downstream of the *OsBRI1* gene. (D) Line 1B-044-17 was tagged 0.7 kb downstream of a gene homologous to *Cf2/Cf5.* (E) Line 1B-037-14 was tagged 3.5 kb upstream of a gene homologous to *transketolase.* (F) Line 1B-042-40 was tagged 1.0 kb downstream of a gene homologous to *oligouridylate binding protein.* W/W = wild-type lines; T/W = heterozygote lines for T-DNA insertion; T/T = homozygote lines for T-DNA insertion.

chemical stimulations would increase GUS-tagging frequency. Considering that approximately 40% of the rice genomic DNA is intragenic, the maximum efficiency should be 20% of the total population if T-DNA is inserted randomly in both orientations. However, if the insertion prefers the intragenic regions, gene-trap efficiency would be higher. In *Arabidopsis,* activation of the reporter gene in a gene-trap vector is as high as 30% (Sundaresan et al 1995). However, because the T-DNA- or transposon-tagged lines contain more than one locus of insertions, actual GUS-positive frequency per insertion would necessarily be lower.

We observed that the GUS-trap efficiency for the pGA2715 lines was much higher than with pGA2707, probably because 35S enhancers were present in the vector. Interestingly, the proportion of organ-preferential tags in all the GUS-positive lines did not differ between the pGA2715 and pGA2707 lines, which implies that the multimerized CaMV 35S enhancers simply elevated the expression level of the nearby genes without altering the original expression pattern. RT-PCR analysis of the tagging lines also showed that the 35S sequence enhanced expression levels of the endogenous genes without changing their patterns. Our observations are consistent with the previous report that the CaMV 35S enhancer caused enhanced expression of the endogenous gene without affecting the expression pattern in some activation-tagging lines of *Arabidopsis* (Neff et al 1999, van der Graaff et al 2000, Weigel et al 2000).

The CaMV 35S enhancer did not always increase the expression level of nearby genes. In our study, only 4 out of the 10 genes in which the enhancers were inserted within 4.5 kb displayed elevated expression, with no enhanced expression being found in the remaining lines. This may have resulted from the presence of insulator elements that prevented the misregulation of genes by restricting the effects of the regulatory elements to specific domains (Oki and Kamakaka 2002). It is possible that this blocking of enhancer activity may arise from the division of the enhancer and promoter elements into separate domains in the nucleus. This is probably facilitated by interactions between these elements and the insulator elements. Alternatively, elevated gene expression in the remaining lines may occur in other tissue types or under conditions that we did not test. That hypothesis is supported by the fact that the CaMV 35S enhancer increases nearby gene expression without altering the original expression pattern (Neff et al 1999, van der Graaff et al 2000, Weigel et al 2000).

Although the 35S enhancer element seemed to efficiently activate nearby genes, only a small number of mutants were isolated from our activation-tagging lines. Weigel et al (2000) and Marsch-Martinez et al (2002), respectively, have reported frequencies of 0.1% and 1% for dominant mutations caused by activation-tagging. These low rates suggest that elevated gene expression by an enhancer may not always produce visible phenotypes. So far, we have isolated nine dominant mutants from 3,290 independent pGA2715-transformed seedlings (unpublished data). We are investigating whether any of these mutant phenotypes are the result of activation-tagging. It has generally been proposed that the tissue-culture process induces somaclonal variants. In the current study, we observed dominant mutants not only from activation-tagging lines but also from untagged lines. Dominant mutant phenotypes that do not cosegregate with T-DNA insertions might be due to somaclonal variation. Tissue culturing may produce a point mutation in a certain gene that causes a dominant negative effect in the genetic pathway. It is also possible that somaclonal variation induces a mutation in an enzyme, which acts in a dose-dependent manner.

To best use our activation-tagging lines, we are employing a "reverse activation-tagging" strategy. A PCR method for sequencing the insertion of a 35S enhancer near a particular gene of interest will help in identifying the activation-tagging line and examining the enhancer effects. A DNA pooling system has been widely used in several plant species, including maize, petunia, *Arabidopsis,* and rice (Krysan et al 1999, Sato et al 1999). PCR screening of the DNA pools, using degenerated primers for more than one isoform, will facilitate tagging-identification and characterization of the gene-family functions (Young et al 2001). We are now establishing pools and superpools of DNA prepared from our activation-tagging lines of rice.

The systematic cataloguing of tagging mutants by random sequencing has begun in *Ds* -tagged *Arabidopsis* (Parinov et al 1999, Ito et al 2002) and Mutator-tagged maize (Hanley et al 2000). Flanking sequences have been determined for the *Tos17*-tagged lines in rice (Hirochika 2001). We are also producing a flanking-sequence database of the activation-tagging lines using an inverse-PCR technique (Spertini et al 1999). Once this database is established, a gene of interest will be searchable *in silico.* From those selected lines, activation of the tagged genes can then be examined via RT-PCR and Northern gel-blot analyses. A particular mutant phenotype can be carefully investigated by considering the specific location, conditions, or time of gene expression. This reverse activation-tagging strategy will provide a good complement to the limitations of forward genetic screening.

References

Borevitz JO, Xia Y, Blount J, Dixon RA, Lamb C. 2000. Activation tagging identifies a conserved MYB regulator of phenylpropanoid biosynthesis. Plant Cell 12:2383-2394.

Chin HG, Choe MS, Lee SH, Park SH, Koo JC, Kim NY, Lee JJ, Oh BG, Yi GH, Kim SC, Choi HC, Cho MJ, Han C. 1999. Molecular analysis of rice plants harboring an *Ac/Ds* transposable elements-mediated gene trapping system. Plant J. 19:615-623.

Fang RX, Nagy F, Sivasubramaniam S, Chua NH. 1989. Multiple *cis* regulatory elements for maximal expression of the cauliflower mosaic virus 35S promoter in transgenic plants. Plant Cell 1:141-150.

Goff SA et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Hanley S, Edwards D, Stevenson D, Haines S, Hegarty M, Schuch W, Edwards KJ. 2000. Identification of transposon-tagged genes by the random sequencing of Mutator-tagged DNA fragments from *Zea mays.* Plant J. 23:557-566.

Hayashi H, Czaja I, Lubenow H, Schell J, Walden R. 1992. Activation of a plant gene by T-DNA tagging: auxin-independent growth in vitro. Science 258:1350-1353.

Hirochika H. 2001. Contribution of the *Tos17* retrotransposon to rice functional genomics. Curr. Opin. Plant Biol. 4:118-122.

Huang S, Cerny RE. Bhat DS, Brown SM. 2001. Cloning of an *Arabidopsis* patatin-like gene, *STURDY,* by activation T-DNA tagging. Plant Physiol. 125:573-584.

Ito T, Meyerowitz EM. 2000. Overexpression of a gene encoding a cytochrome P450, *CYP78A9,* induces large and seedless fruit in *Arabidopsis.* Plant Cell 12:1541-1550.

Ito T, Motohashi R, Kuromori T, Mizukado S, Sakurai T, Kanahara H, Seki M, Shinozaki K. 2002. A new resource of locally transposed Dissociation elements for screening gene-knockout lines *in silico* on the *Arabidopsis* genome. Plant Physiol. 129:1695-1699.

Jeon JS et al. 2000. T-DNA insertional mutagenesis for functional genomics in rice. Plant J. 22:561-570.

Koornneef M, Dellaert LWM, van der Veen JH. 1982. EMS- and radiation-induced mutation frequencies at individual loci in *Arabidopsis thaliana* (L.) Heynh. Mutant Res. 93:109-123.

Krysan PJ, Young JC, Sussman MR. 1999. T-DNA as an insertional mutagen in *Arabidopsis.* Plant Cell 11:2283-2290.

Lee S, Jeon JS, Jung KH, An G. 1999. Binary vectors for efficient transformation of rice. J. Plant Biol. 42:310-316.

Marsch-Martinez N, Greco R, van Arkel G., Herrera-Estrella L, Pereira A. 2002. Activation tagging using the *En-I* maize transposon system in *Arabidopsis.* Plant Physiol. 129:1544-1556.

McElroy D, Zhang W, Cao J, Wu R. 1990. Isolation of an efficient actin promoter for use in rice transformation. Plant Cell 2:163-171.

Mitsuhara I et al. 1996. Efficient promoter cassettes for enhanced expression of foreign genes in dicotyledonous and monocotyledonous plants. Plant Cell Physiol. 37:49-59.

Neff MM, Nguyen SM, Malancharuvil EJ, Fujioka S, Noguchi T, Seto H, Tsubuki M, Honda T, Takatsuto S, Yoshida S, Chory J. 1999. *BAS1:* a gene regulating brassinosteroid levels and light responsiveness in *Arabidopsis.* Proc. Natl. Acad. Sci. USA 96:15316-15323.

Oki M, Kamakaka RT. 2002. Blockers and barriers to transcription: competing activities? Curr. Opin. Cell Biol. 14:299-304.

Omirulleh S, Abraham M, Golovkin M, Stefanov I, Karabaev MK, Mustardy L, Morocz S, Dudits D. 1993. Activity of a chimeric promoter with the doubled CaMV 35S enhancer element in protoplast-derived cells and transgenic plants in maize. Plant Mol. Biol. 21:415-428.

Parinov S, Sevugan M, De Y,Yang WC, Kumaran M, Sundaresan V. 1999. Analysis of flanking sequences from dissociation insertion lines: a database for reverse genetics in *Arabidopsis.* Plant Cell 11:2263-2270.

Sato Y, Sentoku N, Miura Y, Hirochika H, Kitano H, Matsuoka M. 1999. Loss-of-function mutations in the rice homeobox gene *OSH15* affect the architecture of internodes resulting in dwarf plants. Embo J. 18:992-1002.

Spertini D, Beliveau C, Bellemare G. 1999. Screening of transgenic plants by amplification of unknown genomic DNA flanking T-DNA. Biotechniques 27:308-314.

Sundaresan V. 1996. Horizontal spread of transposon mutagenesis: new uses of old elements. Trends Plant Sci. 1:184-191.

Sundaresan V, Springer P, Volpe T, Haward S, Jones JD, Dean C, Ma H, Martienssen R. 1995. Patterns of gene action in plant development revealed by enhancer trap and gene trap transposable elements. Genes Dev. 9:1797-1810.

Suzuki Y, Uemura S, Saito Y, Murofushi N, Schmitz G, Theres K, Yamaguchi I. 2001. A novel transposon tagging element for obtaining gain-of-function mutants based on a self-stabilizing *Ac* derivative. Plant Mol. Biol. 45:123-131.

Terada R, Shimamoto K. 1990. Expression of CaMV 35S-Gus gene in transgenic rice plants. Mol. Gen. Genet. 220:389-392.

van der Fits L, Memelink J. 2000. ORCA3, a jasmonate-responsive transcriptional regulator of plant primary and secondary metabolism. Science 289:295-297.

van der Graaff E, Dulk-Ras AD, Hooykaas PJ, Keller B. 2000. Activation tagging of the *LEAFY PETIOLE* gene affects leaf petiole development in *Arabidopsis thaliana.* Development 127:4971-4980.

Weigel D et al. 2000. Activation tagging in *Arabidopsis.* Plant Physiol. 122:1003-1013.

Young JC, Krysan PJ, Sussman MR. 2001. Efficient screening of *Arabidopsis* T-DNA insertion lines using degenerate primers. Plant Physiol. 125:513-518.

Yu J et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science 296:79-92.

Zubko E, Adams CJ, Machaekova I, Malbeck J, Scollan C, Meyer P. 2002. Activation tagging identifies a gene from *Petunia hybrida* responsible for the production of active cytokinins in plants. Plant J. 29:797-808.

Notes

Authors' address: Department of Life Science and National Research Laboratory of Plant Functional Genomics, Pohang University of Science and Technology (POSTECH), Pohang 790-784, Republic of Korea.

Acknowledgments: This work was supported, in part, by grants from the National Research Laboratory Program of the Korea Institute of Science and Technology Evaluation and Planning (KISTEP) and from the 21st Century Frontier Program of the Crop Functional Genomic Center.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Insertional mutagenesis in rice using the endogenous retrotransposon

H. Hirochika

Insertional mutagenesis is a powerful method for a systematic functional analysis of a large number of genes. In rice, five endogenous active retrotransposons have been found and the most active, *Tos17,* was characterized in detail. *Tos17* is silent under normal conditions and becomes active only under tissue culture conditions. *Tos17* was shown to transpose preferentially into low-copy-number, gene-rich regions, indicating that *Tos17* can be used as an efficient insertional mutagen. A collection of 50,000 regenerated rice lines carrying about 500,000 insertions was produced and these lines are being used for forward and reverse genetic analyses. By using a transposon-tagging strategy, causative genes for more than 20 mutations have been cloned. For reverse genetic studies, two strategies are employed. One is polymerase chain reaction (PCR) screening of mutants of genes of interest. DNA pools derived from 40,000 lines have been produced for screening. By screening 31,000 lines for mutants of 53 genes, mutants of 17 genes have been isolated. Another important strategy is the cataloguing of mutants by sequencing the genomic sequences flanking *Tos17* insertions. Sequences flanking transposed *Tos17* copies are amplified by TAIL (thermal asymmetric interlaced PCR)- and suppression-PCR and directly sequenced. As of June 2002, 14,300 independent flanking sequences from 3,700 lines have been determined and mutants of different classes of genes have been identified.

Draft genomic sequences with 99.8% accuracy of the two major subspecies of rice (*japonica* and *indica*) have been published recently (Yu et al 2002, Goff et al 2002) and a draft sequence of the *japonica* variety with 99.99% accuracy will soon be made available by the International Rice Genome Sequencing Project (IRGSP) (Sasaki and Burr 2000). The next important challenge is to develop a systematic method suitable for discovering the biological functions of all the genes discovered by genomic sequencing. Insertional mutagenesis is most suitable for a systematic functional analysis of a large number of genes in the context of whole plants because many mutant lines can be produced at the same time and induced mutations can be easily detected by simple molecular biological methods. In *Arabidopsis,* whose entire genomic sequencing has been completed (Arabidopsis Genome Initiative 2000), mutant lines have been produced by using insertional mutagens, such as T-DNA (Azpiroz-Leehan and Feldmann 1997, Krysan et al 1999) and maize transposable elements *Ac/Ds* (Parinov et al 1999) and *En/Spm* (Wisman et al 1998, Speulman et al 1999, Tissier et al 1999). To screen mutant lines for reverse genetics, two screening strategies have been employed in these studies—PCR screening of the mutants and random sequencing of insertion sites—and resources for these screening strategies are becoming available. Recent rapid progress in large-scale insertional mutagenesis suggests that mutant populations covering all the genes will soon become available (Parinov and Sundaresan 2000). A large-scale insertional mutagenesis has begun also in rice using T-DNA (Jeon et al 2000), *Ac/Ds* (Enoki et al 1999), and the endogenous retrotransposon *Tos17* (Hirochika 1997, 2001). Since the lines induced by the exogenous insertional mutagens, such as T-DNA and *Ac/Ds,* are transgenic plants, it is necessary to be concerned about the environment. Rice plants are relatively large; therefore, it is not easy to handle thousands of transgenic rice plants in a greenhouse. For this, it is desirable to use endogenous insertional mutagens. Here, I summarize recent progress in insertional mutagenesis in rice using *Tos17* and its application to forward and reverse genetic studies.

Features of *Tos17* as an insertional mutagen

Transposable elements can be classified into two classes based on their mode of transposition. The class II elements, including classical maize transposable elements, transpose through the cut-and-paste mode and thus induce unstable mutations. In contrast, the class I elements (also called retrotransposons) do not induce unstable mutations because they transpose through reverse transcription of an RNA intermediate, the so-called copy-and-paste mode. Reflecting the mode of transposition, the copy number of retrotransposons is usually high (Kumar and Bennetzen 1999). For example, >50,000 copies of *BARE-1* exist in the barley genome (Vicient et al 1999). In contrast to other retrotransposons in plants, the copy number of *Tos17* in the rice genome is quite low, one to five, depending on the cultivar. Nipponbare, selected as a standard cultivar for the IRGSP (Sasaki and Burr 2000), carries only two copies per haploid genome. Its transposition is activated by tissue culture, becoming inactive in regenerated plants (Hirochika et al 1996). The transcript was detected only under tissue culture conditions, indicating that the transposition of *Tos17* is mainly regulated at the transcriptional level. Five to 30 transposed copies were observed in the regenerated plants. Copy number roughly correlated with duration of tissue culture, thus suggesting that the number of mutant lines required for mutant screening can be reduced by prolonging the tissue culture period. However, prolonged culture leads to a reduction in heterogeneity of mutations, possibly because of the selection of specific cell types that may have acquired a higher growth rate (Hirochika et al 1996). To overcome these problems, a 5-month culture period was adopted for the large-scale production of mutant lines. A collection of 50,000 regenerated rice lines has been produced and the mean number of newly transposed copies is estimated to be 10 per line (A. Miyao et al, unpublished).

Commonly used class II elements, such as *Ac/Ds* and *En/Spm* elements, are known to transpose into linked sites (Parinov and Sundaresan 2000). Thus, the original element must be placed near the target gene for efficient tagging. This feature may be useful for an efficient local mutagenesis (Ito et aL 1999). However, this may also restrict the use of saturation mutagenesis. To avoid this problem, a marker gene system selecting only unlinked transpositions has been developed and used efficiently in *Arabidopsis* (Tissier et al 1999). Considering the mechanism of transposition, retrotransposons are expected to transpose into unlinked sites. This was demonstrated with the tobacco retrotransposon *Tto1* (Okamoto and Hirochika 2000) and *Tos17* (Yamazaki et al 2001).

Another important concern is “hot spots” for insertions because well-characterized retrotransposons, such as retrotransposons of yeast, have a strong bias for integration target sites (Voytas 1996). For example, the target site of *Ty3* is restricted to the promoter region of genes transcribed by the RNA polymerase III, whereas *Ty5* prefers silenced chromatin regions. All the available data on target sites of recent transposition indicate that *Tto1* and *Tos17* transpose into unlinked sites scattered throughout the chromosomes, and that they prefer low-copy-number, gene-rich regions (Okamoto and Hirochika 2000, Yamazaki et al 2001). This result was further confirmed by the large-scale analysis of *Tos17* -flanking sequences (see the following section). The preference for low-copy-number, gene-rich regions was also shown in rice with *Ac* (Enoki et al 1999) and T-DNA (Barakat et al 2000).

Unique features of *Tos17* that make it a powerful genetic tool for forward and reverse genetic studies are summarized as follows. (1) Transposition can be regulated since *Tos17* is activated by tissue culture and becomes silent in regenerated plants. (2) Highly mutagenic during tissue culture, *Tos17* transposes preferentially into gene-rich, low-copy-number regions and about ten loci on average are disrupted in each plant regenerated from 5-month-old culture. (3) Integration target loci were widely distributed over the chromosomes so that random insertion for saturation mutagenesis is feasible. (4) Induced mutations are stable and germinally transmitted in the next generation. (5) The original copy number is quite low, one to five, depending on varieties, so that it is easy to identify the transposed copy responsible for the specific mutation. (6) Rearrangements are very rare at junctions between *Tos17* ends and flanking host sequences so that a screen of mutants by PCR and analysis of disrupted genes can be carried out with high efficiency. (7) This transposon system is endogenous so that screening and characterization of mutants in the field are possible without any environmental concern. However, some of the features might also be disadvantageous. For example, transposition via the copy-and-paste mode means that no revertants can be obtained, although revertants are useful for confirming that a gene is tagged and can be obtained from the mutants induced by class II elements.

Forward genetic studies

Traditional transposon tagging is still an important method for cloning important genes for functional analysis. Recently, the feasibility of tagging using *Tos17* has been demonstrated (Agrawal et al 2001) and causative genes for more than 20 mutations have been cloned by using this strategy. R_1 (M_2) generations of regenerated rice were screened for mutants based on the phenotypes in the paddy field. About 40% of the regenerated lines examined showed many kinds of visible mutant phenotypes, such as dwarf, sterile, yellow, albino, virescent, viviparous, brittle, and spotted leaf. In addition to screening in the field, screening in vitro was also conducted to isolate genes involved in salt-stress tolerance and root growth and development. Some of the mutants were chosen and then underwent cosegregation analysis to determine whether the mutations were caused by *Tos17* insertions. Genetic analysis showed that all these mutations were recessive, although some did not segregate in a 1:3 ratio. Because the copy number of *Tos17* is low enough to visualize each transposed copy, the *Tos17* copy causing the specific mutation can be identified by a simple DNA gel blot analysis. Finally, the causative gene can be isolated by using IPCR (inverse PCR) or TAIL-PCR (thermal asymmetric interlaced-PCR) (Liu et al 1995). This situation is quite distinct from the tagging using endogenous transposable elements in other plants, such as maize and petunia, in which the copy number of transposable elements is high (approximately 100 copies) (Maes et al 1999, Walbot 2000). To prove that the cloned genes are causative genes, a straightforward strategy is a complementation test. Another important strategy is the search for allelic mutants by using the PCR-screening method (see the next section). By using this strategy, definite proof was obtained in several cases.

Although gene-tagging with *Tos17* is a powerful strategy for cloning genes, one fundamental problem should be noted: the relatively low tagging efficiency (5% to 10%) (Hirochika 1999, Agrawal et al 2001). This indicates that tissue culture-induced mechanisms other than *Tos17* insertions cause untagged mutations with high frequency. Previously, we have shown that four rice retrotransposons as well as *Tos17* are activated by tissue culture (Hirochika 1999). However, these four retrotransposons may not be a major factor because their activity is at least ten times less than that of *Tos17* (H. Hirochika, unpublished). By increasing the tagging efficiency, it would be possible to avoid tissue culture-induced mutations by finding new conditions under which retrotransposons could be activated or finding new transposable elements that could be activated by tissue culture. It should be mentioned that class II elements are also activated by tissue culture as shown in maize (Peschke et al 1987) and tobacco (Grappin et al 1996). To find active transposable elements, a transposon-trap system using negative selection marker genes is a very powerful method (Grandbastien et al 1989, Tsay et al 1993). An assay to find new transposable elements is currently under way.

Although tagging efficiency with *Tos17* in general is relatively low, some genes were cloned with high efficiency. For example, five mutants exhibiting the brittle culm phenotype were found among 3,500 regenerated lines and all of the five mutations were shown to be caused by insertion of *Tos17*. Causative genes were shown to be cellulose synthase catalytic subunit *(CesA)* genes — *OsCesA4, OsCesA7,* and *OsCesA11* (K. Tanaka et al, unpublished). One possible explanation for the perfect tagging is that *CesA* genes are preferred targets for *Tos17* insertion. This explanation was supported by the finding that two of the five mutations were allelic to two mutations of two genes.

Reverse genetic studies

Considering the increasing availability of rice genomic sequences, the reverse genetic approach to discover gene functions should become more and more important. As already mentioned, two strategies can be employed to screen mutants for reverse genetic studies. One is the PCR screening of mutants and the other is the random sequencing of insertion flanking sequences. As reviewed in this section, some of the features of *Tos17* are most suitable for reverse genetic screening.

The PCR-screening method was first developed in *Drosophila* and has since been used in *Caenorhabditis elegans,* petunia, maize, and *Arabidopsis* (reviewed in Maes et al 1999). The principle of this method is as follows. Four combinations of two gene-specific primers and two insertion-specific primers in forward and reverse orientations are used in separate reactions to detect insertions in a gene of interest, irrespective of their position and orientation. Because PCR is very sensitive, one insertion in a gene of interest can be identified among a pool of thousands of mutants, thus reducing the number of DNA samples required for screening. To identify mutant individuals, a two- or three-dimensional DNA-pooling system is usually adopted. The first direct evidence for the feasibility of using *Tos17* for the PCR-screening strategy was shown by screening for a mutant of the homeobox gene *(OSH15)* (Sato et al 1999). In this case, the mutant was found using a two-dimensional pooling system in a small population consisting of 529 *Tos17*-induced mutant lines. To screen a large population, a three-dimensional system was employed. A total of 40,000 lines carrying about 400,000 *Tos17* insertions were arrayed in a 96-well format and pooled in a three-dimensional matrix. The mutant population of 31,000 lines has been screened for mutants of 53 genes and mutants of 17 genes have been identified (H. Hirochika et al, unpublished). By the analysis of phytochrome-A mutants, functions unique to rice have been found (Takano et al 2001). Although mutants of five out of ten mitogen-activated protein kinase (MAPK) genes have been identified, only the mutant of one gene showed a clear phenotype (T. Watanabe et al, unpublished). The lack of a mutant phenotype can be largely due to gene redundancy. One possible solution is to combine mutations by crossing, as has been successfully demonstrated in *Arabidopsis* (Liljegren et al 2000, Pelaz et al 2000). The existence of multiple allelic mutations in some of the genes screened indicates hot spots for *Tos17* insertion, which enables us to find and confirm the causality of genes and phenotype, while this may be a limiting factor for saturation mutagenesis. To make this system generally applicable to any gene of interest, mutations induced by *Tos17* insertion must be saturated. The success rate (17/53) of PCR screening together with the mutant population size screened suggests that at least 90,000 lines are required for saturation mutagenesis. Considering the existence of hot spots for *Tos17* insertion, this might be an underestimate.

Several problems associated with features inherent in each insertion element have been noted when PCR screening was carried out. For example, some fractions of mutations induced by *Ac* (Enoki et al 1999) or *Mutator* (Walbot 2000) were not inherited in the next generation because the mutations detected were induced in somatic cells. Another problem is that only a fraction of mutants can be detected by PCR screening because the primers cannot bind to T-DNA because of frequent deletions induced at their ends (Krysan et al 1999). Tissue culture-induced activation of *Tos17* seems most suitable for reverse genetic studies because transposition can be regulated strictly and rearrangements of the ends of *Tos17* are only rarely induced (Yamazaki et al 2001).

Although PCR screening seems to be the most efficient approach for reverse genetics, it may not be suitable for the analysis of a large number of genes. Considering large-scale functional genomics in the postsequencing era, a systematic approach to finding mutants for a large number of genes is needed. One of the possible approaches is the cataloguing of insertion mutants by sequencing the genomic DNA sequence flanking insertions (Pavinov and Sundaresan 2000). As has been reported by Hirochika et al (1996), mutants of interesting genes were identified by a small-scale analysis of sequences flanking *Tos17* insertions. In this case, IPCR was used to amplify the flanking sequences. To carry out large-scale sequencing of the *Tos17*-flanking sequences, TAIL- and suppression-PCR were adopted (Miyao et al 1998). By combining these two PCR methods, about 95% of the flanking sequences were amplified. As of June 2002,14,300 independent flanking sequences from 3,700 lines have been determined and assembled into a database (A. Miyao et al, unpublished). By BLAST searches against the flanking sequence database, it is possible to search for mutants of genes of interest *in silico.* The flanking sequence database is accessible at http://tos.nias.affrc.go.jp/ and the mutant seeds are available to the scientific community on request. Reflecting the rapid increase in the publicly available rice genomic sequence data, most of the flanking sequences are mapped on the chromosomes by comparing the flanking sequences with the genomic sequence. Because the ends of the transposed copies are intact and the detected insertions are inherited stably in subsequent generations, the flanking sequence analysis is best suited for the *Tos17* system.

References

Agrawal GK, Yamazaki M, Kobayashi M, Hirochika R, Miyao A, Hirochika H. 2001, Screening of the rice viviparous mutants generated by endogenous retrotransposon *Tos17* insertion: tagging of a zeaxanthin epoxidase gene and a novel *OsTATC* gene. Plant Physiol. 125:1248-1257.

Arabidopsis Genome Initiative. 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana.* Nature 408:796-815.

Azpiroz-Leehan R, Feldmann KA. 1997. T-DNA insertion mutagenesis in *Arabidopsis:* going back and forth. Trends Genet. 13:152-156.

Barakat A, Gallois P, Raynal M, Mestre-Ortega D, Sallaud C, Guiderdoni E, Delseny M, Bernardi G. 2000. The distribution of T-DNA in the genomes of transgenic *Arabidopsis* and rice. FEBS Lett. 471:161-164.

Enoki H, Izawa T, Kawahara M, Komatsu M, Koh S, Kyozuka J, Shimamoto K. 1999. *Ac* as a tool for the functional genomics of rice. Plant J. 19:605-613.

Goff SA and 54 others. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Grandbastien M-A, Spielman A, Caboche M. 1989. *Tnt1,* a mobile retroviral-like transposable element of tobacco isolated by plant cell genetics. Nature 337:376-380.

Grappin P, Audeon C, Chupeau MC, Grandbastien MA. 1996. Molecular and functional characterization of *Slide,* an *Ac* -like autonomous transposable element from tobacco. Mol. Gen. Genet. 252:386-397.

Hirochika H. 1997. Retrotransposons of rice: their regulation and use for genome analysis. Plant Mol. Biol. 35:231-240.

Hirochika H. 1999. Retrotransposons of rice as a tool for forward and reverse genetics. In: Shimamoto K, editor. Molecular biology of rice. Tokyo (Japan): Springer-Verlag. p 43-58.

Hirochika H. 2001. Contribution of the *Tos17* retrotransposon to rice functional genomics. Curr. Opin. Plant Biol. 4: 118-122.

Hirochika H, Sugimoto K, Otsuki Y, Tsugawa H, Kanda M. 1996. Retrotransposons of rice involved in mutations induced by tissue culture. Proc. Natl. Acad. Sci. USA 93:7783-7788.

Ito T, Seki M, Hayashida N, Shibata D, Shinozaki K. 1999. Regional insertional mutagenesis of genes on *Arabidopsis thaliana* chromosome V using the *Ac/Ds* transposon in combination with a cDNA scanning method. Plant J. 17:433-444.

Jeon JS, Lee S, Jung KH, Jun SH, Jeong DH, Lee J, Kim C, Jang S, Yang K, Nam J, An K, Han MJ, Sung RJ, Choi HS, Yu JH, Choi JH, Cho SY, Cha SS, Kim SI, An G. 2000. T-DNA insertional mutagenesis for functional genomics in rice. Plant J. 22:561-570.

Krysan PJ, Young JC, Sussman MR. 1999. T-DNA as an insertional mutagen in *Arabidopsis.* Plant Cell 11:2283-2290.

Kumar A, Bennetzen JL. 1999. Plant retrotransposons. Annu. Rev. Genet. 33:479-532.

Liljegren SJ, Ditta GS, Eshed Y, Savidge B, Bowman JL, Yanofsky MF. 2000. *SHATTER-PROOF* MADS-box genes control seed dispersal in *Arabidopsis.* Nature 404:766-770.

Liu Y-G, Whittier RF. 1995. Thermal asymmetric interlaced PCR: automatable amplification and sequencing of insert end fragment from P1 and YAC clones for chromosomal walking. Genomics 25:674-681.

Maes T, De Keukeleire P, Gerats T. 1999. Plant tagnology. Trends Plant Sci. 3:90-96.

Miyao A, Yamazaki M, Hirochika H. 1998. Systematic screening of mutants of rice by sequencing retrotransposon-insertion sites. Plant Biotechnol, 15:253-256.

Okamoto H, Hirochika, H. 2000. Efficient insertion mutagenesis of *Arabidopsis* by tissue culture-induced activation of tobacco retrotransposons *Tto1.* Plant J. 23:291-304.

Parinov S, Sevugan M, Ye D, Yang WC, Kumaran M, Sundaresan V. 1999. Analysis of flanking sequences from dissociation insertion lines: a database for reverse genetics in *Arabidopsis.* Plant Cell 11:2263-2270.

Parinov S, Sundaresan V. 2000. Functional genomics in *Arabidopsis:* large-scale insertional mutagenesis complements the genome sequencing project. Curr. Opin. Biotechnol. 11:157-161.

Pelaz S, Ditta GS, Baumann E, Wisman E, Yanofsky MF. 2000. B and C floral organ identity functions require *SEPALLATA* MADS-box genes. Nature 405:200-203.

Peschke VM, Phillips RL, Gengenbach BG. 1987. Discovery of transposable element activity among progeny of tissue culture-derived maize plants. Science 238:804-807.

Sasaki T, Burr B. 2000. International rice genome sequencing project: the effort to completely sequence the rice genome. Curr. Opin. Plant Biol. 3:138-141.

Sato Y, Sentoku N, Miura Y, Hirochika H, Kitano H, Matsuoka M. 1999. Loss-of-function mutations in the rice homeobox gene *OSH15* affect the architecture of internodes resulting in dwarf plants. EMBO J. 18:992-1002.

Speulman E, Metz PL, van Arkel G, te Lintel Hekkert B, Stiekema WJ, Pereira A. 1999. A two-component enhancer-inhibitor transposon mutagenesis system for functional analysis of the *Arabidopsis* genome. Plant Cell 11:1853-1866.

Takano M, Kanegae H, Shinomura T, Miyao A, Hirochika H, Furuya M. 2001. Isolation and characterization of rice phytochrome A mutants. Plant Cell 13:521-534.

Tissier AF, Marillonnet S, Klimyuk V, Patel K, Torres MA, Murphy G, Jones JD. 1999. Multiple independent defective suppressor-mutator transposon insertions in *Arabidopsis:* a tool for functional genomics. Plant Cell 11:1841-1852.

Tsay YF, Frank MJ, Page T, Dean C, Crawford NM. 1993. Identification of a mobile endogenous transposon in *Arabidopsis thaliana.* Science 260:342-344.

Vicient CM, Suoniemi A, Anamthawat-Jonsson K, Tanskanen J, Beharav A, Nevo E, Schulman A. 1999. Retrotransposon *BARE-1* and its role in genome evolution in the genus *Hordeum.* Plant Cell 11:1769-1784.

Voytas DF. 1996. Retroelements in genome organization. Science 274:737-738.

Walbot V. 2000. Saturation mutagenesis using maize transposons. Curr. Opin. Plant Biol. 3:103-107.

Wisman E, Hartmann U, Sagasser M, Baumann E, Palme K, Hahlbrock K, Saedler H, Weisshaar B. 1998. Knock-out mutants from an *En-1* mutagenized *Arabidopsis thaliana* population generate phenylpropanoid biosynthesis phenotypes. Proc. Natl. Acad. Sci. USA 95:12432-12437.

Yamazaki M, Tsugawa H, Miyao A, Yano M, Wu J, Yamamoto S, Matsumoto T, Sasaki T, Hirochika H. 2001. The rice retrotransposon *Tos17* prefers low-copy-number sequences as integration targets. Mol. Genet. Genomics 265:336-344.

Yu J and 99 others. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science 296:79-92.

Notes

Author's address: Molecular Genetics Department, National Institute of Agrobiological Sciences, Tsukuba, Ibaraki 305-8602, Japan; e-mail: hirohiko@nias.affrc.go.jp.

Acknowledgments: This work was supported by a project grant from the Ministry of Agriculture, Forestry, and Fisheries of Japan (Rice Genome Project MP-2101, 2102), a grant for the enhancement of Center-of-Excellence, special coordination funds for promoting science and technology in Japan, and the Program for Promotion of Basic Research Activities for Innovative Biosciences.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Marker-assisted evaluation of germplasm resources for plant breeding

Yunbi Xu, T. Ishii, and S.R. McCouch

The evaluation of germplasm resources is required for the continuous improvement of crop plants. Vast genetic resources are available for rice and other crops, but, to date, few of them have been characterized at the molecular level. Automated, high-throughput genotyping systems make large scale marker-assisted germplasm evaluation (MAGE) possible. A pilot study was undertaken to determine the relative utility of restriction fragment length polymorphism (RFLP) and simple sequence repeat (SSR) markers for the molecular characterization of rice germplasm. A set of 236 rice varieties was selected to represent the range of genetic diversity within *Oryza sativa.* The material was analyzed as two subsets, a U.S. collection, with 125 U.S. rice varieties, and a world collection, consisting of 111 diverse varieties collected from 22 other countries. All germplasm accessions were genotyped using 100 RFLP and 60 SSR markers. The resulting data set was used for (1) differentiating cultivars and constructing heterotic groups; (2) identifying germplasm redundancy, underrepresented alleles, and genetic gaps in current collections; (3) monitoring genetic shifts that occur during germplasm storage, regeneration, domestication, and breeding; (4) screening germplasm for novel/superior genes (alleles); and (5) constructing a representative subset or core collection. The results obtained from this data set are presented along with a literature review of other cereal crops. Several MAGE-related issues are also discussed, including the construction of an integrated germplasm database, genotyping cost as a bottleneck for MAGE, germplasm-based association genetics, and a broad-sense concept of germplasm.

Germplasm resources represent the genetic variability required for continuous improvement of crop plants. The old paradigm for germplasm characterization is based on the evaluation of phenotypic variation of entries from a genebank and looking for a clearly defined characteristic that is recognizable in the whole plant. This approach works well when the phenotype is controlled by major genes. For traits such as yield, which is genetically controlled by many genes, it is impossible to distinguish accessions by phenotypic evaluation alone because the same phenotype may be controlled by different genes, and vice versa. As a result, exotic germplasm, which is perceived to be a poor bet for the improvement of most traits based on phenotypic examination, may contain some superior genes (alleles) that lie buried amid the thousands of accessions maintained in genebanks (de Vicente and Tanksley 1993, Xiao et al 1998).

A new paradigm for germplasm characterization is based on genotypic evaluation using molecular markers and/or the integrative power of QTL analysis, which can be used to identify and extract superior genes (alleles) from inferior germplasm. Marker-assisted germplasm evaluation (MAGE) aims to complement phenotypic evaluation by helping define the genetic architecture of germplasm resources and by identifying and managing germplasm that contains alleles associated with traits of economic importance. Molecular markers may allow for characterization based on genes, genotypes, and genomes, which provide more accurate and detailed information than classical phenotypic or passport data. Many features revealed by molecular markers, such as unique alleles, allele frequency, and heterozygosity at marker loci, mirror the genetic structure of germplasm resources at the molecular level. On a more fundamental level, molecular marker information may lead to the identification of useful genes contained in collections and transferal of these genes into well-adapted cultivars. MAGE will play an important role in the procedures related to the acquisition/distribution, maintenance, and use of germplasm (Bretting and Widrlechner 1995, Xu 2003).

Molecular markers can be used for germplasm management in different ways. Markers with known functional alleles or associated with agronomic traits can be used to trace, select, and manage these alleles or traits. Genetic markers revealing multiple bands or representing multiple loci are usually difficult to trace back to specific alleles/loci, so they have to be converted into markers that are locus-specific, such as sequence tagged sites (STSs) or simple sequence repeats (SSRs). Markers in unknown chromosomal regions can be used for fingerprinting and background examination. In this case, any type of marker that detects a high rate of polymorphism is useful as long as it can reveal genome-wide polymorphism. Efficient marker-assisted germplasm management consists of several key components as discussed by Xu (2003). These include (1) suitable genetic markers characterized for number of alleles, polymorphic information content (PIC value), allele sizes and ranges, signal strength, working conditions, and information required for multiplexing; (2) high-density molecular maps so that markers can cover the whole genome and any specific region of interest; (3) established marker-trait associations for traits of agronomic importance; (4) high-throughput genotyping systems; and (5) an efficient data analysis and delivery system. In addition, germplasm resources should be well sampled for each research purpose. In this article, marker-assisted germplasm management and evaluation will be reviewed, along with a report of results from a MAGE project in rice.

Germplasm classification

Understanding the range of diversity and the genetic structure of gene pools is critical for the effective management and use of germplasm resources. Germplasm can be classified on the basis of morphological traits, geographic distribution, evolutionary and breeding history, pedigree, and/or genotypic diversity at molecular marker loci. Several genetic distance or similarity indices have been used as criteria for classification. Both categorical and quantitative data have been used for phenotype-based classification. A broad-based approach to germplasm classification will contribute to our understanding of the genetic structure of subpopulations within a species, how to identify useful gene donors, and the rationale for constructing heterotic groups for hybrid breeding.

The rice example we are going to use throughout this article is taken from a project conducted at Cornell University with basic information reported by Xu et al (2003). A total of 236 rice varieties were used, consisting of two subcollections: (1) the U.S. collection with 125 rice varieties from the U.S. and (2) the world collection with 111 varieties from other countries. All varieties were genotyped using 100 restriction fragment length polymorphism (RFLP) and 60 SSR markers and phenotyped for 12 agronomic traits. A genetic similarity index was computed based on shared allele frequency (S) between each pair of rice accessions, and then $1 - S$ was used as the genetic distance to construct the dendrograms depicting genetic relationships among these rice accessions.

RFLP marker-based analysis of the whole collection of 236 rice cultivars identified two major groups corresponding to the two subspecies, *indica* and *japonica,* respectively. Using SSR markers, however, more subgroups were recognized. Most of the U.S. cultivars belonged to a third group. These polymerase chain reaction (PCR)-based markers that could distinguish closely related accessions were then used to define subgroups within the U.S. cultivar collection. Two subgroups were identified, representing two different types of grain shapes: (1) long grain and (2) medium and short grain, with average grain lengths of 9.7 and 8.4 mm, respectively. The major long-grain cultivars released in Texas tended to cluster in the long-grain subgroup, whereas the medium- and short-grain cultivars released in California formed a cluster in the short-medium subgroup. Within each subgroup, some cultivars were closely clustered. They were either closer in pedigree or more similar in morphology. By comparison of allele frequencies between *indica* and *japonica* cultivars, several subspecies-specific alleles were identified, with one allele existing in more than 99% of *indica* cultivars and another in more than 99% of *japonica* cultivars. For example, the marker *RZ329/Dra*I had 4.3-kb *indica* and 3.3-kb *japonica* alleles, *RZ403/Dra*I had 8.6-kb *indica* and 6.7-kb *japonica* alleles, and *RG181/Dra*I had 3.0-kb *indica* and 2.6-kb *japonica* alleles.

Germplasm classification can be used to construct heterotic groups so that cultivars within each group have a high level of similarity in genetic background. As a result, intergroup hybrids show a higher level of heterosis than within-group hybrids. Commercial maize hybrids are typically made between inbreds from opposite, complementary heterotic groups. Heterotic patterns in many crop species have been established based solely on large numbers of testcrosses and extensive breeding experience. For inbreeding species for which subspecies or subpopulation differences may be older or more pronounced than in cross-pollinating species, DNA-based markers can be used to classify germplasm accessions into different heterotic groups, each with a high level of similarity.

Using diallel crosses among eight *indica* lines representing the parents of the best-performing commercial rice hybrids grown in China, Zhang et al (1995) studied molecular divergence and hybrid performance. Their results suggested the existence of two heterotic groups within *indica,* one composed of rice strains from southern China and the other composed of strains from Southeast Asia. Results from *Brassica* naps, barley, and wheat also supported the conclusion that DNA markers are very useful tools for the construction of heterotic groups. Divergence at molecular marker loci has also been useful in assigning maize inbreds to known heterotic groups previously established in breeding programs and the molecular information agreed with pedigree information (Lee et al 1989, Melchinger et al 1991, Messmer et al 1993).

Heterotic groups should not be considered as closed populations. They should be broadened continuously by introgressing novel alleles to warrant medium- and long-term gains from selection. Heterotic groups consisting of poorly used and unadapted germplasm should be enhanced through joint public-private breeding ventures. Marker-assisted selection (MAS) can be useful in creating, maintaining, and improving heterotic groups. The identification of marker alleles that are specific to each heterotic group will help keep them genotypically separated. MAS can be used to improve the existing heterotic groups through the introgression of complementary genes from one heterotic group or outsourcing of germplasm to another with minimum linkage drag from the donor.

Assessing collection redundancies and gaps

As a large number of germplasm accessions are available for each cultivated plant, many likely represent duplicate or nearly identical samples of the same cultivar, while others embody rare alleles or highly unusual allele combinations, with many genes or alleles still missing in current collections. According to the International Board for Plant Genetic Resources (IBPGR), more than 3.6 million germplasm accessions for different crop species are conserved at international and national genebanks, including 120,000 for wheat, 90,000 for rice, and 25,000 for maize (Iwanaga 1993). The evaluation of genetic diversity will help to understand the genetic structure of existing collections and to design appropriate acquisition strategies. In particular, genetic distance can be calculated to identify particularly divergent subpopulations that might harbor valuable genetic variation that is underrepresented in current holdings.

Germplasm redundancy exists in many germplasm collections because of different names for the same cultivars or duplicate samplings of the same accessions. Pedigree-related cultivars, siblines, and early isogenic lines may represent another type of redundancy because they are genotypically duplicated at most genetic loci. For example, U.S. rice cultivars M5, M301, M103, S201, Calrose, Calrose 76, CS-M3, and Calmochi-202 shared the same panel of alleles at all 100 RFLP loci. All these cultivars can be traced back to a common ancestor, Caloro. In addition, genetic polymorphism could be detected at any of the 60 SSR loci between Calrose and Calrose 76 (Xu et al 2003) because they are isolines, with Calrose 76 representing a variant derived from Calrose via chemical mutagenesis (Rutger et al 1977). Using 15 SSR markers, Dean et al (1999) assayed 19 sorghum [*Sorghum bicolor* (L.) Moench] accessions identified as "Orange" currently maintained by the U.S. National Plant Germplasm System (NPGS). They found that most accessions were genetically distinct, but two redundant groups were found. The variance analysis also indicated that it should be possible to reduce the number of Orange accessions held by NPGS by almost half without seriously jeopardizing the overall amount of genetic variation contained in these holdings. Chavarriaga-Aguirre et al (1999) evaluated genetic diversity and redundancy in a cassava core collection. The core collection (630 accessions) was selected from the base collection (more than 5,500 accessions) on the basis of diversity of origin (country and geographic), morphology, isozyme patterns, and specific agronomic criteria. A small number (1.34%) of potential duplicates were identified from the core collection through isozyme and amplified fragment length polymorphism (AFLP) profiles.

Germplasm collections can be compared for the frequencies of alleles at all marker loci so that distinctive alleles, allele combinations, and allele frequency patterns can be identified. Chromosomal regions containing loci that show the greatest changes in allele frequency between the collections can be located. The rationale for this analysis is to define genomic regions where selection had given rise to allele combinations or allele frequency patterns that distinguished a group of accessions with less diversity from a more diverse accession group. In the rice example, alleles at two RFLP loci (a 6.5-kb allele at CDO686/ *Hin*dIII and a 6.0-kb allele at BCD808/ *Xba*I) and alleles at six SSR loci were represented frequently (17.1-33.6%) in the world collection, but were entirely lacking in the U.S. cultivars. When low-frequency or underrepresented alleles are defined as those that occur in four or fewer U.S. cultivars but are very frequent (i.e., >30% for RFLP and >17% for SSR) in the world collection, alleles underrepresented in the U.S. collection were found at 19 RFLP and 18 SSR loci. Three U.S. cultivars, Della, Rexmont, and Caloro, retained 34 of these 37 low-frequency alleles. Della alone retained 24 (64.9%) of them, all of which could be traced back to two of its ancestral cultivars, Rexoro and Delitus. Selection against these alleles is clear from the fact that modem U.S. rice cultivars have been developed from a small set of germplasm introductions (Dilday 1990), with early cultivars retaining an unusually large number of alleles that show a decline in frequency among later-developed U.S. cultivars.

Monitoring genetic shifts

Maintaining genetic diversity and preventing genetic shifts are important objectives for germplasm conservation. In open-pollinated species, deviations from random mating, primarily in the form of assortative or consanguineous matings, need to be monitored during germplasm regeneration. In maize, deviations from random mating have been widely studied, with emphasis on detailed multilocus isozyme analyses of one or two synthetic or open-pollinated maize cultivars (Kahler et al 1984, Pollak et al 1984, Bijlsma et al 1986). In general, levels of selfing did not exceed those expected under random-mating models, but significant deviations were caused by temporal variation in the pollen pool or by gametophytic selection.

The genetic profiles of germplasm can change during the course of medium- or long-term storage. Storage effects fall into three broad categories: (1) the occurrence of mutations, (2) the occurrence of chromosomal aberrations, and (3) shifts in gene frequencies resulting from differential genotypic viability in heterogeneous populations (Roos 1988). After a comprehensive review of storage effects on seeds, Roos (1988) found little evidence for heritable changes in germplasm attributable to storage-induced chromosomal aberrations, and noted “little need for concern about mutation as a significant factor in altering the composition of germplasm collections.” However, differential seed longevity can markedly reduce genetic variability over time (Bretting and Widrlechner 1995). This is well documented by experiments involving mixtures of eight bean lines (Roos 1984) and four seed storage protein genotypes within a cultivar of wheat (Stoyanova 1991).

Genetic shifts can also be caused by in vitro culture. The genetic stability of germplasm maintained in tissue culture (in vitro) has historically been monitored with karyotypic markers such as chromosome number and morphology (D’Amato 1975) because cytological variability has been considered a primary cause of somaclonal variation. Lassner and Orton (1 983) reported that isozymatically identical in vitro cultures of celery were markedly variable cytologically. More recently, in vitro culture has been shown to induce changes because of the mobilization of transposable elements (Jiang et al 2003, Kikuchi et al 2003, Nakazaki et al 2003). These findings should reinforce the concept that the genetic stability of in vitro cultures should be monitored with a battery of different genetic markers, particularly with transposon-based DNA markers that collectively span the whole genome.

A certain level of heterogeneity could exist in germplasm accessions that are mainly self-pollinated, which provides a buffer for maintaining genetic diversity and preventing genetic shifts. Monitoring heterogeneous accessions will help develop strategies for regeneration of germplasm samples without loss of the allelic diversity provided by heterogeneity. In general, traditional cultivars had a higher level of heterozygosity, as reported in rice by Olufowote et al (1997). Genetic diversity resulting from heterozygosity or heterogeneity was also found within inbred lines from different sources in rice (Olufowote et al 1997) and maize (Gethi et al 2002). In the rice example, a total of 120 (50.6%) of the 236 rice accessions were found to be heterozygous/heterogeneous at one or more RFLP or SSR loci, and the number of heterozygous loci detected in a single rice accession ranged from 0 to 39 (25.3% of the 160 loci). These heterozygous allele patterns could indicate either seed mixtures or true heterozygosity remaining in these cultivars although all accessions had been purified and no visible phenotypic variation was detected.

The existence of off-types is one of the factors contributing to genetic shifts. Off-types are the plants that are different, either phenotypically or genotypically, from the plants developed by breeders. They may result from mechanical mixtures, outcrossing, mutation, or residual genetic variation. Genotypic off-types may severely affect germplasm management and may contribute to reduced performance of commercial cultivars. Off-types may be exaggerated by seed multiplication, contributing to genetic shifts in population structure. Molecular marker technology provides a powerful way of distinguishing both phenotypic and genotypic off-types from the original germplasm sources. Highly informative molecular markers such as SSRs could be used to distinguish two plants with similar genetic backgrounds. Using ten or more SSR markers, rice researchers can easily identify off-types caused by genetic mixture and distinguish them from their distinct originals. The marker information can be used to obtain detailed genotypic information such as where the off-type genotypes may have come from and at what proportion they are detected relative to the "typical" plants. A decision about selection and purification can then be made to refine or purify the germplasm accessions.

Allelic variations of genes originally found in ancestral cultivars or the wild relatives may be gradually lost through domestication and breeding. Modern breeding programs generally rely on a small number of superior accessions, which results in genetic uniformity and loss of diverse alleles that could be important to future breeding programs. Valuable lost genes or alleles can be recovered by going back to the ancestors or wild relatives of our crop species. Using 47 microsatellite markers, Christiansen et al (2002) determined the variation of genetic diversity in 75 Nordic spring wheat cultivars bred during the 20th century. They found that some alleles were lost during the first quarter of the century, whereas several new alleles were introduced in the Nordic spring wheat material during the second quarter of the century.

Identifying unique germplasm

Continuous progress in plant breeding depends on (1) the discovery and production of genetic variation for yield and other agronomic traits and (2) the accurate selection of rare genotypes that possess new or improved attributes resulting from superior combinations of alleles at multiple loci. Over the past century, the development and successful application of modem breeding methodologies has produced most of the high-yielding cultivars and hybrids on which modern farming is based. As the demand for uniform performance and grain quality has increased, new cultivars and hybrids are increasingly derived from adapted, genetically related, and elite modern cultivars/hybrids, while genetically more variable, but less productive, primitive ancestors are excluded from most breeding programs. In a study of pedigree relationships among

140 U.S. rice accessions, Dilday (1990) concluded that all parental germplasm in public cultivars used in the southern U.S. today could be traced back to 22 plant introductions in the early 1900s, and those used in California could be traced to 23 introductions. The same situation is true for soybean and wheat. Virtually all modern U.S. soybean cultivars can be traced back to a dozen strains from a small area in northeastern China, and the majority of hard red winter wheat cultivars in the United States originated from just two lines imported from Poland and Russia (Duvick 1977, Harlan 1987). To broaden the genetic base of specific cultivated species, the genetic diversity within collections must be assessed in the context of the total available genetic diversity for each species. With the use of DNA profiles, the genetic uniqueness of each accession in a germplasm collection or in a population can be determined, and the identity and frequency of individual alleles can be clearly described and characterized (Brown and Kresovich 1996, Smith and Helentjaris 1996).

The sampling of exotic germplasm should emphasize the genetic composition rather than the appearance of exotic accessions. Accessions with DNA profiles most distinct from that of modern germplasm are likely to contain the greatest number of novel alleles. Assuming that most marker alleles having the same molecular weight are likely to be common by descent in a specific varietal group, we are able to trace alleles that are frequent in one specific collection but existed in low frequency or not at all in the other. Examination of the chromosomal distribution of the loci harboring underrepresented alleles indicated that underrepresented alleles in the U.S. rice collection tended to cluster on 11 chromosomal fragments (Xu et al 2003). This raises the question about what genes are located in these regions and whether U.S. breeders have consciously or unconsciously narrowed the range of genetic variation in these regions. It also suggests that molecular marker analysis could be used to identify parents harboring rare or novel alleles in these regions so that the functional significance of the resident genes could be determined using both traditional crossing and sequence-based genomics approaches. Considering the allele frequency profiles across all cultivars will give us some idea of which cultivars may retain or contain the rare genes/alleles and whether these alleles may be important to our future breeding programs.

The germplasm that holds unique alleles may contain unique genetic variation required for trait improvement. In the rice example, 15 (6.4%) of the 236 rice accessions contained unique alleles (those present in only one cultivar) for at least one RFLP locus, and 81 (34.3%) rice accessions had unique SSR alleles. The germplasm accessions identified as having unique alleles also have unusual geographic origins with high genetic diversity and could have potential use in the exploitation of heterosis.

The degree of genetic similarity between any two cultivars can be calculated as the proportion of shared alleles. The most similar accessions share alleles at almost all marker loci while the least similar accessions have few or no alleles in common. When evaluating genetic similarity, shared allele frequencies (SAFs) are averaged over all possible pairs of cultivars. A smaller average similarity indicates a greater genetic difference with respect to the rest of the cultivars in the collection. Based on the averaged SAF, the most diverse accessions can be selected to represent cultivars that host the least-frequent alleles and are genotypically most different from other accessions. From 236 rice cultivars, Xu et al (2003) selected the 16 most diverse accessions (with SAF < 50%) based on RFLP markers and 49 accessions based on SSR markers. Most of these selections, such as Caloro, Cina, Badkalamkati, DGWG, and TN1, were ancestral cultivars that had been used as parents in breeding programs more than 40 years ago, and none of the selections is from the U.S. collection that has a much narrower genetic basis.

Marker-assisted genetic mapping studies involving interspecific crosses have identified novel/superior alleles coming from phenotypically unfavorable distant relatives that enhance the performance of modem cultivars (Xiao et al 1998, Moncada et al 2001, Brondani et al 2002, Nguyen et al 2003, Thomson et al 2003). These novel alleles are present in germplasm collections but have not been previously identified because they are hidden in the inferior phenotype. The valuable alleles identified from *O. rufipogon* that increase yield in commercial cultivars have been used to improve the best hybrids that have been commercialized in China for more than 20 years (Xiao et al 1998), and new hybrids containing these *O. rufipogon* introgressions demonstrate more than a 30% yield advantage over previous Chinese hybrids (Yuan 2002).

Molecular markers are also used for the evaluation of variation among A-genome species of rice. A-genome species consist of two cultivated species (*O. sativa* and *O. glaberrima*) and five wild species (*O. rufipogon, O. glumaepatula, O. longistaminata, O. meridionalis,* and *O. barthii*). Ishii et al (2001) examined allelic diversity at 24 SSR marker loci using 29 cultivars and 30 accessions of wild A-genome species. Although SSR primers were based on sequence information from a single cultivar (*O. sativa* cv. IR36), null alleles (no amplification) were rarely observed (2.8%). Among A-genome species, the highest average SAF was observed between *O. glaberrima* and *O. barthii* (56%), followed by *O. sativa* and *O. rufipogon* (11 %), confirming their cultivar-progenitor relationships. The average SAFs between *O. sativa* and the other five A-genome species were less than 5%. The high level of genetic diversity (reflected in the low SAFs) between *O. sativa* and other A-genome species indicated that marker-assisted genetic mapping using populations derived from interspecific crosses was likely to access many novel alleles and that SSR markers were an efficient tool for mapping in interspecific populations. Bautista et al (2001) studied phylogenetic relationships among A-genome species of rice using RFLP, random amplified polymorphic DNA (RAPD), and SSR markers. They also detected a high level of SSR polymorphism among A-genome species. However, species relationships were more clearly determined using less variable markers such as WLPs and RAPDs. These studies suggested that *O. glumaepatula* (from South America) was relatively closely related to the cultivated species, *O. sativa* and *O. glaberrima,* whereas *O. longistaminata* and *O. meridionalis* were highly differentiated from other A-genome species. This study emphasized the value of using the more conservative RFLP and RAPD markers for phylogenetic reconstruction among evolutionarily diverse species.

Construction of a core collection

As defined by Frankel (1984), a core subset of a germplasm collection contains most of the entire collection's genetic diversity with minimal redundancy. Construction of a core collection involves selecting approximately 10% of the germplasm accessions to represent at least 70% of the genetic variation (e.g., Brown 1989a,b). Combining the use of different types of markers that reveal different levels of genetic diversity will help select a core collection to better represent genome-wide diversity. A combination of phenotypic and genotypic selection, using SAFs as a measure of genetic divergence at the genotypic level, can help construct the core collection.

In the rice example, accessions for the core collection were selected based on SAFs and the frequency of unique RFLP and SSR alleles. Subsets of various sizes were selected (representing 5% to 50% of the U.S. and world collections), using random selection as a control. For each sample size, 200 replications were analyzed through a resampling technique and the number of alleles in each subgroup was compared with the total number of alleles identified in the larger collection from which the subsets were sampled. The following conclusions were obtained (Xu et al 2003): (1) more samples were needed to represent the world collection, which was more diverse than the U.S. collection, which contained more pedigree-related cultivars; (2) combining the use of SAF and unique alleles improved the representativeness of the core collection; (3) core collections selected based on SAF required fewer samples than random selection for the same level of representativeness; and (4) more samples were needed to adequately represent genetic diversity if highly polymorphic markers were used (e.g., SSRs vs RFLPs). A cultivar subset (13% of the entire collection), selected based on both shared allele frequencies and number of unique alleles detected, represented 94.9% of the RFLP alleles but only 74.4% of the SSR alleles. It can be expected that selection criteria based on additional sources of information will further improve the value and representativeness of core collections.

In barley, Russell et al (2000) found that 19 "foundation genotypes" (landraces and key progenitors) contained 72% of the alleles detected at 28 SSR loci present in the 101 sampled cultivars based on a retrospective analysis of currently successful spring barley cultivars developed from foundation genotypes. A set of 44 selected cultivars could encompass all of the alleles. For crops with larger collections, core subsets have been designated for a more concentrated distribution pattern within the NPGS. Crops with cores established include alfalfa, barley, chickpea, clover, lentil, medic, peanut, bean, pea, safflower, and wheat (Clark et al 1997). Several types of data were used for each crop, with geographic origin usually one of the first criteria for selection. Morphological as well as molecular markers were also used to analyze genetic differences.

When molecular markers are developed from DNA sequences with unknown function, identical marker alleles in two collections may not necessarily mean that the two collections share identical functional genes linked to the marker locus. Genetic variation for important phenotypic traits could be lost if core collections are based solely on the use of DNA markers. As the genome sequence is deciphered and the function of many genes is determined, gene-specific markers with identified functional nucleotide polymorphisms (FNP) will become available for many genes. Core collections of germplasm constructed using FNP could be assembled to represent a "core collection" of genes. As gene structure-function relationships are clarified with greater precision, it will be possible to focus attention on genetic diversity within the active sites of a structural gene or within key promoter regions. This will make it productive to screen large germplasm collections for FNP, targeting the search for alleles that are likely to be phenotypically relevant at specific loci. From a primary collection, a user who had identified an accession or accessions of interest would move to the next level of information, where clusters of germplasm known to represent a broader spectrum of diversity within a specific gene pool, or a specific trait, could be defined. The second level of investigation could be conducted using carefully designed sets of molecular markers known to target specific traits or regions of the genome. The construction of core collections using these approaches may help establish heterotic groups and choose parents for establishing base populations.

Germplasm genotyping database

Plant geneticists and breeders can use the data from a germplasm evaluation project as a guide in choosing the most efficient crosses for genetic studies and breeding. The rice example given in this article provides preliminary polymorphism data for many pairwise combinations of parents. Theoretically, the data set with 236 rice cultivars provides polymorphism surveys for $236 \times 235/2 = 27{,}730$ possible cross combinations, including thousands of *indica/indica, indica/japonica,* and *japonica/japonica* crosses. With an increasing number of markers surveyed on a variety of germplasm accessions and as more data flow into the database from multiple sources, it will be increasingly possible to determine the genetic constitution and genetic relationships among a wide range of parental lines, cultivars, and wild relatives. This also provides the foundation for developing hypotheses based on association genetics to relate agronomically important phenotypes to the presence or absence of specific molecular marker alleles.

A comprehensive DNA fingerprinting of crop gene pools, including as many cultivars, hybrid parents, and progenies as possible, is the first step for using MAS in plant breeding. These data can be integrated with both phenotypic information and pedigree information. A database of DNA marker alleles for the elite gene pool of a crop provides information on specific DNA polymorphisms that is needed to design, execute, and analyze genetic mapping experiments, targeted at specific traits or specific crosses. The same database serves as a classification tool, describing the overall levels and patterns of variation within the crop gene pool and illustrating subdivisions within a gene pool such as heterotic groups. Such information is useful in making predictions about the performance of new cultivars and hybrids, or selecting parents for crosses that are likely to yield new gene combinations or afford an optimal degree of performance.

An efficient approach to the screening of germplasm involves the ability to rapidly create a nested series of core collections, based on information about geographic, phenotypic, and genotypic diversity stored in a database. The construction of such a system would require a large-scale effort to provide genotypic information using a standard set of markers that could serve as a reference point. As new markers and marker systems were developed, they could be overlaid onto the essential framework of diversity established previously. An increasingly powerful information system could be developed if data models were made explicit and the data structures were modular so that new types of genetic information could be readily incorporated as they became available. By accumulating historical information in a systematic way, germplasm collections would rapidly gain in value because they could be screened computationally for essential molecular and phenotypic characteristics of interest.

Databases for whole genomic sequences for several important species, both dicots and monocots, are available, allowing directed discovery of genes in higher plants and classification of alleles present in a wide range of breeding germplasm. As indicated by Sorrells and Wilson (1997), the identification of the genes controlling a trait and knowledge of their DNA sequence would facilitate the classification of variation in a germplasm pool based on gene fingerprinting or characterization of variation in key DNA sequences. Classification of functional sequence variants within genes such as FNP at a large number of targeted loci would substantially reduce the amount of work required to determine their relative breeding value and lead to the identification of superior alleles.

It is important for all researchers to follow general rules for reporting their genotyping and phenotyping results. One direction for the use of a germplasm database is to combine information collected from global research efforts. Facilitating cross talk among currently existing genome databases specializing in sequence information or expression data with databases documenting phenotypic and genotypic variation will add value to all sources of information.

Future prospects

A bottleneck currently limiting the extensive use of molecular markers in germplasm management is the high cost per data point. The cost of molecular genotyping depends on marker type and its capacity in high-throughput analysis. For example, the cost of SNP analysis is now about US$0.20-0.30 per genotype, with a cost of only a few cents per genotype expected in the coming years (Jenkins and Gibson 2002). With well-established marker systems and sequencing facilities, genotyping with SSR markers costs about $0.30-0.80 per data point, depending on marker multiplexing and the number of markers genotyped for each sample (Xu et al 2002). There are several ways to reduce the cost of marker evaluation. First, increasing the throughput using automated genotyping and data-scoring systems can help increase the daily data output (Coburn et al 2002). Second, the optimization of marker systems, including facilities and personnel, will result in less cost per data point.

Genomic research has helped establish an information flow from molecular markers to genetic maps to sequences to genes and to functional alleles. Apparently, however, there is still a gap between sequence-based information targeting genes and alleles and breeding-related information targeting germplasm, pedigrees, and phenotypes. Phenotypic evaluation still provides the foundation for functional analysis of genes even though a complete draft of the genomic sequence of rice is available. Integration of breeding-related phenotypic evaluation with the high-throughput evaluation of mutants in a genomics context will hasten progress toward understanding the functions of all plant genes in the years ahead. This information will enhance an effort to use MAGE effectively to achieve a substantial increase in the efficiency of germplasm management in the years to come.

The breadth of genetic information from thousands of DNA polymorphisms and the depth of phenotypic measurements hold promise for identifying marker-trait correlations using association genetics. At a fundamental level, both genetic association and linkage rely on the co-inheritance of adjacent DNA variants. Linkage studies capitalize on this by identifying haplotypes that are inherited intact over several generations, while association studies rely on the retention of adjacent DNA variants over many generations. Thus, association studies can be regarded as very large linkage studies of unobserved hypothetical pedigrees (Cardon and Bell 2001). Recombination is the primary force that eliminates linkage and disrupts association over generations, while mutation is the one that obscures associations. Previous attempts were made in rice to detect marker-trait associations based on the use of unmapped RAPD markers and a wide array of *O. sativa* genotypes that were not analyzed for population substructure (Virk et al 1996). Using the data set described in this paper, genetically mapped markers were also used to identify marker-trait associations (Xu 2002, Y. Xu and S.R. McCouch, Cornell University, unpublished data). A comparison of marker-trait associations in different cultivar groups demonstrated that both phenotypic variation and pedigree relationship among rice accessions strongly influenced the detection of associations. Several highly consistent allele-trait associations were revealed among multiple alleles at specific loci. However, evidence of allelic associations or marker-trait associations did not always imply that two loci were linked. Spurious associations can be produced by random genetic drift, founder effect, mutation, selection, and/or population admixture and stratification (Sham 1997, Jannink and Walsh 2002). For several reasons, enthusiasm is great at present about the promise of association studies for uncovering the genetic components of complex traits in humans: dense SNP maps across the genome, elegant high-throughput genotyping techniques, simultaneous comparison of groups of loci, statistical measures for assessing genome-wide significance, and phenotypic insights as the basis for comparative genomic studies among different human groups are all available. These conditions have already been or will soon be satisfied in plants as well, and association studies are beginning to emerge in maize (Thornsbeny et al 2001) and *Arabidopsis* (Nordberg et al 2002). These studies bring together the power of genomics with the richness of crop germplasm collections and promise to provide new insights into the genetic bases of domestication and productivity of our major food crops.

In the age of genomics, the value of germplasm resources, including whole plants, seeds, plant parts, tissues, and clones, from distinct species and synthetic germplasm and all types of mutants is receiving new attention. The ultimate goal of germplasm conservation is to maintain diversity of the genes and gene combinations (Xu and Luo 2002). Information about germplasm resources is increasingly extracted from studies involving the relationship between genome sequence and the biological and evolutionary significance in the context of genetic resources. This information can be translated across species in a comparative context and thus the effective management of germplasm resources today involves both the practical management of seeds, tissues, clones, cells, and mutant stocks and the effective management of large reservoirs of electronic information that helps us decipher the value and meaning of the genetic information contained within each germplasm accession.

References

Bautista NS, Solis R, Kamijima O, Ishii T. 2001. RAPD, RFLP and SSLP analyses of phylogenetic relationships between cultivated and wild species of rice. Genes Genet. Syst. 76:71-79.

Bijlsma R, Allard RW, Kahler AL. 1986. Nonrandom mating in an open-pollinated maize population. Genetics 112:669-680.

Bretting PK, Widrlechner MP. 1995. Genetic markers and plant genetic resource management. Plant Breed. Rev. 13:11-86.

Brondani C, Rangel N, Brondani V, Ferreira E. 2002. QTL mapping and introgression of yield-related traits from *Oryza glumaepatula* to cultivated rice (*Oryza sativa*) using microsatellite markers. Theor. Appl. Genet. 104:1192-1203.

Brown ADH. 1989a. The case for core collections. In: Brown ADH, Frankel OH, Marshall RD, Williams JT, editors. The use of plant genetic resources. Cambridge (UK): Cambridge University Press. p. 136-156.

Brown ADH. 1989b. Core collection: a practical approach to genetic resources management. Genome 31:818-824.

Brown SM, Kresovich S. 1996. Molecular characterization for plant genetic resources conservation. In: Paterson AH, editor. Genome mapping in plants. Austin, Tex. (USA): R. G. Landes Co. p 85-93.

Cardon LR, Bell JI. 2001. Association study designs for complex diseases. Nat. Rev. Genet. 2:91-99.

Chavarriaga-Aguirre P, Maya MM, Tohme J, Duque MC, Iglesias C, Bonierbale MW, Kresovich C, Kochert G. 1999. Using microsatellites, isozymes and AFLPs to evaluate genetic diversity and redundancy in the cassava core collection and to assess the usefulness of DNA-based markers to maintain germplasm collections. Mol. Breed. 5:263-273.

Christiansen MJ, Anderson SB, Ortiz R. 2002. Diversity changes in an intensively bred wheat germplasm during the 20th century. Mol. Breed. 9:1-11.

Clark RL, Shands HL, Bretting PK, Eberhart SA. 1997. Germplasm regeneration: developments in population genetics and their implications. Crop Sci. 37:1-6.

Coburn J, Temnykh S, Paul E, McCouch SR. 2002. Design and application of microsatellite marker panels for semi-automated genotyping of rice (*Oryza sativa* L.). Crop Sci. 42:2092-2099.

D'Amato F. 1975. The problem of genetic stability in plant tissues and cell cultures. In: Frankel O, Hawkes JG, editors. Crop genetic resources for today and tomorrow. Cambridge (UK): Cambridge University Press. p 333-348.

Dean RE, Dahlberg JA, Hopkins MS., Kresovich S. 1999. Genetic redundancy and diversity among 'Orange' accessions in the U.S. national sorghum collection as assessed with simple sequence repeat (SSR) markers. Crop Sci. 39:1215-1221.

de Vicente MC, Tanksley SD. 1993. QTL analysis of transgressive segregation in an inter-specific tomato cross. Genetics 134:585-596.

Dilday RH. 1990. Contribution of ancestral lines in the development of new cultivars of rice. Crop Sci. 30:905-911.

Duvick DN. 1977. Major USA crops in 1976. In: Day PR, editor. Annals of the New York Academy of Sciences. New York, NY (USA): New York Academy of Sciences. 287:86-96.

Frankel O. 1984. Genetic perspectives of germplasm conservation. In: Arber W, Limensee K, Peacock WJ, Starlinger P, editors. Genetic manipulation: impact on man and society. Cambridge (UK): Cambridge University Press. p 161-170.

Gethi JG, Labate JA, Lamkey KR, Smith ME, Kresovich S. 2002. SSR variation in important U.S. maize inbred lines. Crop Sci. 42:951-957.

Harlan JR. 1987. Gene centers and gene utilization in American agriculture. In: Yeatman CW, Kafton D, Wilkes G, editors. Plant genetic resources: a conservation imperative. Boulder, Colo. (USA): Westview. p 111-129.

Ishii T, Xu Y, McCouch SR. 2001. Nuclear- and chloroplast-microsatellite variation in A-genome species of rice. Genome 44:658-666.

Iwanaga M. 1993. Enhancing links between germplasm conservation and use in a changing world. In: International crop science I. Madison, Wis. (USA): Crop Science Society of America. p 407-413.

Jannink JL, Walsh B. 2002. Association mapping in plant populations. In: Kang MS, editor. Quantitative genetics, genomics and plant breeding. Wallingford (UK): CAB International. p 59-68.

Jenkins S, Gibson N. 2002. High-throughput SNP genotyping. Comp. Funct. Genom. 3:57-66.

Jiang N, Bao Z, Zhang X, Hirochika H, Eddy SR, McCouch SR, Wessler SR. 2003. An active DNA transposon family in rice. Nature 421:163-167.

Kahler AL, Gardner CO, Allard RW. 1984. Nonrandom mating in experimental populations of maize. Crop Sci. 24:350-354.

Kikuchi K, Terauchi K, Wada M, Hirano Y. 2003. The plant MITE mPing is mobilized in anther culture. Nature 421: 167-170.

Lassner MW, Orton TJ. 1983. Detection of somatic variation. In: Tanksley SD, Orton TJ, editors. Isozymes in plant genetics and breeding. Vol. 1A. Developments in plant genetics and breeding, 1. Amsterdam (Netherlands): Elsevier. p 209-217.

Lee M, Godshalk EB, Lamkey KR, Woodman WL. 1989. Association of restriction length polymorphism among maize inbreds with agronomic performance of their crosses. Crop Sci. 29:1067-1071.

Melchinger AE, Messmer MM, Lee M, Woodman WL, Lamkey KR. 1991. Diversity and relationships among U.S. maize inbreds revealed by restriction fragment length polymorphism. Crop Sci. 31:669-678.

Messmer MM, Melchinger AE, Herrmann RG, Boppenmaier J. 1993. Relationships among early European maize inbreds. II. Comparisons of pedigree and RFLP data. Crop Sci. 33:944-950.

Moncada P, Martinez CP, Borrero J, Chatel M, Gauch H, Guimarães E, Tohme J, McCouch SR. 2001. Quantitative trait loci for yield and yield components in an *Oryza sativa* × *Oryza rujipogon* BC_2F_2 population evaluated in an upland environment. Theor. Appl. Genet. 102:41-52.

Nakazaki T, Okumoto Y, Horibata A, Yamahira S, Teraishi M, Nishida H, Inoue H, Tanisaka T. 2003. Mobilization of a transposon in the rice genome. Nature 421:170-172.

Nguyen BD, Brar DS, Bui BC, Nguyen TV, Pham LN, Nguyen HT. 2003. Identification and mapping of the QTL for aluminum tolerance introgressed from the new source *Oryza rufipogon* Griff. into *indica* rice (*Oryza sativa* L.). Theor. Appl. Genet. 106:583-593.

Nordberg M, Borevitz JO, Bergelso J, Berry CC, Chory J, Hagenblad J, Kreitman M, Maloof JN, Noyes T, Oefner PJ, Stahl EA, Weigel D. 2002 The extent of linkage disequilibrium in *Arabidopsis thaliana.* Nat. Genet. 30:190-193.

Olufowote JO, Xu Y, Chen X, Park WD, Beachell HM, Dilday RH, Goto M, McCouch SR. 1997. Comparative evaluation of within-cultivar variation of rice (*Oryza sativa* L.) using microsatellite and RFLP markers. Genome 40:370-378.

Pollak LM, Gardner CO, Kahler AL, Thomas-Compton M. 1984. Further analysis of the mating system in two mass selected populations of maize. Crop Sci. 24:793-796.

Roos EE. 1984. Genetic shifts in mixed bean populations. I. Storage effects. Crop Sci. 24:240-244.

Roos EE. 1988. Genetic changes in a collection over time. HortScience 23:86-90.

Russell JR, Ellis RP, Thomas WTB, Waugh R, Provan J, Booth A, Fuller J, Lawrence P, Young G, Powell W. 2000. A retrospective analysis of spring barley germplasm development from ‘foundation genotypes’ to currently successful cultivars. Mol. Breed. 6:553-568.

Rutger JN, Peterson ML, Hu CH. 1977. Registration of Calrose 76 rice. Crop Sci. 17:978.

Sham P. 1997. Statistics in human genetics. New York (USA): John Wiley & Sons.

Smith S, Helentjaris T. 1996. DNA fingerprinting and plant variety protection. In: Paterson AH, editor. Genome mapping in plants. Austin, Tex. (USA): R. G. Landes Company. p 95-110.

Sorrells ME, Wilson WA.1997. Direct classification and selection of superior alleles for crop improvement. Crop Sci. 37:691-697.

Stoyanova SD. 1991. Genetic shifts and variations of gliadins induced by seed aging. Seed Sci. Technol. 19:363-371.

Thomson MJ, Tai TH, McClung AM, Hinga ME, Lobos KB, Xu Y, Martinez C, McCouch SR. 2003. Mapping quantitative trait loci for yield, yield components, and morphological traits in an advanced backcross population between *Oryza rufipogon* and the *Oryza sativa* cultivar Jefferson. Theor. Appl. Genet. (In press.)

Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES. 2001. *Dwarf8* polymorphisms associate with variation in flowering time. Nat. Genet. 28:286-289.

Virk PS, Ford-Lloyd BV, Jackson MT, Pooni HS, Clemeno TP, Newbury HJ. 1996. Predicting quantitative variation within rice germplasm using molecular markers. Heredity 76:296-304.

Xiao J, Li L, Grandillo S, Yuan L, Tanksley SD, McCouch SR. 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon.* Genetics 150:899-909.

Xu Y. 2002. Global view of QTL: rice as a model. In: Kang MS, editor. Quantitative genetics, genomics and plant breeding. Wallingford (UK): CAB International. p 109-134.

Xu Y. 2003. Developing marker-assisted selection strategies for breeding hybrid rice. Plant Breed. Rev. (In press.)

Xu Y, Luo L. 2002. Biotechnology and germplasm resource management in rice. In: Luo L, Ying C, Tang S, editors. Rice germplasm resources. Wuhan (China): Hubei Sci. Tech. Publisher. p 229-250.

Xu Y, Lobos KB, Clare KM. 2002. Development of SSR markers for rice molecular breeding. In: Proceedings of the Twenty-Ninth Rice Technical Working Group (RTWG) Meeting, 24-27 February 2002. Little Rock, Ark. (USA): RTWG. p 49.

Xu Y, Beachell HM, McCouch SR. 2003. A marker-based approach to broadening the genetic base of rice (*Oryza sativa* L.) in the U.S. Crop Sci. (Submitted.)

Zhang Q, Gao YJ, Saghai Maroof MA, Yang SH, Li JX. 1995. Molecular divergence and hybrid performance in rice. Mol. Breed. 1: 133-142.

Notes

Authors' addresses: Yunbi Xu, RiceTec, Inc., P.O. Box 1305, Alvin, TX 77512, USA; T. Ishii, Laboratory of Plant Breeding, Faculty of Agriculture, Kobe University, Nada-ku, Kobe 657, Japan; S.R. McCouch, Plant Breeding Department, Cornell University, Ithaca, NY 14853-1901, USA.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Molecular breeding of rice for drought tolerance

B. Courtois, R. Lafitte, S. Robin, L. Shen, M.S. Pathan, H. Nguyen

Water deficit is an increasingly important constraint limiting rice production, highlighting the need for varieties with improved drought tolerance and technologies that increase water-use efficiency. Drought tolerance, however, is a complex character resulting from the interaction of many quantitative component traits. Marker-based genetic studies permitted the identification of reliable QTLs for root traits and osmotic adjustment. To demonstrate the value of marker-aided selection to manipulate QTLs, we describe two examples of introgression of QTLs into elite material undertaken in the framework of an upland rice breeding program. The first study targeted root depth. Several QTLs from Azucena, a deep-rooted variety, were introgressed into IR64 through three cycles of backcrosses with selection based on marker information alone. The evaluation of the BC_3F_3 families showed what progress could be expected and how progress was affected by lack of precision in QTL positions. For the second study, targeting osmotic adjustment, we used the advanced backcross QTL analysis method, which allows the simultaneous discovery and transfer of interesting QTLs, a procedure that appeared more adapted to a breeding program. We transferred QTLs for osmotic adjustment from IR62266, an indica donor, into IR60080-46A, a japonica elite line, conducted QTL analysis in a BC_3F_3 population, and outlined a strategy to construct improved near-isogenic lines. The candidate gene approach was used to associate genes with QTLs in this population. Association studies based on linkage disequilibrium in breeders' working collections could allow further progress by locating QTLs more precisely.

From an evolutionary point of view, rice is an aquatic crop that has been only secondarily adapted to nonflooded environments. Rice is therefore more sensitive to periods of water deficit than any other cereal. About 45% of the total rice area is currently planted without irrigation. In the irrigated areas, the cost of irrigation has increased substantially. Competition for water between rice production and nonagricultural activities is increasing and water shortages sometimes occur even in the irrigated areas. Varieties with improved drought tolerance as well as technologies for increasing water-use efficiency are needed to cope with this situation. Drought tolerance, however, is a complex character resulting from many interacting component traits. Stable yield under water-limited conditions is the final breeders' target but the selected material also needs to perform well under well-watered conditions. Since it is rather difficult to evaluate yield reliably under stress because of drought's unpredictable nature, most teams choose to work on morphological or physiological traits assumed to be well correlated with yield under stress. There is a long list of potentially valuable secondary traits, which are generally classified into three mechanisms: escape, avoidance, or true tolerance. The choice of the secondary trait(s) to focus on depends on the nature of the drought situations in the target ecosystems (upland, rainfed lowland, or irrigated) and environments (phenological stage of occurrence, duration, and severity of the water deficits) and supposes therefore that a good initial agroclimatic characterization has been undertaken.

In this paper, we will develop the case of upland rice, but most of the strategy presented would apply to rainfed lowland rice as well. The different agroecological zones of upland rice production identified in Asia as well as the overall framework of the breeding program for these drought-prone environments were described in detail in Courtois and Lafitte (1999). Traditional upland rice varieties shaped by generations of selection pressure under aerobic conditions are among the most drought-tolerant rice varieties. The deep and thick root system of these varieties is one of the traits recognized as contributing to their drought tolerance and is said to be correlated with yield under water-limited conditions. An important objective of upland rice breeders is therefore to keep this quality in the improved varieties while improving yield potential.

Osmotic adjustment, which is the ability of a plant cell to actively accumulate solutes in a water-deficit situation, resulting in the maintenance of high turgor, is low in most upland varieties. Improvement in this trait could therefore bring a significant improvement in drought tolerance. Its effect on yield under water-limited situations, however, is unknown in rice.

Most traits involved in drought tolerance have been shown to be quantitative. Genetic studies of quantitative traits were boosted by the development of molecular marker technology. Molecular markers allow localization with precision of the various genes controlling a trait and evaluation of their individual effects. Moreover, markers allow breeders to manipulate genes by selecting favorable alleles at markers tightly linked with the genes. They now constitute an invaluable tool for breeders to improve selection efficiency.

This paper retraces the approach we chose and results we obtained in using molecular markers to improve both root depth and osmotic adjustment of upland rice to contribute to improved drought tolerance.

Mapping QTLs for root depth

The first study attempting to locate the genes controlling root morphology in the rice genome and tag them with tightly linked molecular markers was undertaken by Champoux et al (1995). The population they used, however, was strongly skewed toward the parent with a poor root system. There was a need to develop the same type of study on more agronomically sound crosses. We analyzed root morphology in a doubled-haploid (DH) population of 105 lines derived from a cross between IR64, a shallow-rooted but very productive indica cultivar, and Azucena, a deep-rooted japonica variety (Yadav et al 1997). Distant crosses were preferred at that time because of polymorphism constraints, which have since disappeared with the development of highly polymorphic markers such as microsatellites. The choice of fixed lines was also mandatory when dealing with drought-tolerance traits, which need replications and are sensitive to genotype × environment interactions.

The experiment was conducted under greenhouse conditions. The broad-sense heritabilities of root depth and deep root weight, 0.77 and 0.60, respectively, were reasonable. QTL analysis using simple interval mapping showed that both traits were quantitatively controlled with QTLs on chromosomes 1, 2, 3, 5, 6, 7, 8, and 9 for root depth and on chromosomes 1, 6, 7, and 9 for deep root weight. The QTLs on chromosomes 1, 6, 7, and 9 were common between both traits. All favorable alleles came from the japonica parent. Individual QTLs accounted for from 4% to 21% of the phenotypic variability, with the QTL on chromosome 7 being the only strong one, while the multiple QTL model accounted for 23% to 49%. Although additive × additive epistasis was not very frequent (close to 5% of the tested pairs), some nonallelic interactions between markers located on different chromosomes, involved in additive effects or not, had magnitudes large enough to mask QTL detection.

Since the studies of Champoux et al (1995) and Yadav et al (1997), both conducted under aerobic conditions, other studies aiming at QTL identification have been undertaken with different populations, but with protocols similar enough to permit comparisons (Ito et al 1999, for a review). Various conditions (aerobic, anaerobic, and hydroponic) were explored (Price and Tomo 1997, Kamoshita et al 2002) and root QTLs were detected in all of them. The target traits were constitutive root morphology (root depth, root thickness, root length density in various soil layers, root to shoot ratio) and root penetration through compacted soils or hardpans (Ray et al 1996, Ali et al 2000, Price et al 2000). A relatively clear pattern can now be obtained for root QTLs across genetic backgrounds (Zheng et al 2000, Zhang et al 2001), though we still lack an extensive comparative study positioning all QTLs on a single map. In parallel, Kamoshita et al (2002) assessed the influence of experimental conditions on the results, confirming the suspected importance of G × E and, to a lesser extent, QTL × E interactions. Hemamalini et al (2000) and Price et al (2002) also explored the field of adaptive response under stress conditions, finding some degree of consistency in the QTLs detected in contrasting moisture regimes. Several of these studies have identified root QTLs in the same regions as Yadav et al (1997), therefore limiting the risk that they could be false-positives. Among those, segments on chromosomes 1, 2, 7, and 9 appeared particularly promising to us.

Introgression of QTLs for root depth

After genetic dissection of the trait, the next step was to use the identified QTLs to improve elite material. Successful integration of mapping results into applied breeding programs had been done for major genes, but no example was available for QTLs in rice. To test the efficiency of marker-aided selection (MAS) to manipulate QTLs, and following up on our previous QTL analysis, we conducted a study aimed at introgressing alleles for root depth, basing selection on molecular information alone (Shen et al 2000). We used the DH lines of the IR64 × Azucena population as the starting point of the program. The positive alleles at the QTLs came from Azucena, the deep-rooted variety, and IR64, the target for introgression, was used as the recurrent parent in three cycles of marker-assisted backcrosses. The four QTLs on chromosomes 1,2,7, and 9 were manipulated independently to produce near-isogenic lines (NILs) introgressed with one QTL. We used the fact that some parental lines carried several QTLs to directly create NILs carrying the QTLs from both chromosomes 1 and 7. We selected the plants heterozygous at the QTL during the backcross process on the basis of markers alone as shown in Figure 1. Because of the relative uncertainty on the QTL position and the size of the donor segments in the parental DH lines, we used several markers per segment (from 2 to 6). Results of simulations had shown that the control obtained by three markers optimally placed gave satisfactory results even for confidence intervals of the QTL as large as 60 cM (Hospital and Charcosset 1997).

We genotyped BC_3F_2 progenies, selected plants with Azucena alleles at the QTLs, and assessed the return to the recurrent parent. The phenotypic evaluation of BC_3F_3 families showed that, except in the case of the QTL on chromosome 2, the introgressed QTLs were expressed in the recipient background with the expected effects (Shen et al 2001). The analysis of the results showed that the preferred approach is one that localizes the QTL with the smallest confidence interval possible, allows detection of QTLs linked in the repulsion phase, and takes into account epistasis. Greenhouse and field evaluations of the performance of these lines showed reduced tillering in all lines and variations for plant height. Although pleiotropic effects of the QTLs cannot be excluded for tillering, these results were attributed to linkage drag since the introgressed segments had been deliberately made rather large to limit the risks associated with imprecision in QTL location. Linkage drag can deeply affect the phenotype even in lines with less than 3% of the donor parent in the genome, showing the need to fine-map the QTLs to smaller intervals.

A more thorough evaluation of the material under aerobic field conditions with different water availability situations showed that all lines with increased root-depth QTLs performed better than the lines without increased root depth, and that some produced higher yield than IR64 in both situations (Lafitte, unpublished results). These lines are candidates for further in-depth work to fine-map the significant areas.

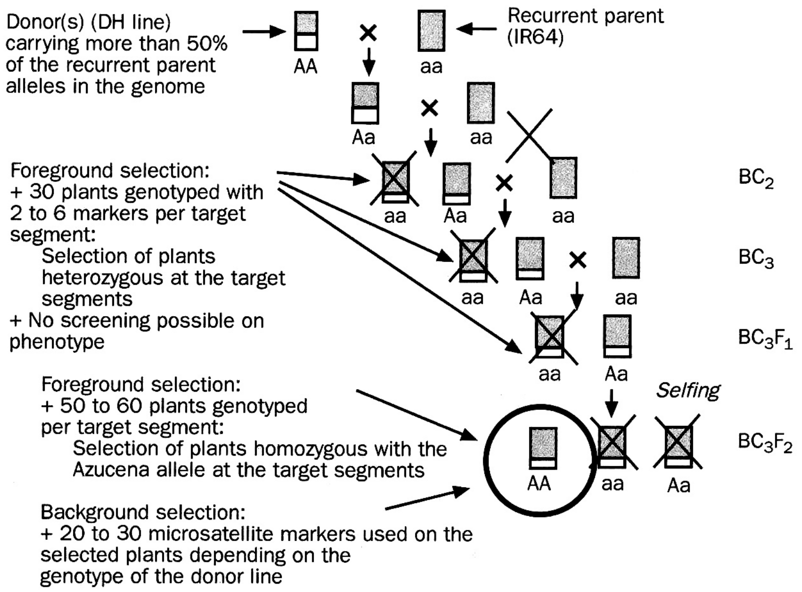


Fig. 1. Scheme used for foreground and background marker-aided selection in the transfer of QTLs for root depth.

Simultaneous detection and introgression of QTLs for osmotic adjustment

In standard breeding programs, QTL information is seldom available in the appropriate genetic background. The method used for root QTL introgression, which separates mapping work from marker-aided selection, was typical of the approach of early work. Nowadays, other options are available. The advanced backcross (ABC) QTL analysis method allows the simultaneous discovery and transfer of interesting QTLs from an unadapted donor to an elite variety (Tanksley and Nelson 1996). We used this method to transfer QTLs for osmotic adjustment (OA) from IR62266, an indica donor, to IR60080-46A, a japonica elite line. Osmotic adjustment is one of the parameters contributing to true drought tolerance in rice. Indica cultivars are known to have high OA capacity, whereas japonica cultivars do not. We developed an ABC population of 150 BC_3F_3 families that we genotyped using microsatellites and RFLP markers (Fig. 2). Each of these families was expected to have a few segments from the donor introgressed at random. We evaluated OA under greenhouse conditions using the rehydration technique. As expected with limited random introgressions, the distribution was centered around the recurrent parent. None of the ABC lines had an OA close to that of the donor parent, though 14 of them had significantly higher OA than the mean of the population. Using the composite interval mapping technique,

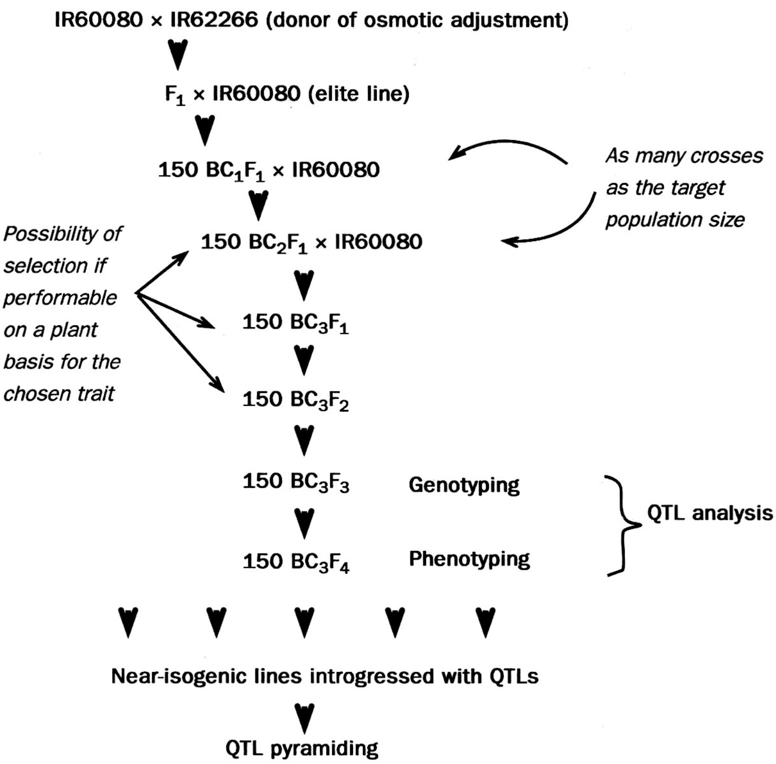


Fig. 2. Scheme used for developing an advanced backcross population introgressed with QTLs for osmotic adjustment.

we detected 14 QTLs located on chromosomes 1, 2, 3, 4, 5, 7, 8, and 10, together explaining 58% of the phenotypic variability, as shown in Figure 3 (Robin et al 2000). Most, but not all, of the alleles for greater OA came from the donor parent. On chromosome 8, two QTLs were linked with the favorable alleles associated in repulsion. The QTL location was in good agreement with previous studies on this trait (Lilley et al 1996, Zhang et al 2001). Comparative mapping across taxa provides an additional way to identify the important QTLs or validate them: the QTL on chromosome 8 is conserved in wheat and barley.

The BC3F3 lines carried the favorable alleles at the homozygous or heterozygous stage at up to eight QTLs, with two of them coming from the recurrent parent and therefore being present in most of the lines.

There are several options for the pursuit of the work. We could continue the BC scheme with MAS to reduce the portion of introgressed segments on the carrier chromosomes and improve the return toward the recurrent parent on the noncarrier chromosomes. A few well-placed markers would be enough to cover the noncarrier

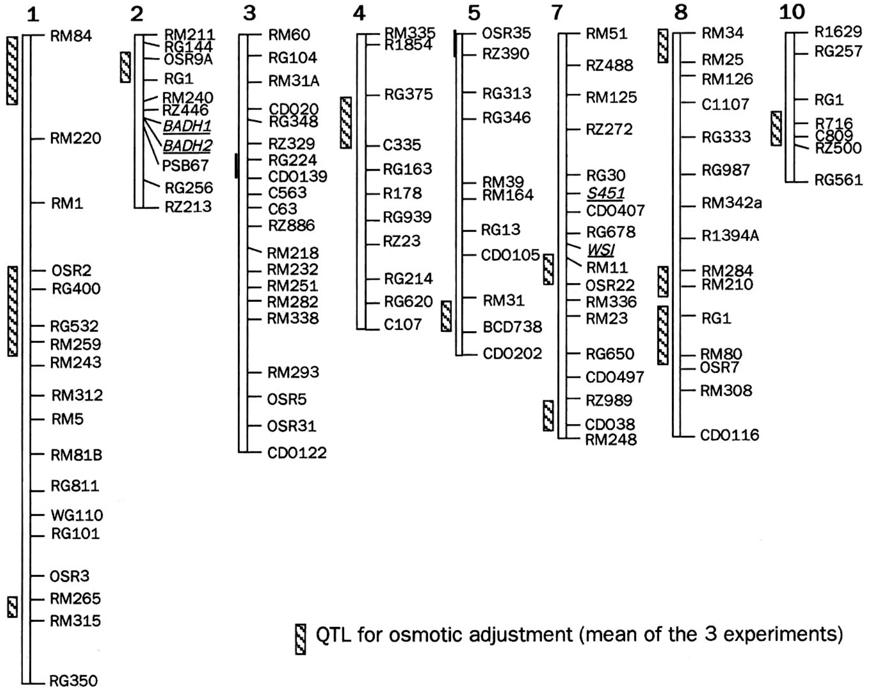


Fig. 3. QTL for osmotic adjustment detected in the IR62266 x IR60080 BC_3F_3 population. Candidate genes are underlined.

chromosomes but, for the carrier chromosomes, several markers in the target zone will be necessary to locate the QTLs into a smaller interval. The results of the root-depth work showed clearly that strong linkage drag could be a source of unexpected results. It is certainly easier to undertake the "cleaning" operations at this stage rather than later, when several QTLs will have been pyramided, although the number of QTLs carried by the best lines, and therefore to follow through with MAS, is already high. With more segments to follow at the same time, more plants must be analyzed to recover the proper ones. Fortunately, no selection is needed for the two QTLs for which the favorable allele comes from the recurrent parent. A phenotypic evaluation will have to be carried out at the end of the new BC process to see if the locations of the QTLs can be narrowed down.

Intercrossing these lines will be necessary in any case to recover isogenic lines with a level of OA similar to that of the donor parent. Graphical genotyping allowed evaluation of the complementarity between the top lines to construct the ideal genotype. To reach the objective in one round of crosses is not possible. Moreover, it may not be the best economy of resources. The minimal population size needed increases exponentially with the number of QTLs being manipulated and, as shown by Hospital and Charcosset (1997), even in the best situations, the maximum number of targets should not exceed five or six. It would be more efficient to try to obtain the best lines in two or more generations of recurrent crossing, which would require genotyping of a smaller number of lines, although the time gain might not be as high as in the first option (Charmet et al 2001).

In addition to their value in breeding programs, such NILs are useful for testing physiological hypotheses concerning the value of OA. It is unlikely that OA could help to improve yield under stress in all situations, but such material would allow definition of those situations and drought conditions in which OA could be most useful.

The advanced backcross strategy appeared to be an appropriate method to speed up the process of introgression of promising traits into elite material. If phenotypic information can be used in combination with molecular information at all generations, the efficiency of the method should even be higher.

Mapping candidate genes

Marker-assisted selection programs would benefit from a better understanding of the genes underlying QTLs. Moreover, the gene itself or a portion of it would constitute the best marker to suppress the risk of losing the marker-gene linkage through recombination in the MAS process. Cloning major QTLs for height or duration has been successfully achieved in rice (e.g., *sd1* by Ashikari et al 2002; *Hd1* by Yano et al 2000), but the enterprise is more difficult when the QTL effect is small and the phenotypic evaluation is complex. Meanwhile, the availability of the rice sequence and progress in functional genomics in various cereals are leading to the identification of many genes that can putatively be involved in pathways leading to improved drought tolerance that can be proposed as candidates. These genes can be used as probes to check for cosegregation with the detected QTLs. We established a list of 35 candidate genes for OA, found seven polymorphic in our cross, and were able to map six of them on the IR60080 × IR62266 population. Most of them mapped on chromosomal segments where no QTL was detected. On the other hand, WS1, a cDNA induced during water stress, mapped on chromosome 7 near a QTL. Although the use of candidate genes seems to be particularly attractive, these results highlight some of the difficulties in the approach. A first limitation is the number of possible genes to be tested, which increases exponentially with the development of genomics. A second one is the need for polymorphism in the cross of interest. Lastly, a cosegregation is not a proof of causality: several genes affecting the same trait are often found in clusters and, because of a lack of precision in QTL location, it is not possible to determine which one is responsible for the phenotype.

Perspectives: association studies

With mapping populations of ordinary size, QTLs are located with a confidence interval that is rather typically large (20 to 30 cM). The large size of the segments to be manipulated creates problems in their use as shown in the example of the NILs for root depth. To improve the precision of their location, association studies based on linkage disequilibrium (LD) in natural populations have emerged as a promising field of research, following a trend started with human genetics. Breeders constantly evaluate germplasm as potential parents in their hybridization schemes and therefore have phenotypic data on numerous accessions that could be used for association studies. Remington et al (2001) showed that it was possible to locate QTLs with a 5,000-fold greater resolution in maize using LD instead of current mapping populations. LD in rice may not decrease as rapidly as in maize, but, because of the early domestication of rice 5,000 years ago and its annual nature, it is not expected to span a very long distance. Glaszmann (1986), evaluating LD between two isozyme loci in a population of 2,280 accessions from the world rice collection, showed that LD could still be strong at 1 cM distance. By using a significantly higher marker density in the areas where major QTLs are identified and assessing allelic variation among accessions of working collections whose phenotype is known, it should be possible to locate the QTLs with a better precision than with mapping populations. Depending on the distance of decay of LD, this may make it possible to achieve a very high marker density in the areas of interest. The sequencing of the rice genome gives access to additional markers, notably microsatellites. Bacterial artificial chromosome (BAC) libraries can be used for the same purpose. If their density is too low in the area of interest, single nucleotide polymorphisms (SNPs) would have to be used. We are currently developing this approach on a well-characterized collection of upland rice varieties and intend to piggy-back on phenotypic data accumulated in the framework of our breeding program.

Conclusions

Molecular mapping studies have been a very efficient way to improve our understanding of the genetics of drought-tolerance traits such as root morphology and osmotic adjustment. Mapping results for performance under field conditions are slowly accumulating but, because of the large variation in results caused by different water-deficit situations, we still have a long way to go before we will have a clear view of what genomic areas affect a given trait in a given water-deficit situation. Data are particularly needed for performance under a stress at the reproductive stage, for which few studies have been published. The examples of marker-aided selection involving QTLs for drought-tolerance traits are too few to predict the exact role this technique will play among breeders' tools, but the two examples presented here show that it leads to promising results. The examples also highlight the need for marker-aided recurrent selection schemes to solve the problem of manipulating many QTLs at once. To improve the precision of QTL location and decrease linkage drag, association studies based on linkage disequilibrium may prove to be interesting in rice, but most of the progress in future years will probably come from progress in identifying the genes underlying the QTLs and developing better markers based on the genes themselves.

References

Ali ML, Pathan MS, Zhang J, Bai G, Sarkarung S, Nguyen HT. 2000. Mapping QTLs for root traits in a recombinant inbred population from two indica ecotypes in rice. Theor. Appl. Genet. 101:756-766.

Ashikari M, Sasaki A, Ueguchi-Tanaka M, Itoh H, Nishimura A, Datta S, Ishiyama K, Saito T, Kobayashi M, Khush GS, Kitano H, Matsuoka M. 2002. Loss-of-function of a rice gibberellin biosynthetic gene, *GA20 oxidase* (*GA20ox-2*), led to the rice "green revolution." Breed. Sci. 52:143-150.

Champoux MC, Wang G, Sarkarung S, Mackill DJ, O'Toole JC, Huang N, McCouch SR. 1995. Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. Theor. Appl. Genet. 90:969-981.

Charmet G, Robert N, Perretant MR, Gay G, Sourdille P, Gross C, Bernard S, Bernard M. 2001. Marker-assisted recurrent selection for cumulating QTLs for bread-making related traits. Euphytica 119:89-93.

Courtois B, Lafitte R. 1999. Improving rice for drought-prone environments. In: Ito O, O'Toole J, Hardy B, editors. Genetic improvement of rice for water-limited environments. Los Baños (Philippines): International Rice Research Institute. p 35-56.

Glaszmann JC. 1986. Linkage disequilibrium between Est-2 and Amp-3 in rice varieties. Int. Rice Res. Newsl. 33-56.

Hemamalini GS, Sashidar HE, Hittalmani S. 2000. Molecular marker-assisted tagging of morphological and physiological traits under two contrasting moisture regimes at peak vegetative stage in rice. Euphytica 112:69-78.

Hospital F, Charcosset A. 1997. Marker-assisted introgression of quantitative trait loci. Genetics 147:1469-1485.

Ito O, O'Toole J, Hardy B, editors. 1999. Genetic improvement of rice for water-limited environments. Proceedings of the Workshop on Genetic Improvement of Rice for Water-Limited Environments, 1-3 Dec. 1998. Los Baiios (Philippines): International Rice Research Institute. 353 p.

Kamoshita A, Zhang J, Sipongco J, Sarkarung S, Nguyen HT, Wade LJ. 2002. Effect of phenotyping environment on identification of QTLs for rice root morphology under anaerobic conditions. Crop Sci. 42:255-265.

Kamoshita A, Wade LJ, Ali ML, Pathan MS, Zhang J, Sarkarung S, Nguyen HT. 2002. Mapping QTLs for root morphology of a rice population adapted to rainfed lowland conditions. Theor. Appl. Genet. 104:880-893.

Lilley JM, Ludlow MM, McCouch SR, O'Toole JC. 1996. Locating QTL for osmotic adjustment and dehydration tolerance in rice. J. Exp. Bot. 47:1427-1436.

Price AH, Tomos AD. 1997. Genetic dissection of root growth in rice. II. Mapping quantitative trait loci using molecular markers. Theor. Appl. Genet. 95:143-152.

Price AH, Steele KA, Moore BJ, Barraclough PB, Clark LJ. 2000. A combined RFLP and AFLP linkage map of upland rice used to identify QTLs for root penetration ability. Theor. Appl. Genet. 100:49-56.

Price AH, Steele KA, Moore BJ, Jones RGW. 2002. Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes. II. Mapping QTL for root morphology and distribution. Field Crops Res. 76:25-43.

Ray JD, Yu LX, McCouch SR, Champoux MC, Wang G, Nguyen HT. 1996. Mapping quantitative trait loci associated with root penetration ability in rice. Theor. Appl. Genet. 92:627-636.

Remington DL, Thornsberry JM, Matsuoka Y, Wilson LM, Whitt SR, Doebley J, Kresovich S, Goodman MM, Buckler ES. 2001. Structure of linkage disequilibrium and phenotypic associations in the maize genome. Proc. Natl. Acad. Sci. USA 98(20):11479-11484.

Robin S, Courtois B, Yankel C, Pathan S, Carandang S, Lanceras R, Amante M, Li Z, Lafitte HR, Nguyen HT. 2000. Molecular dissection of osmotic adjustment in upland rice using the advanced backcross QTL approach. Paper presented at the 4th International Rice Genetics Symposium, 22-27 Oct. 2000, Los Baños, Philippines.

Shen L, Courtois B, McNally KL, Robin S, Li Z. 2000. Developing near-isogenic lines of IR64 introgressed with QTL for deeper and thicker roots through marker-aided selection. In: Ito O, O'Toole J, Hardy B, editors. Genetic improvement of rice for water-limited environments. Los Baños (Philippines): International Rice Research Institute. p 275-292.

Shen L, Courtois B, McNally KL, Robin S, Li Z. 2001. Evaluation of near-isogenic lines introgressed with QTLs for root depth through marker-aided selection. Theor. Appl. Genet. 103:q75-83.

Tanksley SD, Nelson JC. 1996. Advanced back-cross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. Theor. Appl. Genet. 92:191-203.

Yadav R, Courtois B, Huang N, McLaren G. 1997. Mapping genes controlling root morphology and root distribution in a double-haploid population of rice. Theor. Appl. Genet. 94:619-632.

Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y, Sasaki T. 2000. *Hd1,* a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the *Arabidopsis* flowering time gene *Constans.* Plant Cell 12:2473-2483.

Zhang J, Zheng HG, Aarti A, Pantuwan G, Nguyen TT, Tripathy JN, Sarial AK, Robin S, Babu RC, Nguyen BD, Sarkarung S, Blum A, Nguyen HT. 2001. Locating genomic regions associated with components of drought resistance in rice: comparative mapping within and across species. Theor. Appl. Genet. 103: 19-29.

Zheng HG, Babu CR, Pathan MS, Ali L, Huang N, Courtois B, Nguyen HT. 2000. Quantitative trait loci for root penetration ability and root thickness: comparison of genetic backgrounds. Genome 43:53-61.

Notes

Authors' addresses: B. Courtois, CIRAD-AMIS, TA40/03, Avenue Agropolis, 34398 Montpellier, Cedex 5, France; R. Lafitte, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; S. Robin, Tamil Nadu Agricultural University, Trichy 620 009, Tamil Nadu, India; L. Shen, Texas Tech University, Lubbock, TX 79409-2122, USA; M.S. Pathan and H. Nguyen, University of Missouri, Department of Agronomy, Columbia, MO 65211, USA.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Marker-based analysis of genetic drag between blast-resistance and yield-trait genes in rice

Kangle Zheng, Jieyun Zhuang, Jianli Wu, Rongyao Chai, Liyong Cao, Hei Leung, Yeyang Fan, Mingzhong Jin, Zhiming Rao

Based on major genes and QTL mapping for blast resistance and QTL mapping for yield traits in the same recombinant inbred line (RIL) population, genetic drag between the resistance-gene and yield-trait QTLs on chromosome 6 and between resistance QTLs and yield-trait QTLs on chromosome 7 was found. In our study, the QTLs for yield traits involved in the drag to the major resistance gene were finely mapped using two sets of RILs, each of which was composed of RILs carrying alleles on all the QTLs detected for yield-component traits on chromosomes 2, 3, and 7 from different parents based on the genotypes of the flanking DNA markers. The RILs within each set had different recombinations of alleles on marker loci. The control of genotypes on important loci for the traits studied in other parts of the genome increased the power to detect QTLs in the target region. More QTLs were detected for grain yield, spikelet fertility, number of filled grains per panicle, total number of spikelets per panicle, and grain weight in the 35-cM region. Some QTLs were mapped within an interval of the target region.

Rice is one of the major food crops in China. The key points in durable development of rice production involve the continuous increase in yield potential, improvement of pest resistance and stress tolerance, and improvement of grain quality. Genetic improvement has been effective in reaching these goals. The recently developed DNA markers and molecular maps are useful tools for the genetic improvement of crops (Tanksley et al 1989).

Rice yield and its components (panicle number per plant, grain number per panicle, spikelet fertility, and grain weight) are all quantitative traits. Polygenes control the yield potential of a rice variety. Rice materials usually show better productivity in demonstration trials. In addition, the actual yields of rice varieties in commercial production are always lower than their respective potential yields mainly because of pests and environmental stresses. So, from a practical point of view, an increase in actual yield relies on an increase in both yield potential and resistance/tolerance. As a matter of fact, the resistances to diseases and/or insects of many newly developed varieties with higher yield potential are not as good as expected. In the Southern China Rice Regional Trial distributed in 15 provinces, only 24.2% of the 33 advanced breeding lines were resistant to blast in the group of early maturing crop for indica rice during 1986-90. In the same group, the percentages of lines resistant to bacterial blight or brown planthopper were 21.1% and 15.2%, respectively. In the group of late-maturing crop for indica rice of the same trial during the same period, 36.4%, 45.5%, and 45.5% of the 11 advanced breeding lines were resistant to blast, bacterial blight, or brown planthopper, respectively. The percentages of the lines with resistance to two pests were 12.1% in the early group for indica rice and 36.4% in the late group for indica rice (Yang et al 1995). Most of the tested advanced lines showed higher yield potential but were susceptible to diseases, implying that there might be genetic drag between yield-component traits and disease resistance. In recent years, mapping and cloning for major genes as well as quantitative trait loci (QTL) for disease resistance were reported in crops (McCouch et al 1994, Wang et al 1994, Song et al 1995, Wang ZX et al 1999). QTL mapping and effect analysis for yield traits were also reported (Lin et al 1996, Li et al 1998). However, mapping for disease-resistance genes was separated from mapping for yield-trait QTLs in different populations in most cases. Evidence for genetic drag between disease resistance and yield traits was reported preliminarily in rice (Zhuang et al 2002).

We developed an F_8 recombinant inbred population from an indica cross (Zhong 156/Gumei 2) using single-seed descent. In this population, a major gene with resistance only to leaf blast was mapped on chromosome 12, a major gene with resistance to both leaf and neck blast with the same isolate was mapped to chromosome 6, and QTLs conferring partial resistance to leaf blast with two different isolates of the fungus were mapped. In the same population, QTL mapping for yield-component traits was also carried out. Genetic drag between yield potential and blast resistance was found. Genetic dissection of the QTLs involved in the drag was investigated.

Development of recombinant inbred lines (RILs)

The F_8 recombinant inbred population from an indica cross (Zhong 156/Gumei 2) was developed. The female parent Zhong 156 is a commercial indica rice variety developed at the China National Rice Research Institute (CNRRI). It had shown resistance to a wide spectrum of blast fungus at the vegetative stage, but was susceptible at the reproductive stage (Wu et al 1992). The male parent Gumei 2 is a semidwarf indica rice variety with durable blast resistance. In a long-term evaluation in natural nurseries of blast hot-spots across different rice-growing regions in China, six out of a total of 38,000 rice accessions tested showed high levels of resistance for 12 years or more, among which Gumei 2 was the only semidwarf variety (Peng et al 1996). This population contained 304 RILs.

A linkage map was constructed with 168 DNA markers including restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA

(RAPD), resistance gene analog (RGA), and simple sequence length polymorphism (SSLP) covering all 12 chromosomes. This map spanned 1,447.9 cM (Rao 2002).

Genetic mapping of blast-resistance genes

Mapping of major genes for resistance to leaf and neck blast

Two major genes, tentatively assigned as *Pi24*(t) and *Pi25*(t), were mapped onto chromosomes 12 and 6, respectively. *Pi24*(t) conferred resistance to leaf blast only, and its resistance allele was from Zhong 156. *Pi25* (t) conferred resistance to both leaf and neck blast, with the same isolate, and its resistance allele was from Gumei 2 (Zhuang et al 1997, 2002). *Pi24* (t) was flanked by a RAPD marker (N7) and an RGA marker (Nlrr-3). The genetic distance between N7 and Nlrr-3 was 0.8 cM. *Pi25* (t) was flanked by an RFLP marker (RG456) and a RAPD marker (A7) and the locus was 1.5 cM from RG456 and 1.8 cM from A7 (Rao 2002).

The effectiveness of the resistance gene from Gumei 2 in field conditions was examined in an early test in 1998. The RILs were planted in a blast hot-spot in Fujian Province, where the prevailing isolate and the genetic structure of the pathogen were unknown. At that time, the genetic distances between *Pi-25* (t) and the established flanking markers were 2.6 and 5.2 cM. Among 133 resistant lines, 98 possessed Gumei 2 alleles at both marker loci flanking *Pi-25* (t), 20 lines possessed the Gumei 2 and Zhong 156 alleles at either flanking loci, and only 8 lines possessed Zhong 156 alleles at both loci. On the other hand, only 7 out of 101 susceptible lines possessed Gumei 2 alleles at both flanking loci (Wu et al 1999). The association between genotypes of flanking markers and resistance performance suggested that *Pi25* (t) was responsible for the resistance in the field. It was also evident that markers linked to resistance genes would provide a reliable means for the selection of resistant lines.

Mapping of QTLs for partial resistance to leaf blast

Evaluation of partial resistance to leaf blast. In our early screening, Gumei 2 was resistant to leaf blast while Zhong 156 was susceptible to leaf blast with two isolates, Ca89 and 99-30-1. One hundred and forty-four RILs and 129 RILs susceptible to Ca89 and 99-30-1 were chosen to analyze partial resistance to leaf blast, respectively. Ca89 was from the International Rice Research Institute (IRRI) and 99-30-1 was from the Plant Protection Institute of the Zhejiang Academy of Agricultural Sciences (ZAAS). Spray inoculation (Marchetti et al 1987) and a complete randomized block design with three replications were used. Ca89 was inoculated in the greenhouse at IRRI (Wu 2000) and 99-30-1 was inoculated at ZAAS.

Plants were scored 7 days after inoculation. Diseased leaf area (DLA), lesion size (LS), and lesion number (LN) were used as parameters for partial resistance. DLA was visually estimated in 10 plants randomly selected from each line. LS and LN were measured on the fourth leaf of the 10 plants. Mean values of three replications for each parameter were used for QTL analysis. Normal distributions were observed for all parameters for disease resistance. Significant and positive correlations were

Table 1. QTLs for partial resistance to leaf blast in Zhong 156/Gumel 2 recombinant inbred line population.

QTL	Isolate	Interval	LOD	A[a]	%Var[b]
qDLA-8	Ca89	RM2532A1_9	4.6	0.53	5.0
qDLA-12	99-30-1	RM20-RM19	2.7	-4.42	5.9
qLS-1-1	99-30-1	S2A1_5-XN5	2.4	-0.47	9.1
qLS-1-2	Ca89	RM212-Pk34_1	3.6	-0.29	6.8
qLN-2	Ca89	Clrr3-RG25	2.9	0.56	5.2
qLN-7-1	99-30-1	Pk12_2-RM214	5.6	1.93	12.3
qLN-7-2	99-30-1	RZ395_RM234	3.5	−1.53	8.2
qLN-8	Ca89	RM2542A1_9	3.9	0.64	4.4
qLN-11	99-30-1	RZ525-RZ816	2.6	−1.57	4.9

[a] The genetic effect of the given QTL when a maternal allele was replaced by a paternal allele. [b] Variation explained by the given QTL.

shown between the parameters for the same isolate. The correlation coefficient between DLA and LN for the same isolate (Ca89) was 0.74.

Data analysis. QTLMapper 1.01b of the mixed linear model (Wang DL et al 1999) was employed to determine QTLs conditioning partial-resistance parameters. Important markers were selected with stepwise regression analysis (P <0.O01). Background genetic variation (BGV) caused by main and epistatic effects of important markers was controlled by BGV control mode A. The threshold of LOD>2.4 was chosen for claiming a putative QTL. QTLs were designated as proposed by McCouch et al (1997). Taking into account all QTLs detected for the same trait on the same chromosome, the suffix following the chromosome number was given from top to bottom. In the mapping of QTLs for yield traits, the same procedures were used.

QTLs with partial resistance to leaf blast. Nine QTLs were detected to have significant additive effects for three parameters of partial resistance to leaf blast with two isolates (Table 1). For DLA, *qDLA-8* and *qDLA-12* were detected for DLA for Ca89 and 99-30-1, respectively. For LS, *qLS-1-1* and *qLS-1-2* were detected for 99-30-1 and Ca89, respectively. Five QTLs were detected for LN, including *qLN-2* and *qLN-8* for Ca89 and *qLN-7-1, qLN-7-2,* and *qLN-11* for 99-30-1. The variations explained by individual QTLs ranged from 4.87% to 12.33%. The three QTLs for LN for Ca89 could explain 25.41% of the total phenotypic variation. The two QTLs (*qDLA-8* and *qLN-8*) located in the same interval coincided with the correlation between the performance of the parameters DLA and LN to the same isolate. The values of additive effects of four QTLs were positive, indicating the presence of partial-resistance alleles in a susceptible parent.

Genetic mapping for yield-trait genes

Phenotyping of yield-component traits

In 1996 and 1998, 148 RILs with similar heading dates and two parents were transplanted in the paddy field at CNRRI, Hangzhou, China, with two replications using

Table 2. Correlation coefficients between yield traits In 304 recombinant inbred lines derived from Zhong 156/Gumel 2.

Yield trait^{a}	NFGP^{b}	TNSP	SF	TGWT	GYD
NP	−0.135*	-0.125*	0.169**	0.163**	0.480**
NFGP		0.859**	0.500**	0.040	0.650**
TNSP			0.090	0.077	0.529**
SF			0.213**	0.426**	
TGWT					0.264**

^{a} NP = number of panicles, NFGP = number of filled grains per panicle, TNSP = total number of spikelets per panicle, SF = spikelet fertility, TGWT = 1,000-grain weight. ^{b}** = significant at 1% level, * = significant at 5% level.

a randomized complete block design. Nine plants in a row per replication were planted and the middle five plants were harvested at maturity for trait evaluation.

Six traits—grain yield per plant (GYD), number of panicles per plant (NP), number of filled grains per panicle (NFGP), total number of spikelets per panicle (TNSP), spikelet fertility (SF), and 1,000-grain weight (TGWT)—were measured. Mean values over two replications in each year were used for analysis.

Normal distributions were observed for each of the six yield traits in 1996 and 1998. Highly positive significant correlations between the phenotype performance in 1996 and 1998 were observed. The correlation coefficients obtained were from 0.236 for GYD to 0.685 for TGWT. Significant and positive correlations were shown between grain yield and each of its component traits, among which NFGP and TGWT showed the highest and lowest correlations with GYD, respectively (Table 2). As shown in Table 2, the correlations between NP and NFGP and between NP and TNSP were negative.

Correlations between resistance and yield traits

Table 3 shows the correlations between resistance parameters and yield. With the isolate Ca89, the only significantly positive correlation was between DLA and NP, although significantly negative correlations were observed between DLA and NFGP, DLA and TNSP, and LN and NFGP. With the isolate 99-30-1, the only significant correlation was detected between DLA and NP, which was negative.

QTLs for yield-component traits

A total of 22 QTLs were detected to have significant additive effects on the six yield traits (Table 4). These QTLs were distributed in 15 separate intervals of nine different chromosomes. The numbers of QTLs detected for each yield trait ranged from 1 for NP to 6 for TGWT. The total percentage of variation explained by all the QTLs detected for each trait ranged from 19.4% for NP to 73.1% for TNSP.

Two QTLs, *qNFGP-2* and *qGYD-2,* were mapped in the same interval with similar LOD scores and the same direction of additive effects, which coincide with the performance correlation between the traits. QTLs underlying the correlated traits

Table 3. Correlation coefficients between yield traits and blast-resistance parameters in subpopulations of recombinant inbred lines derived from Zhong 156/Gumel 2.

Yield trait [a]	Resistance parameters/subpopulation sizes					
	DLA89 [b] /144	LS89 /144	LN89 /144	DLA99 [c] /129	LS99 /129	LN99 /129
NP	0.169*	-0.044	0.122	-0.176*	-0.140	-0.142
NFGP	-0.173*	–0.082	-0.170*	0.095	0.050	0.069
TNSP	-0.153*	–0.086	-0.105	0.078	-0.027	0.092
SF	-0.021	0.019	-0.094	0.021	0.117	–0.020
TGWT	0.147	0.108	0.161	0.007	0.030	-0.007
GYD	0.041	-0.094	-0.001	-0.011	-0.039	-0.030

[a] NP = number of panicles, NFGP = number of filled grains per panicle, TNSP = total number of spikelets per panicle, SF = spikelet fertility, TGWT = 1,000-grain weight, GYD = grain yield per plant. [b] The suffix 89 represents the isolate Ca89. [c] The suffix 99 represents the isolate 99-30-1. * = significant at 5% level.

Table 4. QTLs for yield traits in a Zhong 156/Gumei 2 recombinant inbred line population.

QTL	Interval	LOD	A[a]	%Var[b]	Σ%Var[c]
qNP-2	RM263-CG1	4.5	0.52	19.4	19.4
qNFGP-2	Clrr_3Xlrr_5	4.3	–5.33	5.8	
qNFGP-6	K17-Pk34_6	5.8	–5.99	7.3	
qNFGP-7-1	Pk12_2-Pk12_3	14.5	12.54	32.1	
qNFGP-7-2	RM182-RM10	4.1	6.12	7.7	
qNFGP-10	RG241BS2A1_4	6.1	-6.46	8.5	68.9
qTNSP-2	RZ401-RM263	8.7	–7.94	9.6	
qTNSP-7-1	Pk12_2-Pk12_3	16.6	15.93	38.5	
qTNSP-7-2	RM10-RZ264	2.8	5.35	4.3	
qTNSP-10	RG241BS2A1_4	9.0	–8.54	11.1	
qTNSP-12	RM20-RM19	3.9	5.08	3.9	73.1
qSF-6	RM136-K17	7.2	–3.48	18.4	
qSF-12	RM20-RM19	9.4	–3.78	21.8	40.3
qTGWT-1-1	RG532-Xlrr_7	2.5	–0.44	4.3	
qTG-WT-1-2	RM212-Pk34_2	3.5	-0.48	5.0	
qTGWT-3	Pk34_11-S2A1_3	12.6	1.07	24.8	
qTGWT-5	S2A1_6-Pk34_10	5.9	0.61	8.2	
qTGWT-7	RZ264-RZ626	9.4	-0.87	16.6	
qTGWT-8	RG978-RM29b	3.5	-0.46	4.6	63.5
qGYD-1	RM23-RM24	3.9	0.86	7.5	
qGYD-2	Clrr_3-Xlrr_5	3.6	-0.85	7.3	
qGYD-7	Pk12_3-RM2	6.3	1.47	21.9	36.8

[a] The genetic effect of the given QTL when a maternal allele was replaced by a paternal allele. [b] Variation explained by the given QTL. [c] Subtotal of the variation explained by all the QTLs detected for the same trait.

between NFGP and TNSP, between TGWT and GYD, and between SF and TNSP were also found in the same intervals, respectively.

Clusters of QTLs were found on chromosomes 2, 3, and 7, which played major roles for yield traits. The percentages of variation explained by all the QTLs on these three chromosomes were 19.4% for NP, 45.2% for NFGP, 52.4% for TNSP, 41.4% for TGWT, and 29.2% for GYD. In further fine mapping of QTLs for yield traits on chromosome 6, RILs with alleles from the same parent on these QTLs were selected based on the genotypes of the flanking markers of the intervals.

Genetic drag between resistance loci and yield QTLs

Although the two QTLs for yield traits on chromosome 12 were apart from the interval in which *Pi-24* (t) was located, the two QTLs for yield traits on chromosome 6 were mapped in intervals in which *Pi-25* (t) was located (Fig. 1). The QTL *qNFGP-6* detected with a LOD score of 5.8 and that explained 7.3% of the phenotypic variation had an additive effect of 6.0%. QTL *qSF-6* detected with a LOD score of 7.2 and that explained 18.4% of the phenotypic variation had an effect of 3.5%. In both cases, the Gumei 2 alleles acted to reduce the trait value. Since the resistance allele at *Pi-25* (t) was derived from Gumei 2, genetic drag between *Pi-25* (t) and QTLs for yield traits was evident.

One of the partial-resistance QTLs, *qLN-7-1,* was detected with a LOD score of 5.6 and it explained 12.3% of the phenotypic variation. The allele from Gumei 2 increased lesion number by 1.93. Three yield-trait QTLs (*qNFGP-7, qTNSP-7,* and *qGYD-7*) were also detected in the same region and alleles from Gumei 2 increased the number of grains by 12.54, the number of spikelets by 15.93, and grain yield by 1.47 grams. Susceptible alleles for partial resistance and favorable alleles for yield coexisted in the same region of the chromosome.

On another region of chromosome 7, *qLN-7-2* was detected and its allele from Gumei 2 decreased lesion number by 1.53. A yield QTL, *qTGWT-7,* was detected in the interval adjacent to *qLN7-2.* The Gumei 2 allele on *qTGWT-7* decreased grain weight by 0.87 grams.

These results indicated that genetic drag between disease-resistance genes and yield-trait genes was common. This drag could be between the major gene and QTL or between one QTL and another QTL, and it could explain why most of the varieties developed so far with high yield potential were susceptible to pests.

Genetic dissection of the genomic region for *qSF-6* and *qNFGP-6*

To finely map the QTLs for yield-component traits in the two-LOD support intervals, which covered about 35 cM on chromosome 6, two sets of RILs were selected. Set 1 consisted of seven RILs (A3, A5, A7, A8, A9, A12, and A14) carrying Gumei 2 alleles on all QTLs detected for yield-component traits on chromosomes 2, 3, and 7 based on the genotypes of the flanking DNA markers. Set 2 consisted of seven RILs

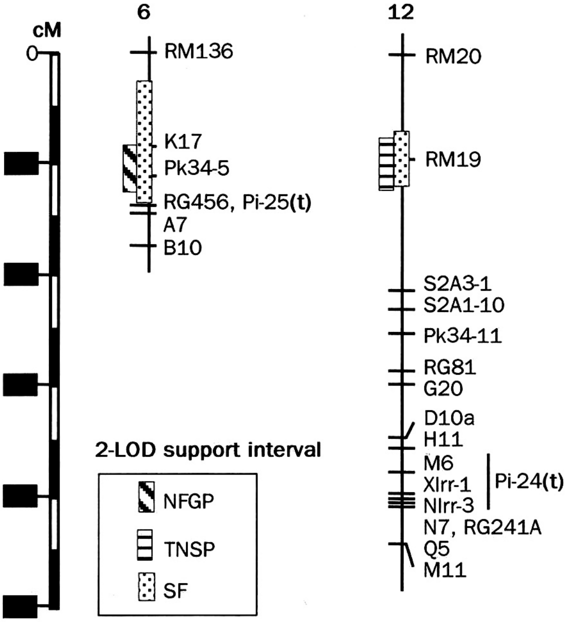
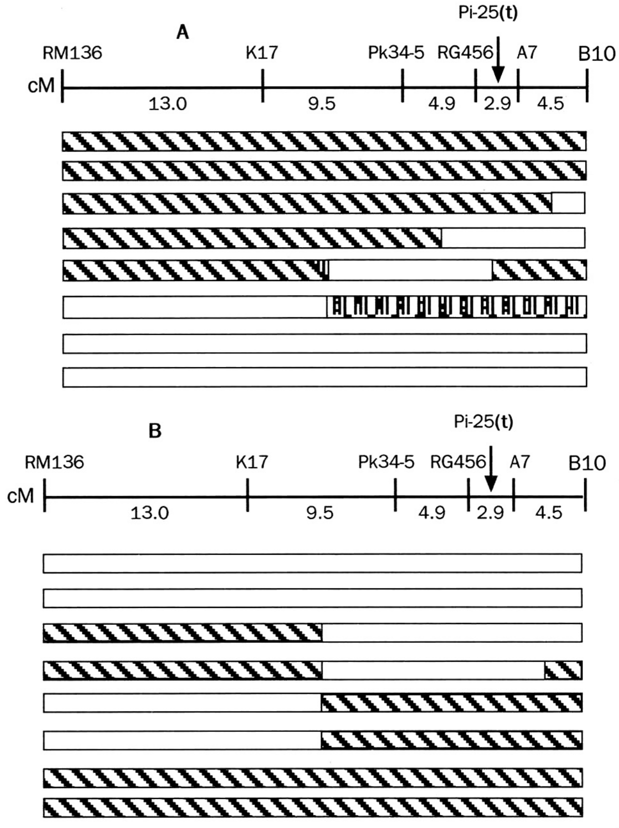


Fig. 1. Parts of the linkage map of chromosomes 6 and 12 showing locations of blast-resistance genes and QTLs for yield traits. NFGP = number of filled grains per panicle, TNSP = total number of spikelets per panicle, SF = spikelet fertility.

(I1, I3, I6, I7, I8, I10, and I12) carrying Zhong 156 alleles. The RILs within each set had different recombinations of alleles on marker loci. They were grown in two seasons in 2001, with two replications and 30 hills per replication per line. The first growing was sown on 24 May and transplanted on 18 June, and the other sown on 12 June and transplanted on 30 June. GYD, SF, NFGP, TNSP, and TWGT were measured and used for evaluating the significance of the differences among the RILs by the least significant difference (LSD) test.

Figure 2 depicts the marker genotypes in the target region of RILs involved in the test and their means for the yield traits. In Figure 2A, different RILs in set 1 were significantly different from Gumei 2 depending on the traits. For GYD, significant differences were found in three RILs: A9 showed a lower value, whereas A12 and A14 showed higher values, implying that there might be two QTLs for GYD with different directions of the effect within the target region. A12 showed higher values for both SF and NFGP and had the alleles on all the marker loci from Zhong 156 in the target region. For TNSP, A9 had a higher value and only one allele on B10 from Zhong 156, but A3 with all the Gumei 2 alleles also had a higher value. For TGWT, significant differences were found in five RILs: A8, A7, and A5 increased the value, whereas A12 and A14 decreased the value, implying that there might be two QTLs



	GYD	SF	NFGP	TNSP	TGWT
Gumei 2	624.8	61.0	63.2	103.8	28.3
A3	616.5	56.5	84.9	149.2*	28.9
A9	429.0*	66.0	101.2	150.2*	27.5
A8	535.8	68.7	100.1	143.3	29.6*
A7	594.3	58.6	76.8	132.2	29.9*
A5	665.3	76.5	107.3	139.6	30.0*
A12	814.3*	90.3*	116.3*	128.4	23.5*
A14	839.8*	75.4	93.0	123.8	26.8*

	GYD	SF	NFGP	TNSP	TGWT
Zhong 156	738.5	82.1	107.5	127.6	30.6
I12	723.8	72.4	97.3	133.4	28.2
I10	494.8*	69.4*	91.4	130.5	28.9
I8	695.5	76.4	132.5	173.3*	29.4
I7	628.0	62.1*	81.2	129.4	28.1
I3	601.5	55.8*	92.8	165.6	28.3
I6	508.0*	76.0	78.1	102.7	27.7*
I1	704.8	84.7	116.4	137.7	27.5*

Fig. 2. Delineation of recombinations in the 35-cM target region on chromosome 6 and yield-trait means among two sets of RILs. Statistically significant differences between RILs and their respective controls (LSD, *P* <0.05) are marked as *. (A) Set 1 contained seven RILs in which the alleles on all QTLs detected for yield traits on chromosomes 2, 3, and 7 were from Gumei 2 based on the genotypes of the flanking DNA markers. The control in this set was Gumei 2. (B) Set 2 contained seven RiLs in which the alleles on all QTLs detected for yield traits on chromosomes 2, 3, and 7 were from Zhong 156 based on the genotypes of the flanking DNA markers. The control in this set was Zhong 156. GYD = grain yield per plant, SF = spikelet fertility, NFGP = number of filled grains per panicle, TNSP = total number of spikelets per panicle, TGWT = 1,000-grain weight.

with different directions of the effect within the target region. In Figure 2B, different RILs in set 2 were significantly different from those of Zhong 156 depending on the traits. For GYD, significant differences were found in two RILs. Both I10 and I6 showed lower values and they had Gumei 2 alleles on shared marker loci, implying that the QTL for GYD might be located between RM136 and K17. For SF, I10, I7, and I3 had the lowest values. I7 and I3 had Gumei 2 alleles from Pk34-5 to B10, whereas I10 had Gumei 2 alleles on RM136 and K17. A significant higher value of TNSP was detected in I8 and a putative QTL could be considered on either end of the region. For TGWT, I6 and I1 had significantly higher values and both of them had an identical genotype in this region, implying that there might be a QTL for TGWT.

With the two sets of RILs in each of which the alleles of previously detected yield-trait QTLs on chromosomes 2, 3, and 7 were all from the same parent and alleles from different parents were recombined differently in the target region, significant differences between RILs and parents were detected for more traits and QTLs for more yield traits could be considered in this region. In our previous work, only two QTLs (*qSF-6* and *qNFGP-6*) were detected in this region. The present results implied that QTLs for each of the yield traits existed in this region. Since most of the RILs showing higher yield carried Zhong 156 alleles in the interval RM136-KI7, one of the QTLs for GYD might be in this interval and the higher-value allele was from Zhong 156. For SF, although A5 and A14 did not show significant differences with Gumei 2, three RILs—A5, A12, and A14—all had Zhong 156 alleles in the interval RM136-K17 and showed higher values, implying that the QTL for spikelet fertility might be in this interval. The Gumei 2 alleles in the RM136-K17 interval decreased spikelet fertility with both backgrounds of the yield-trait QTLs on chromosomes 2, 3, and 7. However, in set 2, where the background alleles were from Zhong 156, the Gumei 2 alleles in other intervals within the target region also decreased the value, indicating that the coadaptive epistasis between the target region and other parts of the genome affected the trait performance. This kind of epistasis is even obvious in the case of TWGT. In set 1 with background from Gumei 2, though Zhong 156 alleles on part of the region increased the value, all the Zhong 156 alleles in the whole region increased the trait value. In set 2 with background alleles from Zhong 156, all Gumei 2 alleles in the whole region decreased the value.

Future perspectives

Based on the major gene and QTL mapping for blast resistance and QTL mapping for yield traits in the same RIL population, genetic drag between the resistance gene and yield-trait QTLs on chromosome 6 and between resistance QTLs and yield-trait QTLs on chromosome 7 was found. In our study, the QTLs for yield traits involved in the drag to the major resistance gene were finely mapped using two sets of RILs, each of which was composed of RILs carrying alleles on all QTLs detected for yield-component traits on chromosomes 2, 3, and 7 from different parents based on the genotypes of the flanking DNA markers. The RILs within each set had different recombinations of alleles on marker loci. The control of genotypes on important loci for the traits studied in other parts of the genome increased the power to detect QTLs in the target region.

Paterson et al (1990) proposed substitution mapping as a method for fine-mapping QTLs, in which a series of near-isogenic lines (NILs) differing in recombination in the QTL regions was compared for the quantitative trait being mapped. NILs have the advantage of being genetically uniform throughout the rest of their genomes, which makes it easier to study the effects of a single QTL. Using a set of recombinant lines (subNILs) derived from the original NIL TA523, a QTL from wild tomato (*Lycopersicon hirsutum*) chromosome 1 affecting fruit characteristics and agronomic traits was finely mapped. QTLs affecting brix and total yield were mapped to opposite extremes of the 40-cM introgressed segment and linkage of the two loci rather than pleiotropy was evident (Monforte and Tanksley 2000). The rice photoperiod sensitivity gene *Hd3* was finely mapped using a large segregating population derived from an advanced backcross progeny. Two tightly linked loci, *Hd3a* and *Hd3b,* were identified in the *Hd3* region. Analysis of daylength response in NILs of *Hd3a* and *Hd3b* showed that the Kasalath allele at *Hd3a* promotes heading under short-day conditions while that at *Hd3b* causes late heading under long-day and natural conditions (Monna et al 2002). We need to further fine-map the yield-trait QTLs involved in genetic drag to blast-resistance genes. Development of NILs and a high-density molecular linkage map from our RILs should provide a solution.

References

Li ZK, Pinson SRM, Paterson AH, Stansel JW. 1998. Genetic dissection of the source-sink relationship in rice. Mol. Breed. 4:419-426.

Lin HX, Qian HR, Zhuang JY, Lu J, Min SK, Xiong ZM, Huang N, Zheng KL. 1996. RFLP mapping of QTLs for yield and related characters in rice (*Oryza sativa* L.). Theor. Appl. Genet. 92:920-927.

Marchetti MA, Lai X, Bollich CN. 1987. Inheritance of resistance to *Pyriculuria oryzae* in rice cultivars grown in the United States. Phytopathology 77:799-804.

McCouch SR, Nelson RJ, Tohme J, Zeigler RS. 1994. Mapping of blast resistance genes in rice. In: Zeigler RS, Leong SA, Teng PS, editors. Rice blast disease. Wallingford (UK): CAB International in association with the International Rice Research Institute. p 167-186.

McCouch SR, Cho YG, Yano M, Paul E, Blinstrub M, Morishima SR, Kinoshita T. 1997. Report on QTL nomenclature. Rice Genet. Newsl. 14: 11-13.

Monforte AJ, Tanksley SD. 2000. Fine mapping of a quantitative trait locus (QTL) from *Lycopersicon hirsutum* chromosome 1 affecting fruit characteristics and agronomic traits: breaking linkage among QTLs affecting different traits and dissection of heterosis for yield. Theor. Appl. Genet. 100:471-479.

Monna L, Lin HX, Kojima S, Sasaki T, Yano M. 2002. Genetic dissection of a genomic region for quantitative trait locus *Hd3* into two loci, *Hd3a* and *Hd3b,* controlling heading date in rice. Theor. Appl. Genet. 104:772-778.

Paterson AH, DeVerna JW, Lanini B, Tanksley SD. 1990. Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes in an interspecies cross of tomato. Genetics 124:735-742.

Peng SQ, Huang FY, Sun GC, Liu EM, Sun YJ, Ai RX, Zhao JX, Bai SZ, Xiao FH. 1996. Studies on durable resistance to blast disease in different latitudes for rice. Sci. Agric. Sin. 29(2):52-58.

Rao ZM. 2002. Genetic dissection and molecular analysis of blast resistance in rice (*Oryza sativa* L.). Ph.D. thesis. The Graduate School, Chinese Academy of Agricultural Sciences.

Song WY, Wang GL, Chen L, Kim HS, Pi LY, Gardner J, Holsten T, Wang B, Zhai WX, Zhu LH, Fauquet C, Ronald P. 1995. A receptor kinase-like protein encoded by the rice disease resistance gene Xu-21. Science 270:1804-1806.

Tanksley SD, Young ND, Paterson AH, Bonierbale MW. 1989. RFLP mapping in plant breeding: new tools for an old science. Biotechnology 7:257-264.

Wang DL, Zhu J, Li ZK, Paterson AH. 1999. Mapping QTLs with epistasis effects and QTL x environment interactions by mixed linear model approaches. Theor. Appl. Genet. 99:1256-1264.

Wang GL, Mackill DJ, Bonman JM, McCouch SR, Champoux MC, Nelson RJ. 1994. RFLP mapping of genes conferring complete and partial resistance to blast in a durably resistant rice cultivar. Genetics 136:1421-1434.

Wang ZX, Yano M, Yamanouchi U, Iwamoto M, Monna L, Hayasaka H, Katayose Y, Sasaki T. 1999. The *Pib* gene for rice blast resistance belongs to the nucleotide binding and leucine-rich repeat class of plant disease resistance genes. Plant J. 19:55-64.

Wu JL, Zhuang JY, Fan YY, Li DB, Leung H, Zheng KL. 1999. Effectiveness of a resistance gene from Gumei 2 against leaf and neck blast under field conditions in China. Rice Genet. Newsl. 16:90-92.

Wu JL. 2000. Gene mapping and candidate gene profiling to accumulate blast resistance in rice (*Oryza sativa* L.). Ph.D. thesis. Zhejiang University.

Wu ML, Zhao ML, Li XM, Zhuang JY, Ma LY, Peng YC, Xia XJ. 1992. Zhong 156, a high-yielding early-season indica rice variety. CNRRI annual report 1991. Beijing (China): Chinese Agricultural Press. p 19-20.

Yang SH, Xiong ZM, Chen ZQ, Cai GH, Xie FX, Zhang GH. 1995. Analysis of the varieties in the Southern China Rice Regional Trial during the “7th Five-Year Plan” period and future breeding prospects. Sci. Agric. Sin. 28:49-55.

Zhuang J-Y, Chai R-Y, Ma W-B, Lu J, Jin M-Z, Zheng K-L. 1997. Genetic analysis of blast resistance at vegetative and reproductive stages in rice. Rice Genet. Newsl. 14:62-64.

Zhuang JY, Ma WB, Wu JL, Chai RY, Lu J, Fan YY, Jin MZ, Leung H, Zheng KL. 2002. Mapping of leaf and neck blast resistance genes with resistance gene analog, RAPD and RFLP in rice. Euphytica 128:363-370.

Notes

Authors' addresses: Kangle Zheng, Jieyun Zhuang, Jianli Wu, Liyong Cao, Yeyang Fan, Zhiming Rao, National Center for Rice Improvement, China National Rice Research Institute, Hangzhou 310006, China; Jianli Wu, Hei Leung, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; Rongyao Chai, Mingzhong Jin, Institute of Plant Protection, Zhejiang Academy of Agricultural Sciences, Hangzhou 3 10021, China. Email:zhengkangle@china.com.

Acknowledgments: The research presented in this chapter was supported by the Natural Science Foundation of Zhejiang Province, China (300006), the National Natural Science Foundation of China (30070400), the Asian Rice Biotechnology Network, and the Rockefeller Foundation International Rice Biotechnology Program.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Mark——— assisted dissection and pyramiding of complex traits in rice

M. Yano, H.X. Lin, Y. Takeuchi, Y. Nonoue, T. Ando, A. Shomura, T. Shimizu, I. Kono,
Y. Takahashi, U. Yamanouchi, S. Konishi, Z.-W. Liang, T. Ueda, and T. Sasaki

Recent progress in rice genome analysis has made it possible to dissect complex traits into individual genetic factors by means of a marker-assisted approach. Using heading date as a model for complex traits, we have performed a comprehensive detection and characterization of quantitative trait loci (QTLs) using different types of progeny and near-isogenic lines for QTLs. The results clearly indicate that many QTLs, including those with minor effects, can be dealt with as single Mendelian factors. We have also performed molecular dissection of heading date by using map-based cloning of QTLs. The identification of genes involved in heading in rice facilitates not only the development of diagnostic markers for heading date in rice breeding but also our understanding of the genetic control of flowering time in short-day plants. To extend this approach to other complex traits of rice, we have developed several series of chromosomal segment substitution lines. In collaboration with other groups, we have used a marker-assisted approach to analyze plant type, preharvest sprouting, seed longevity, tolerance of abiotic stresses such as cold temperature and nutrient imbalances, and Al tolerance. This approach will contribute greatly to the establishment of marker-assisted breeding in rice.

Recent progress in rice genome analysis has provided a powerful tool for plant genetics and breeding. DNA markers, such as restriction fragment length polymorphism (RFLP), simple sequence repeats, and single nucleotide polymorphisms, have been used in the genetic analysis of agronomically important traits such as disease and pest resistance, plant height, and grain quality. These markers are also used in the genetic analysis of quantitative traits such as heading date, environmental stress tolerance, and yield-related traits. These marker-assisted approaches have made it possible to clone the genes involved in such complex traits at the molecular level (Alonso-Blanco and Koornneef 2000, Yano 2001). Tightly linked DNA markers or causal genes themselves can be used in marker-assisted selection in breeding programs. This paper summarizes our recent progress in the marker-assisted genetic and molecular dissection of several complex traits (mainly heading date) in rice.

Genetic and molecular dissection of heading date

A phenotype-based approach to the genetic analysis of heading date in mutants and natural variants has allowed the identification of several genes involved in the photoperiodic response (photoperiod sensitivity) (Yokoo et al 1980, Yamagata et al 1986, Yokoo and Okuno 1993, Okumoto and Tanisaka 1997). A series of tester lines for several photoperiod sensitivity genes has been developed to facilitate the genetic analysis of flowering time in rice (Yamagata et al 1986). This analysis has contributed much to the understanding of heading date in rice. However, the nature of the quantitative inheritance of heading date has hindered the performance of more detailed analyses, including the analysis of epistatic interactions of genes and accurate determination of the chromosomal locations of genes. In the last decade, progress in the development of DNA markers has made it possible to use quantitative trait locus (QTL) analysis to clarify the genes controlling heading date in rice (Yano and Sasaki 1997).

We have performed a QTL analysis of heading date using several types of progeny derived from a single cross between Nipponbare (japonica) and Kasalath (indica) and have identified 15 QTLs controlling heading date in rice (Yano et al 1997, Lin et al 1998, 2002, 2003, Yamamoto et al 2000).

The development of near-isogenic lines (NILs) by marker-assisted selection, in which a small chromosomal segment including the detected QTL of the donor cultivar Kasalath was substituted into the Nipponbare genetic background, has brought many advantages for the genetic analysis of flowering time in rice (for a review, see Yano and Sasaki 1997). For example, the QTL-NILS can be used in the characterization of photoperiodic response, epistatic interaction analysis, and fine genetic linkage mapping for target QTLs. Five QTLs — *Hd1, Hd2, Hd3, Hd5,* and *Hd6* —were found to confer photoperiod sensitivity (Lin et al 2000,2003, Yamamoto et al 2000). Genetic analysis using QTL-NILS detected the existence of an epistatic interaction between the QTLs (Lin et al 2000,2003, Yamamoto et al 2000, Monna et al 2002).

QTL-NILS can also be used for the fine mapping of target QTLs. Seven QTLs — *Hd1, Hd2, Hd3, Hd4, Hd5, Hd6,* and *Hd9* — were mapped precisely on a genetic linkage map as single Mendelian factors (Yamamoto et al 1998, 2000, Lin et al 2002, 2003). Moreover, high-resolution mapping enabled us to dissect two tightly linked loci, *Hd3a* and *Hd3b,* in the *Hd3* region (Monna et al 2002). These results clearly demonstrate that the genetic mechanisms controlling rice heading date can be dissected into their genetic components by a series of QTL analyses.

A major QTL, *Hdl,* which controls response to photoperiod, was cloned by means of a map-based cloning strategy (Yano et al 2000). Hdl is an ortholog of *CONSTANS (CO)* in *Arabidopsis* (Putterill et al 1995). Structural analysis of *Hdl* demonstrated that the major gene controlling the response to photoperiod, *Photoperiod sensitivity 1 (Se1),* is allelic to *Hdl.* High-resolution, fine-scale genetic mapping of *Hd6,* another

QTL involved in photoperiod sensitivity (Yamamoto et al 2000), delimited the candidate for *Hd6* to a 26.4-kb genomic region. Complementation analysis proved that *Hd6* encodes the a subunit of protein kinase CK2 (CK2a) (Takahashi et al 2001). This result indicates that *CK2*a plays an important role in the photoperiod response of flowering in rice. *Hd3a,* which is located on the short arm of chromosome 6 and is involved in the promotion of heading under short-day conditions, was also identified by a map-based strategy (Kojima et al 2002). *Hd3a* showed a high level of similarity to *FT* (Kobayashi et al 1999), which promotes flowering in *Arabidopsis.* The successful cloning of these three heading date QTLs clearly contributed to our understanding of the genetic control mechanism of heading date in rice (Yano et al 2001).

Mapping populations

In QTL analysis, primary mapping populations, such as F2, recombinant inbred lines, and doubled-haploid lines, are often used to detect the chromosomal regions controlling target traits. However, these materials are not enough to allow us to proceed to fine mapping and characterization of target QTLs. Secondary mapping populations, such as chromosome segment substitution lines (CSSLs) or NILs, will be required to facilitate more comprehensive analysis of target QTLs. Secondary mapping populations have been developed in tomato (Eshed and Zamir 1995), *Brassica napus* (Howell et al 1996), *Arabidopsis* (Koumproglou et al 2002), and rice (Kubo et al 2002).

We also developed novel CSSLs from a cross between an elite japonica cultivar, Koshihikari, and an indica cultivar, Kasalath (T. Ebitani and M. Yano, unpublished data). The selection was based on marker-assisted selection using RFLP and cleaved amplified polymorphic sequences. Chromosome segments substituted in the CSSLs overlapped in at least two lines and the 12 rice chromosomes were covered by the substituted segments of 39 CSSLs. Only one target chromosome segment was substituted with that of Kasalath in each CSSL, leaving the other chromosomal regions homozygous for Koshihikari. The percentage of the chromosomal region of the homozygous Kasalath allele within each line varied from 1% to 9% of the whole genome. We measured days to heading for each CSSL under natural field conditions at Toyama, Japan. It varied from 91 to 128 days in the CSSLs. A significant difference from the isogenic control Koshihikari was observed in 19 CSSLs. As a result, 14 putative QTLs for heading date were detected. Our previous QTL analysis for heading date using BC_1F_3 plants derived from the same cross revealed only four QTLs involved in the phenotypic variation (Yamamoto et al 2001). Thus, the statistical power of QTL detection is clearly greater in CSSLs than in BC_1F_3 plants. The CSSLs developed in this study will be very useful for the genetic analysis of quantitative traits such as heading date, plant height, resistance to preharvest sprouting, and tolerance of cool temperatures at the booting stage. The CSSLs will also be useful as candidate parental lines for the map-based cloning of genes of interest. In addition, Koshihikari, the recurrent parent of the CSSLs, is an elite rice variety in Japan. Thus, the CSSLs may be used directly as material for rice breeding programs once favorable characteristics are found in them.

Exploitation of useful genes in natural variants

Marker-based genetic approaches can be used to analyze other complex traits as well as heading date. Several primary mapping populations, including backcross inbred lines (BILs) and doubled-haploid lines, have been developed to facilitate the analysis of complex traits (Yano 2001).

Five putative QTLs affecting seed dormancy were detected on chromosomes 3, 5, 7 (two regions), and 8 by using the BILs derived from a backcross of Nipponbare/Kasalath//Nipponbare. The genetic effects of those QTLs have been verified by using NILs for each QTL. QTLs for seed dormancy *(Sdr1)* and heading date *(Hd8)* had been mapped to approximately the same region on chromosome 3 (Lin et al 1998). To clarify whether *Sdr1* and *Hd8* could be dissected genetically, we carried out fine mapping by using advanced backcross progenies. As a result, *Sdr1* and *Hd8* were mapped to different loci. We thus successfully dissected two tightly linked QTLs by a marker-based approach (Y. Takeuchi and M. Yano, unpublished data).

To identify the chromosomal regions controlling cool-temperature tolerance at the booting stage of rice, we performed QTL analysis with doubled-haploid lines derived from crosses between two cultivars, Akihikari (moderately cool-temperature sensitive) and Koshihikari (cool-temperature tolerant). Three QTLs were mapped, one to each of chromosomes 1, 7, and 11. For each QTL, alleles from Koshihikari increased the degree of cool-temperature tolerance (Takeuchi et al 2001).

QTLs controlling seed longevity in rice were identified by using 98 BILs derived from a cross between the japonica cultivar Nipponbare and the indica cultivar Kasalath. Three putative QTLs—*qLG-2, qLG-4,* and *qLG-9*—were detected on chromosomes 2, 4, and 9, respectively (Miura et al 2002). Kasalath alleles increased the seed longevity in these QTLs.

QTLs for A1 tolerance were mapped in a population of 183 BILs derived from a cross of Koshihikari and Kasalath (Ma et al 2002). Three putative QTLs controlling A1 tolerance were detected on chromosomes 1, 2, and 6. Kasalath QTL alleles on chromosomes 1 and 2 reduced A1 tolerance, but the allele on chromosome 6 increased tolerance. The existence of QTLs for A1 tolerance was confirmed in substitution lines for corresponding chromosomal segments (Ma et al 2002).

QTL analysis for tolerance of P deficiency was conducted by using 98 BILs derived from a cross between Nipponbare and Kasalath. Lines were grown on P-deficient soil and were evaluated for their tolerance. Three QTLs were identified for dry weight and four for P uptake (Wissuwa et al 1998). For both traits, the QTL linked to marker C443 on chromosome 12 had a major effect. Furthermore, a major QTL for P uptake, *Pup1,* on chromosome 12 has been mapped as a single Mendelian factor by using advanced backcross progenies in a substitution mapping approach (Wissuwa et al 2002).

Phenotypic differences in plant type-either erect or spreading stub—were observed in advanced backcross progenies from a cross between Nipponbare and Kasalath. The inheritance and chromosomal location of the gene involved in this difference have been determined through the analysis of RFLP markers and advanced backcross progenies (Yamamoto et al 1997). The spreading stub is controlled by a single dominant gene from Kasalath, and the tentatively designated locus *Spk* (t) was mapped on chromosome 9 by using RFLP markers (Yamamoto et al 1997).

Conclusions

Marker-assisted approaches have contributed to our understanding of many kinds of complex traits in rice, including plant morphology and environmental stress tolerance. These approaches have enabled us not just to identify the genes involved in complex traits, but to identify them at the molecular level. Once we have identified tightly linked markers, NILs for target traits with minimum introgressed chromosomal segments from donor varieties can be readily and quickly developed by marker-assisted selection. In addition, we will be able to introduce genes derived from different donor varieties into elite rice cultivars by using a variety of NILs and DNA markers (trait pyramiding). This strategy has not yet been applied in phenotype-based selection in rice breeding. Marker-based approaches have led to a paradigm change in the breeding of rice and other crop species.

References

Alonso-Blanco C, Koornneef M. 2000. Naturally occurring variation in *Arabidopsis:* an underexploited resource for plant genetics. Trends Plant Sci. 5:22-29.

Eshed Y, Zamir D. 1995. An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield-associated QTL. Genetics 141:1147-1162.

Howell PM, Marshall DF, Lydiate DJ. 1996. Towards developing intervarietal substitution lines in *Brassica napus* using marker-assisted selection. Genome 39:348-358.

Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T. 1999. A pair of related genes with antagonistic roles in mediating flowering signals. Science 286:1960-1962.

Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M. 2002. *Hd3a,* a rice ortholog of the *Arabidopsis FT* gene, promotes transition to flowering downstream of *Hd1* under short-day condition. Plant Cell Physiol. 43:1096-1105.

Koumproglou R, Wilkes TM, Townson P, Wang XY, Beynon J, Pooni HS, Newbury HJ, Kearsey MJ. 2002. STAIRS: a new genetic resource for functional genomic studies of *Arabidopsis.* Plant J. 31:355-364.

Kubo T, Aida Y, Nakamura K, Tsunematsu H, Doi K, Yoshimura A. 2002. Reciprocal chromosome segment substitution series derived from *japonica* and *indica* cross of rice (*Oryza sativa* L.). Breed. Sci. 52:319-325.

Lin HX, Ashikari M, Yamanouchi U, Sasaki T, Yano M. 2002. Identification and characterization of a quantitative trait locus, *Hd9,* controlling heading date in rice. Breed. Sci. 52:35-41.

Lin HX, Liang ZW, Sasaki T, Yano M. 2003. Fine mapping and characterization of quantitative traits loci *Hd4* and *Hd5* controlling heading date in rice. Breed. Sci. 53. (In press.)

Lin HX, Yamamoto T, Sasaki T, Yano M. 2000. Characterization and detection of epistatic interactions of three QTLs, *Hd1, Hd2,* and *Hd3,* controlling heading date in rice using nearly isogenic lines. Theor. Appl. Genet. 101:1021-1028.

Lin SY, Sasaki T, Yano M. 1998. Mapping quantitative trait loci controlling seed dormancy and heading date in rice, *Oryza sativa* L., using backcross inbred lines. Theor. Appl. Genet. 96:997-1003.

Ma JF, Shen R, Zhao Z, Wissuwa M, Takeuchi Y, Ebitani T, Yano M. 2002. Response of rice to AI stress and identification of quantitative trait loci for AI tolerance. Plant Cell Physiol. 43:652-659.

Miura K, Lin SY, Yano M, Nagamine T. 2002. Mapping quantitative trait loci controlling seed longevity in rice (*Oryza sativa* L.). Theor. Appl. Genet. 104:981-986.

Monna L, Lin HX, Kojima S, Sasaki T, Yano M. 2002. Genetic dissection of a genomic region for a quantitative trait locus, *Hd3,* into two loci, *Hd3a* and *Hd3b,* controlling heading date in rice. Theor. Appl. Genet. 104:772-778.

Okumoto Y, Tanisaka T. 1997. Trisomic analysis of a strong photoperiod-sensitivity gene *E1* in rice (*Oryza sativa* L.). Euphytica 95:301-307.

Putterill J, Robson F, Lee K, Simon R, Coupland G. 1995. The *CONSTANS* gene of *Arabidopsis* promotes flowering and encodes a protein showing similarities to zinc finger transcription factors. Cell 80:847-857.

Takahashi Y, Shomura A, Sasaki T, Yano M. 2001. *Hd6,* a rice quantitative trait locus involved in photoperiod sensitivity, encodes the alpha subunit of protein kinase CK2. Proc. Natl. Acad. Sci. USA 98:7922-7927.

Takeuchi Y, Hayasaka H, Chiba B, Tanaka I, Shimano T, Yamagishi M, Nagano K, Sasaki T, Yano M. 2001. Mapping quantitative trait loci controlling cool-temperature tolerance at booting stage in temperate *japonica* rice. Breed. Sci. 51:191-197.

Wissuwa M, Wegner J, Ae N, Yano M. 2002. Fine mapping of *Pup1:* a major QTL increasing phosphorus uptake of rice from a phosphorus-deficient soil. Theor. Appl. Genet. 105:890-897.

Wissuwa M, Yano M, Ae N. 1998. Mapping of QTLs for phosphorus deficiency tolerance in rice (*Oryza sativa* L.). Theor. Appl. Genet. 97:777-783.

Yamagata H, Okumoto Y, Tanisaka T. 1986. Analysis of genes controlling heading time in Japanese rice. In: Rice genetics. Manila (Philippines): International Rice Research Institute. p 351-359.

Yamamoto T, Kuboki Y, Lin SY, Sasaki T, Yano M. 1998. Fine mapping of quantitative trait loci, *Hd-1, Hd-2* and *Hd-3,* controlling heading date of rice as single Mendelian factors. Theor. Appl. Genet. 97:37-44.

Yamamoto T, Lin HX, Sasaki T, Yano M. 2000. Identification of heading date quantitative trait locus *Hd6* and characterization of its epistatic interactions with *Hd2* in rice using advanced backcross progeny. Genetics 154:885-891.

Yamamoto T, Sasaki T, Yano M. 1997. Genetic analysis of spreading stub using *indica/japonica* rice backcrossed progenies. Breed. Sci. 47:141-144.

Yamamoto T, Taguchi-Shiobara F, Ukai Y, Sasaki T, Yano M. 2001. Mapping quantitative trait loci for days-to-heading, and culm, panicle and internode lengths in a BC_1F_3 population using an elite rice variety, Koshihikari, as the recurrent parent. Breed. Sci. 5 1:63-71.

Yano M. 2001. Genetic and molecular dissection of naturally occurring variation. Curr. Opin. Plant Biol. 4:130-135.

Yano M, Harushima Y, Nagamura Y, Kurata N, Minobe Y, Sasaki T. 1997. Identification of quantitative trait loci controlling heading date in rice using a high-density linkage map. Theor. Appl. Genet. 95:1025-1032.

Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y, Sasaki T. 2000. *Hd1,* a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the *Arabidopsis* flowering time gene *CONSTANS.* Plant Cell 12:2473-2483.

Yano M, Kojima S, Takahashi Y, Lin HX, Sasaki T. 2001. Genetic control of flowering time in rice, a short-day plant. Plant Physiol. 127:1425-1429.

Yano M, Sasaki T. 1997. Genetic and molecular dissection of quantitative traits in rice. Plant Mol. Biol. 35:145-153.

Yokoo M, Kikuchi F, Nakane A, Fujimaki H. 1980. Genetical analysis of heading time by aid of close linkage with blast, *Pyricularia oryzae,* resistance in rice. B. Natl. I. Agric. Sci. D 31:95-126.

Yokoo M, Okuno K. 1993. Genetic analysis of earliness mutations induced in the rice cultivar Norin 8. Jpn. J. Breed. 43:1-11.

Notes

Authors' addresses: M. Yano, Z.-W. Liang, T. Ueda, T. Sasaki, National Institute of Agrobiological Sciences, 2-1-2 Kannondai, Tsukuba 305-8602, Japan; H.X. Lin, Shanghai Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, 300 Fenglin Road, Shanghai 200032, China; Y. Takeuchi, Y. Nonoue, T. Ando, A. Shomura, T. Shimizu, I. Kono, Y. Takahashi, U. Yamanouchi, S. Konishi, Institute of the Society for Techno-Innovation of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki 305-0854, Japan. E-mail: myano@nias.affrc.go.jp, phone: +81-29-8-38-7443, Fax: +81-29-8-38-7468.

Acknowledgments: We thank Drs. K. Miura, J.F. Ma, M. Wissuwa, and T. Yamamoto and Mr. H. Hayasaka for their collaboration in the genetic analysis of the complex traits described in this paper. The genetic studies described here were supported by the Program for Promotion of Basic Research Activities for Innovative Biosciences (PROBRAIN) from the Bio-oriented Technology Advancement Institution (BRAIN) and Rice Genome Project (DM-I 103 and DM 1806) from the Ministry of Agriculture, Forestry, and Fisheries.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Introgression for agronomic traits from *Oryza grandiglumis* into rice, *O. sativa*

S.N. Ahn, S.J. Kwon, J.P. Suh, K.H. Kang, H.J. Kim, H.G. Hwang and H.P. Moon

Introgression has been achieved from wild species *Oryza grandiglumis* (2n=48, CCDD, Acc. No. 101154) into *O. sativa* subsp. *japonica* cv. Hwaseongbyeo. Hwaseongbyeo was used as a recurrent parent and *O. grandiglumis* as a donor parent. An advanced introgression (backcross) line, HG101, produced from a single plant from BC_5F_3 families resembled Hwaseongbyeo, but it showed differences from Hwaseongbyeo in several traits, including days to heading. To detect the introgressions, 300 microsatellite markers of known chromosomal position were used for the parental survey. Of the 300 markers, 50 (15%) showed polymorphism.

To identify and characterize the effects of alien genes introgressed into HG101, F_2 and F_3 lines from the cross Hwaseongbyeo/HG101 were developed and evaluated for 12 agronomic traits. Several lines outperformed Hwaseongbyeo in several traits, including days to heading. Genotypes were determined for 150 F_2 plants using simple sequence repeat (SSR) markers. QTL analysis was carried out to determine the relationship between marker genotype and traits evaluated. Three QTLs on chromosomes 1, 8, and 11 were significantly associated with culm length. Two QTLs on chromosome 11 were significantly associated with panicle number and panicle length and one QTL detected on chromosome 11 affected days to heading. Several QTLs on chromosomes 8 and 11 controlling culm length have not been detected in previous studies between *Oryza* cultivars, indicating potentially novel alleles from *O. grandiglumis.* The QTLs detected in this study could be a rich source of natural genetic variation underlying the evolution and breeding of rice.

The genus *Oryza* has two cultivated and 22 wild species (2n=24 or 48). The wild relatives of *Oryza* representing different genomes are an important reservoir of genetic variability for agronomic traits such as biotic and abiotic stresses and for improved yield potential (Brar and Khush 1986, 1997, Moncada et al 2001, Xiao et al 1998). Tissue culture and molecular techniques are available to overcome incompatibility frequently found in hybrids between distantly related species and to monitor the introgression and transfer of genes from wild species. *Oryza grandiglumis* is distributed in tropical regions of Central and South America. Some accessions of *O. grandiglumis* show strong vegetative growth and are resistant to diseases and insect pests (Vaughan 1994, Yu et al 1997). Recent progress in plant genome analysis has made it possible to examine naturally occurring allelic variation underlying complex traits. Quantitative trait loci (QTL) analysis can provide information relevant to agricultural traits by using molecular markers to identify specific regions of the genome affecting any measurable trait (Tanksley 1993). Several QTLs, including yield, yield components, and morphological traits from *O. sativa* cultivars, have been identified in the past decade (McCouch and Doerge 1995, Yano and Sasaki 1997).

This study was carried out using an introgression line (a backcross progeny), HG101, developed from the cross *O. sativa* cv. Hwaseongbyeo/*O. grandiglumis* (1) to identify regions of the genome related to agronomic traits of interest for characterization of the molecular mechanism underlying natural genetic variation, (2) to identify trait-improving alleles from *O. grandiglumis* and selectively transfer novel alleles into the background of Hwaseongbyeo to develop useful bridging lines and to broaden the genetic base of Korean rice cultivars, and (3) to determine the conservation of QTLs across other rice cultivars.

To our knowledge, this report represents the first report of a genetic study conducted on an interspecific cross of *O. sativa/O. grandiglumis.*

Materials and methods

Plant materials and field trials

Interspecific backcross progenies were developed from the cross between the elite japonica cultivar Hwaseongbyeo used as a recurrent parent and the wild species *O. grandiglumis* (IRGC Acc. No. 101 154) with the CCDD genome as a donor parent. Among them, one BC_5F_6 introgression line (HG101) was selected. HG101 was produced from a single plant from BC_5F_3 families, which was subsequently self-pollinated for three more generations. HG101 differed from Hwaseongbyeo in several traits, including culm length and days to heading and these differences can be attributed to the *O. grandiglumis* chromosome segments introgressed into HG101. To evaluate the effects of these segments on the agronomic traits, 150 F_2 and F_3 lines derived from the cross Hwaseongbyeo/HG101 were developed and evaluated for 12 traits, including culm length and grain length, in the field at the Chungnam National University, Daejeon, Korea. The field planting followed a completely randomized block design with two replications. For each line within a replication, 30-day-old seedlings were transplanted to a row with 30 plants per row. The middle 10 plants in the row of each plot were evaluated for 12 traits (days to heading, culm length, panicle length, panicles per plant. spikelets per panicle, fertility, 1,000-grain weight, grain yield, grain length, grain width, grain thickness, amylose content) based on the Standard Evaluation System (Standard Evaluation System 1995).

SSR genotyping and statistical analysis

A total of 300 simple sequence repeat (SSR) markers of known chromosomal position were used to survey the parents for polymorphism (Temnykh et al 2000,2001). The markers showing polymorphism between Hwaseongbyeo and HG101 were used for genotype analysis of 150 F_2 plants. SSR analysis was carried out as described in Panaud et al (1996). Polymerase chain reaction (PCR) products were run on 4% polyacrylamide denaturing gel during 2 h at 1,800-2,000 V, and marker bands were revealed using silver staining.

Statistical analysis was performed using QGENE (Nelson 1997) and Data Desk 4.0 (Data Description Inc. 1992). Pearson correlation coefficients were calculated for the traits evaluated. Single-point regression was used to determine the effect of each marker on each trait measured on the F_2 and F_3 using QGENE. Regions of the genome were identified as putatively containing a QTL if a significant effect was observed for a single marker/trait combination at a single location with $P < 0.001$ or significant effects were observed in the same direction for a marker/trait combination at two or more locations with $P < 0.05$. The percent phenotypic variance (% PV) associated with each significant QTL was calculated from the regressions of each marker/phenotype combination.

Results

Morphology of HG101

HG101 resembled the *O. sativa* parent, Hwaseongbyeo. However, it differed from Hwaseongbyeo in several traits, including culm length and days to heading (Table 1, Ahn et al 2001). HG101 showed delayed heading and short culm length compared with Hwaseongbyeo. Also, the grain characteristics (grain weight and length and amylose content) of HG101 were different from those of Hwaseongbyeo. HG101 was resistant to three *Pyricularia grisea* isolates that were collected and are genetically stable and routinely used for studies in Korea (Ryu et al 1987). Several independent studies demonstrated that resistance to each of the three isolates in several rice accessions is under a single dominant gene and the resistance genes were mapped using molecular markers (Choi et al 2000, Kim et al 1995). Genes for blast resistance are of great interest and value for rice improvement in Korea. We are investigating the allelic relationships of these genes with other known genes for resistance. The most notable feature of HG101 is the absence of undesirable traits of *O. grandiglumis,* such as grain shattering and tall plant stature.

Correlations among traits

Correlations among traits were calculated and the significant correlation coefficients were observed among the traits (data not shown). The strongest correlation was found between 1,000-grain weight and panicles per plant, and significant correlations were also found between panicle length and culm length, panicles per plant and panicle length, spikelets per panicle and culm length, and spikelets per panicle and panicle length. In agreement with previous studies, yield showed positive correlations with

Table 1. Comparison of agronomic characteristics of the parents and HG101.

Accession	Days to heading (d)	Culm length (cm)	Panicle length (cm)	Grain fertility (%)	Grain length (mm)	Grain width (mm)	1,000 grain wt. (g)	Amylose content (%)	Blast isolate reaction		
									KI-313	KI-409	KI-1113a
O. grandiglumis	180	174	45	20.5	–	–	–	–	R[a]	R	R
Hwaseongbyeo	108	81	20	90.5	5.03	2.84	21.5	20.5	S	S	S
HG101	117	75	21	61.9	5.53	3.08	26.9	15.5	R	R	R

[a] R = resistant, S = susceptible.

panicles per plant and spikelets per panicle. Negative correlations existed between days to heading and panicle length, panicles per plant and panicle length, spikelets per panicle and days to heading, and 1,000-grain weight and panicles per plant.

Frequency distribution of traits and QTL analysis

The frequency distribution of phenotypes for each trait in the parents and F_2 and F_3 lines is shown in Figure 1. Transgressive segregants were observed for all traits measured. The F_2 plants were genotyped with 30 markers that detected *O. grandiglumis* alleles in HG101 (Fig. 2). Distorted segregation was observed in some genomic regions (data not shown). RM411 on chromosome 3 showed distortion toward the Hwaseongbyeo allele and RM214 on chromosome 7 showed distortion toward the HG101 allele. Segregation distortion is common in interspecific crosses and has been widely documented (reviewed in Xu et al 1997). The region on chromosome 3 has also been found to be similarly skewed in other studies. In the F_2 progenies from a cross between Nipponbare and Kasalath, the significant deviation toward the Kasalath genotype was found on chromosome 3, which is presumably due to the gametophyte gene (*ga*-2) (Harushima et al 1996).

One-way ANOVA was carried out to detect associations of introgression with morphological traits. Significant QTLs were detected for agronomic traits as summarized in Table 2. Seven QTLs associated with agronomic traits were identified for the F_2 and F_3 of the cross Hwaseongbyeo/HG101. One QTL was significantly associated with days to heading. The phenotypic variance explained by this QTL was 16.0%. Three QTLs on chromosomes 1, 8, and 11 were significantly associated with culm length. In all cases, the HG101 alleles decreased culm length. The phenotypic effect of the three QTLs ranged from 2.2 to 3.0 cm. The phenotypic variance explained by each QTL ranged from 16.7% to 23.2%. One QTL on chromosome 11 was significantly associated with panicle length. The HG101 alleles increased panicle length with the phenotypic effect of the QTL being 0.2 cm. The phenotypic variance explained by each QTL was 11.2%. One significant QTL on chromosome 11 was associated with grain length. The HG101 allele increased the grain length and this QTL explained 16.2% of the observed phenotypic variance. Screening of more markers is under way to identify the introgression undetected previously and to map those markers in the F_2 and F_3 populations.

Discussion

One of the objectives was to identify novel beneficial alleles from *O. grandiglumis* for yield and yield components. We identified *O. grandiglumis* alleles related to yield components, including loci for culm length. The number of QTLs identified in this study is probably an underestimation because the genotypes of F_2 plants were not determined for all the polymorphic markers between the parents and some of the chromosomal regions harboring introgressions might have been undetected with the SSR markers used. As was evidenced for culm length in this study, of particular interest is the demonstration that some of the novel genetic variation observed in the

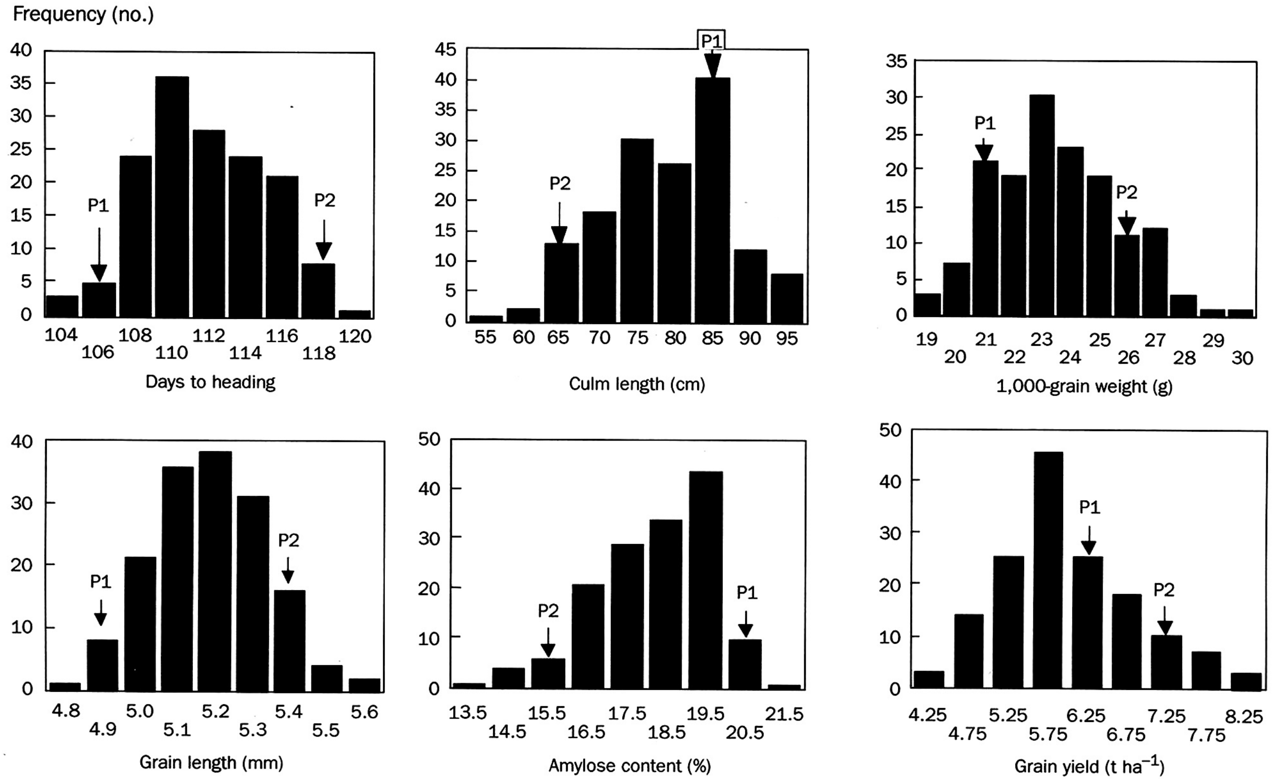


Fig. 1. Frequency distribution of six traits in the F_2 and F_3 populations (P1 = Hwaseongbyeo, P2 = HG101).

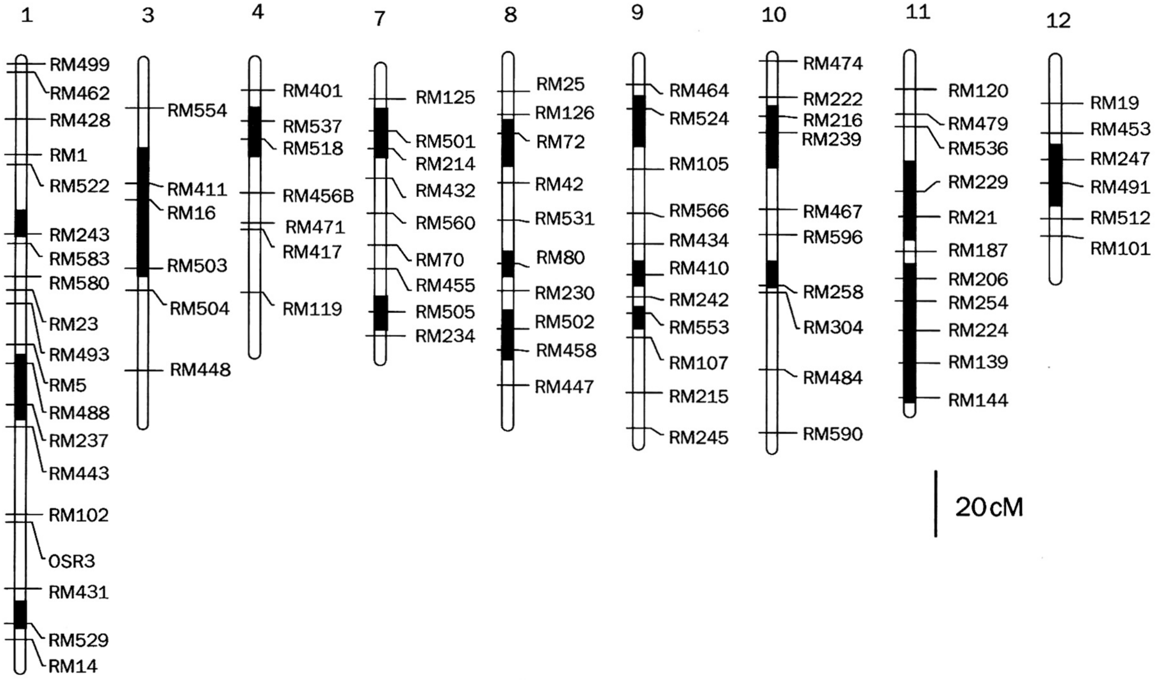


Fig. 2. A partial SSR map of rice derived from a backcross population (Temnykh et al 2001). Scale in Kosambi cM is shown on the right. Chromosome number is on the top and loci names are listed to the right of the chromosome. Solid black regions mark the specific *O. grandiglumis* introgressions.

Table 2. QTLs detected for traits based on single-point analysis in F_2 and F_3 populations.

Trait	Marker	Chrom.	*P*	R^2(%)	H/H[a]	H/G	G/G	Allele effect
Days to heading(d)	RM229	11	0.002	16.0	120.0	121.0	123.0	1.5
Culm length (cm)	RM488	1	0.0009	16.7	85.8	81.9	80.8	2.5
	RM80	8	0.002	18.3	82.5	82.0	78.2	2.2
	RM229	11	0.004	23.2	82.5	82.1	76.5	3.0
Panicle no.	RM224	11	0.046	10.2	11.0	11.0	13.0	1.0
Panicle length (cm)	RM144	11	0.03	11.2	19.5	19.7	19.9	0.2
Grain length (mm)	RM229	11	0.0001	18.3	5.01	5.11	5.18	0.09

[a] H/H, H/G, G/G: Hwaseong homozygotes, Hwaseong/HG101 heterozygotes, and HG101 homozygotes, respectively.

advanced backcross progenies of the interspecific cross involves positive transgressive variation. The fact that the positive or trait-enhancing alleles come from the agronomically unfavorable wild parent provides evidence that phenotypic performance turns out to be a poor predictor of genetic potential. These results are comparable with those of previous studies that reported trait-enhancing alleles from the same *O. rufipogon* accession (Moncada et al 2001, Xiao et al 1998), although the *O. rufipogon* accession was phenotypically inferior to *O. sativa.* With more markers mapped, it is expected that more trait-improving QTLs from HG101 can be identified.

This study aimed to determine the degree of conservation of QTLs across rice cultivars and environments. The detection of QTLs across cultivars and species might provide additional evidence for the existence of conserved loci controlling the traits of interest. The limited number of QTLs detected in this study prevented a direct comparison of QTLs. However, some inferences could be made. For example, the QTL on chromosome 1 affecting culm length in this study appears to share a similar region as d-18 (Kinoshita et al 1974), although this remains to be clarified. Several alleles such as QTLs on chromosomes 8 and 11 controlling culm length have not been detected in previous QTL studies between *Oryza* cultivars, indicating potentially novel alleles from *O. grandiglumis.* Genome-wide comparisons will be possible as more QTLs are detected and accumulated in this study.

Trait correlations or similar genomic locations of QTLs affecting different traits may be attributable to either pleiotropy of single genes or tight linkage of several genes that individually influence specific traits. In a previous study by Xiao et al (1996), pleiotropy was suggested for three chromosomal regions that were simultaneously associated with 1,000-grain weight and grains per plant or 1,000-grain weight and grains per panicle. These yield components showed highly negative correlations and three significant QTLs associated with 1,000-grain weight were mapped to the same positions as three QTLs affecting grains per plant and grains per panicle. In this study, one genomic region was associated with more than one trait, indicating linkage and/or pleiotropic effects. The HG101 allele at the locus RM229 on chromosome 11 increased the number of days to heading and grain length, and also decreased culm length. To better understand the characteristics of this locus, the development of further generations of near-isogenic lines (NILs) containing the fine-mapped QTLs is under way.

The results obtained in this study indicate that *O. grandiglumis* contains QTL alleles that are likely to improve agronomically important traits in elite cultivars. It is proposed that NILs containing individual introgressions associated with positive QTLs from *O. grandiglumis* be developed from this population and evaluated in a wide range of environments, so that QTL × environment interactions can be assessed. Construction of NILs is in progress to characterize these trait-enhancing QTLs in the Hwaseongbyeo genetic background.

References

Ahn SN, Kwon SJ, Suh JP, Kang KH, Kim HJ, Song MT, Hwang HG, Moon HP. 2001. Identification of introgressions in a backcross progeny derived from the cross between *Oryza sativa* and *O. grandiglumis*. Korean J. Breed. 33:318-323.

Brar DS, Khush GS. 1986. Wide hybridization and chromosome manipulation in cereals. In: Evans DH, Sharp WR, Ammirato PV, editors. Handbooks of plant cell culture. Vol. 4. Techniques and applications. New York (USA): MacMillan Publishing Co. p 221-263.

Brar DS, Khush GS. 1997. Alien introgression in rice. Plant Mol. Biol. 35:35-47.

Choi HC, Kim YG, Hong HC, Hwang HG, Ahn SN, Moon HP, Han SS, Ryu JD. 2000. Development of blast-resistant multilines and its blast infection and yield performance in rice. Treatises Crop Res. 1:9-18.

Data Description, Inc. 1992. Data Desk: statistics guide. Ithaca, N.Y. (USA): Data Description, Inc.

Harushima Y, Kurata N, Yano M, Nagamura Y, Sasaki T, Minobe Y, Nakagara M. 1996. Detection of segregation distortions in an indica-japonica rice cross using a high-resolution molecular map. Theor. Appl. Genet. 92:145-190.

Kim YK, Kim YJ, Choi HC, Han SS. 1995. Inheritance of leaf blast reactions to four races of blast fungus in segregating populations of eight rice crosses. RDA J. Agric. Sci. 37:283-298. (In Korean.)

Kinoshita T, Takamure I, Mori K, Shinbashi N. 1974. Character expression and inheritance mode of three kinds of dwarf rice: genetical studies on rice plant, LXI. Res. Bull. Farm Hokkaido Univ. 19:64-75. (In Japanse/English.)

McCouch SR, Doerge RW. 1995. QTL mapping in rice. Trends Genet. 11:482-487.

Moncada P, Martinez CP, Borrero J, Chatel M, Gauch Jr. H, Guimarães E, Tohme J, McCouch SR. 2001. Quantitative trait loci for yield and yield components in an *Oryza sativa* × *Oryza rufipogon* BC_2F_2 population evaluated in an upland environment. Theor. Appl. Genet. 102:41-52.

Nelson JC. 1997. QGENE: software for marker-based genome analysis and breeding. Mol. Breed. 3:239-245.

Panaud O, Chen X, McCouch SR. 1996. Development of microsatellite markers and characterization of simple sequence length polymorphism (SSLP) in rice (*Oryza sativa* L.). Mol. Gen. Genet. 252:597-607.

Ryu JD, Yeh WH, Han SS, Lee YH, Lee EJ. 1987. Regional and annual fluctuation of races of *Pyricularia oryzae* during 1977-1985 in Korea. Korean J. Plant Pathol. 3:174-179.

Standard Evaluation System in Agricultural Experiments and Research. 1995. Rural Development Administration Press, Suwon, Korea. (In Korean.)

Tanksley SD. 1993. Mapping polygenes. Annu. Rev. Genet. 27:205-233.

Temnykh S, Cartinhour S, Park W, Ayres N, Hauck N, Lipovich L, Cho YG, McCouch SR. 2000. Mapping and genome organization of microsatellite sequences in rice (*Oryza sativa* L.). Theor. Appl. Genet. 100:697-712.

Temnykh S, De Clerck G, Lukashova A, Lipovitch L, Cartinhour S, McCouch SR. 2001. Computational and experimental analysis of microsatellites in rice (*Oryza sativa* L.): frequency, length variation, transposon associations, and genetic marker potential. Genome Res. 11:1441-1452.

Vaughan DA. 1994. The wild relatives of rice (a genetic resources handbook). Los Baños (Philippines): International Rice Research Institute. p 38-39.

Xiao J, Li J, Yuan L, Tanksley SD. 1996. Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific cross. Theor. Appl. Genet. 92:230-244.

Xiao J, Li J, Grandillo S, Ahn SN, Yuan L, Tanksley SD, McCouch SR. 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon.* Genetics 150:899-909.

Xu Y, Zhu L, Xiao J, Huang N, McCouch SR. 1997. Chromosomal regions associated with segregation distortion of molecular markers in F_2, backcross, doubled haploid, and recombinant inbred populations in rice (*Oryza sativa* L.). Mol. Gen. Genet. 253:535-545.

Yano M, Sasaki T. 1997. Genetic and molecular dissection of quantitative traits in rice. Plant Mol. Biol. 35:145-153.

Yu GJ. Kwak TS, Kang KH, Moon HP. 1997. Efficiency of backcrossing and ovule culture in an interspecific cross between *O. sativa* L. and *O. grandiglumis* Prod. Korean J. Breed. 29:448-452.

Notes

Authors' addresses: S.N. Ahn, H.J. Kim, Department of Agronomy, Chungnam National University, Daejeon 305-764; S.J. Kwon, National Institute of Agricultural Biotechnology, RDA, Suwon 441-100; J.P. Suh, K.H. Kang, H.G. Hwang, H.P. Moon, National Crop Experiment Station, RDA, Suwon 441-100, Korea.

Acknowledgments: This study is part of the BioGreen21-supported project "Improvement of Selection Efficiency and Development of New Rice Cultivars Using Molecular Markers."

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Characterization, mapping and cloning of useful genes of the cultivated African rice *O. glaberrima*

A. Ghesquiere, M. Lorieux, L. Albar, S. Heuer, K. Miezan, G. Reversat, M.-Ndjiondiop, and M. Jones

This paper summarizes the efforts made by the West Africa Rice Development Association (WARDA) and the Institut de Recherche pour le Développement (IRD) during recent years to develop genetic tools and plant material required for the identification of genetic novelties provided by the African cultivated rice species *Oryza glaberrima.* This research focused on mapping and introgressions of *O. glaberrima* in the *O. sativa* indica genetic background since only conventional approaches can be developed to overcome or bypass strong effects of sterility barriers. A genetic map based on microsatellite markers was first established on a backcross population derived between IR64 and an *O. glaberrima* accession (Tog5681) identified as a potential donor for resistance to rice pests. Advanced backcross populations on IR64 were selected from the mapping population and monitored by molecular markers to construct progressively introgressed lines in a "contig" fashion. These lines now provide a framework for characterizing and assessing genetic variation of *O. glaberrima.* Advanced progenies were also analyzed to characterize the genetic basis of male sterility. A good general interspecific recombination ability indicated that positional cloning of *O. glaberrima* useful genes is feasible and different projects have begun with this aim. Nevertheless, a better analysis of sterility genes as well as an appropriate breeding scheme are key points to developing a more rational use of *O. glaberrima* genetic resources.

Oryza glaberrima Steud. is the African cultivated rice species. It was domesticated from the wild annual rice *O. breviligulata* A. Chev. & Roehr (= *O. barthii* A. Chev.) long before the introduction of the Asian cultivated rice *O. sativa* L. in West Africa during the 15th or 16th century (Portéres 1950). Isozyme polymorphism first clarified that *O. glaberrima* was a true cultivated species deriving from a domestication independent from that of *O. sativa* (Second 1982). Markers derived from DNA polymorphism at the cytoplasmic level (Dally and Second 1990) and at the nuclear restriction fragment length polymorphism (RFLP) level (Wang et al 1991, Second and

Ghesquière 1995) confirmed this hypothesis and close relationships with *O. breviligulata.* Nowadays, *O. glaberrima* tends to be replaced by *O. sativa* because of its low yield potential (high shattering, lodging susceptibility). Farmers are still growing African rice under poor crop management or adverse ecological conditions. The genetic diversity of *O. glaberrima* is substantially lower than that of *O. sativa* and no classification into different subspecies, such as *indica* and *japonica* in *O. sativa,* is recognized (Second 1982). Two major agroecotypes can be distinguished: a floating photosensitive type and an erect type cultivated in upland or in moderately inundated conditions. Another striking trait is the very strong reproductive barrier separating *O. glaberrima* from *O. sativa,* which includes pollen sterility as well as female sterility (Bougerol and Pham 1989, Sano 1985, Sano et al 1979). Both sterility effects and the rapid recovery of parental types in hybrid derivatives hampered the use of *O. glaberrima* in rice genetics and breeding programs. Recently, the use of anther culture on backcross plants was found to be efficient for deriving interspecific doubled-haploid (DH) lines at the origin of NERICA (New Rice for Africa) varieties released by WARDA for rainfed conditions (Jones et al 1997b). In addition, extensive evaluation of *O. glaberrima* accessions allowed us to identify potential donors for tolerance of abiotic stresses (acidity, iron toxicity, drought, Sano et al 1984) as well as resistance to or tolerance of several rice pests endemic in Africa (see Jones et al 1997a for a review). *O glaberrima* showed original patterns of blast resistance (Silue and Nottéghem 1991). Some accessions have very high resistance to rice yellow mottle virus (Ndjiondjop et al 1999, John et al 1985) and insect resistance, including resistance to stem borers and African rice gall midge (ARGM) (Sauphanor 1985). Resistance to several species of nematodes (*Heterodera sacchari* and *Meloidogyne* spp.) has also been identified (Reversat and Destombes 1998). Moreover, physiological traits and plant architecture characteristics of *O. glaberrima* are favorable for weed competitiveness (Dingkhun et al 1997). For a more complete incorporation of *O. glaberrima* genetic resources in plant breeding, a collaborative research initiative was launched in 1997 among international institutes from the Consultative Group on International Agricultural Research (IRRI, CIAT, WARDA), Cornell University (USA), Institut de Recherche pour le Développement (IRD, France), and Yunnan Academy of Agricultural Sciences (YAAS, China). This contribution reports the results and achievements made at IRD in collaboration with WARDA to develop molecular tools and resources required for characterizing and identifying novelties provided by *O. glaberrima.*

Developing an interspecific genetic map based on microsatellite markers

An interspecific backcross population was derived from IR64 (an indica high-yielding variety from IRRI) and Tog5681, an *O. glaberrima* accession highly resistant to rice yellow mottle virus (Ndjiondjop et al 1999) and to *H. sacchari* (Reversat and Destombes 1998). A total of 144 BC, individuals were obtained when using IR64 as a recurrent parent and were scored for various polymerase chain reaction (PCR) markers, including microsatellites (Chen et al 1997, Panaud et al 1996, Wu and Tanksley 1993) and sequence-tagged sites (STS) (Inoue et al 1994), and completed by some convenient amplified fragment length polymorphism (AFLP) markers. The resulting map finally comprised 119 markers (94 simple sequence length polymorphism — SSLP, 21 STS, 1 AFLP, and 3 random amplified polymorphic DNAs—RAPDs), giving a total map length of 1,923 cM and a mean interval length of 17 cM (Fig. 1) (Lorieux et al 2000). Except for local small and nonsignificant inversions, comparison of the interspecific map with similar microsatellite rice maps established on an indica x japonica recombinant inbred line (RIL) (Akagi et al 1996) or IR64 × Azucena DH lines (Chen et al 1997) gave an excellent colinearity and recombination along chromosomes. Segregation distortion is a very frequent phenomenon found in rice-mapping studies, particularly when remote crosses involving indica × japonica varieties (McCouch et al 1988, Kurata et al 1994) or cultivated x wild species (Causse et al 1994) are used. On this map, the most evident distortion was observed at the end of chromosome 6 for markers OSR19 and OSR25, both contained in the waxy gene. This corresponded to the sporo-gametophytic sterility gene S_{10}, found to be tightly linked to the waxy gene by Sano (1990). This model of gamete eliminator relies on a complete sterility of the pollen and on a total elimination of female gametes carrying the *O. sativa* allele for S_{10} in heterozygous F_1 genotypes. Other sterility genes were probably acting on pollen viability or female fertility but here they were completely masked by the S_{10} effect in the BC_1 population. The effects of S_{10} on segregation distortions can explain the rapid recovery of parental types in advanced interspecific progenies usually observed in many breeding experiments. Nevertheless, the construction of a genetic linkage map provided good evidence that there is a good general ability of interspecific genetic recombination between the two cultivated rice species, which is confirmed by cytogenetical observations and chromosome pairing (Ohmido and Fukui 1995).

Constructing introgressed interspecific isolines in a contig pattern

The development of suitable progenies for mapping studies and quantitative trait loci (QTL) characterization in interspecific progenies derived from *O. glaberrima* are strongly hampered by the very high sterility of F_1 and early backcross progenies, particularly when indica varieties are used. To overcome this sterility problem, we have begun developing a set of fixed lines, each bearing a chromosomal fragment of around 15–20 cM introgressed from *O. glaberrima* in the *O. sativa* genetic background (Ghesquikre et al 1997). Fragments belonging to the different lines will be arranged in a contiguous pattern in such a way that the totality of the fragments will represent the whole genome of *O. glaberrima.* This strategy is based on the assumption that, considering the low genetic diversity of *O. glaberrima,* a single interspecific combination can probably reveal a large proportion of the variation provided by *O. glaberrima,* including possible transgressive variations. Consequently, this process was supposed to mimic to some extent the reciprocal introgression process that

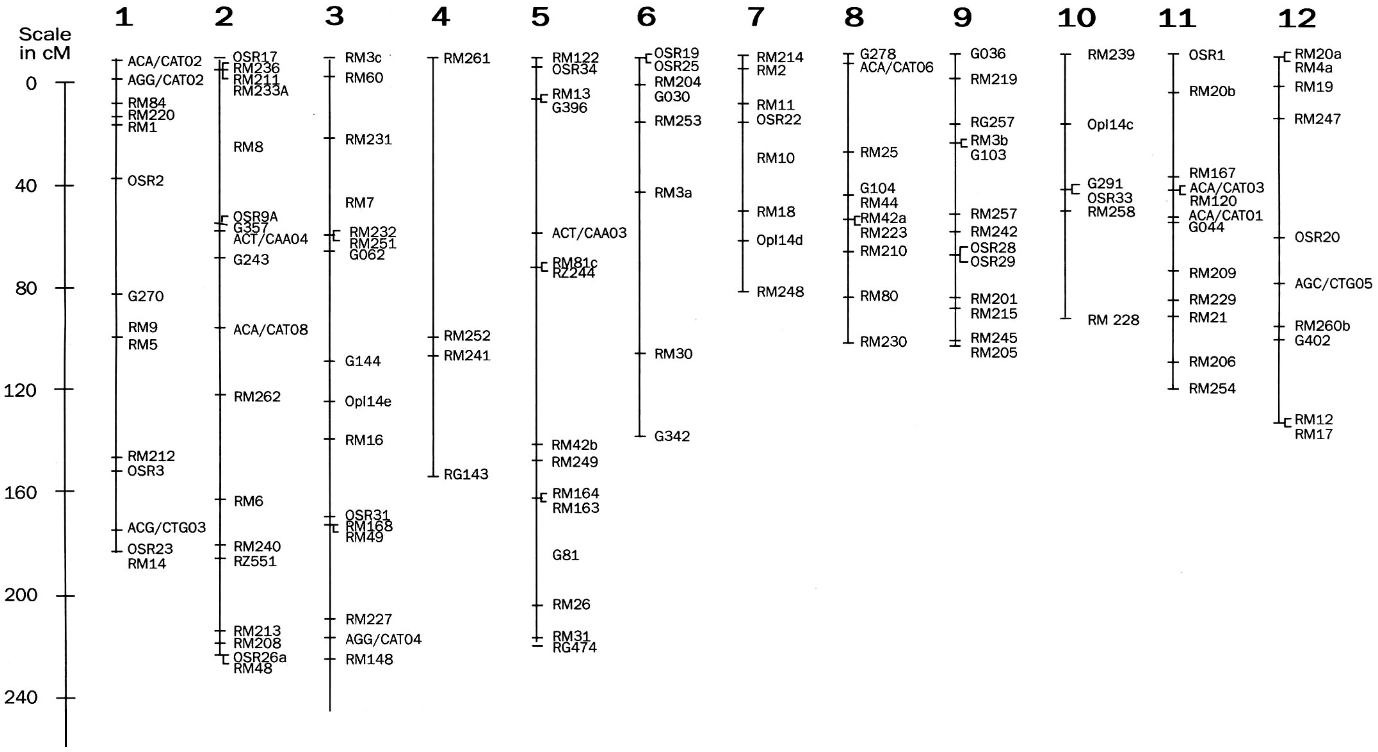


Fig. 1. Interspecific *O. sativa* × *O. glaberrima* simple sequence repeat (SSR)-based genetic map.

occurred between indica and japonica varieties and resulted in the large genetic diversity currently observed in *O. sativa.*

Sixteen BC_1 plants were selected for an appropriate allelic configuration of PCR markers mapped in the interspecific backcross. Introgression was monitored at each step by genotyping with a core set of 97 microsatellite and STS markers.

This process led to the production of 30 BC_2F_1, 203 BC_3F_1, and 40 BC_2F_2 individuals. Ratios of heterozygous loci in the successive generations conformed to those expected and indicated the good success of crosses. A graphical genotyping analysis of all BC_3F_1 and BC_2F_2 allowed us to select 49 BC_3F_1 with appropriate configuration to represent as best as possible the *O. glaberrima* genome in a contiguous pattern. Only fertile BC_3 or BC_3 plants with available corresponding BC_4F_1 progenies were retained in this selection. Two BC_2F_2 lines were also kept to fill a gap on chromosome 2. The resulting 51 genotypes were sorted according to their allelic composition (Fig. 2) and, for some missing data, the probability of the presence of the targeted fragment was deduced from the pedigree of the BC progenies. Therefore, except for a fragment of about 17 cM on chromosome 10, which has been lost, all the other markers have been checked or are supposed to be present in the selected BC_3 with high probability (P >0.95-0.99) (Fig. 3). Typically, most selected plants displayed one to four alien fragments scattered on different chromosomes as expected by simulation analyses and with variable size according to the map position of spanning markers. Pooling the alien segments of *O. glaberrima* showed that the overall distribution of introgression in the selected 51 plants was significantly reduced by marker selection to give a mean value around 58 cM. Fertility was progressively restored during the backcross process and the percentage of partially fertile genotypes in our glasshouse conditions was 1.4% in BC_1F_1, 33% in BC_2F_1, 54% in BC_3F_1, and 100% in BC_2F_2. The fertility restoration in BC_2F_1, BC_3F_1, and BC_2F_2 could be explained by recovery of homozygosity at the S_{10} locus on chromosome 6 and/or at various other loci. Another sterility gene might be localized on chromosome 3 close to marker RM231 as it also corresponded to segregation distortion in one *O. sativa* X *O. longistaminata* and five different indica x japonica segregating populations (Xu et al 1997).

Analyzing F_1 fertility and fertility restoration in advanced progenies

Sterility of interspecific F_1 hybrids was extensively analyzed at WARDA (St. Louis, Senegal) among various combinations of *O. glaberrima* and *O. sativa* parents. Seven varieties of *O. sativa* (Aus373, Dular, Peta, Ketan, Nangka, N22, and Patong) harboring various sets of neutral sterility alleles (S^n) on three to six S loci ($S_5{}^n$, $S_7{}^n$, $S_9{}^n$, $S_{15}{}^n$, $S_{16}{}^n$, $S_{17}{}^n$; Ikehashi and Wan 1996) were crosses with four *O. glaberrima* accessions (Tog5681, Tog5674, Tog5672, and CG17). Monitoring of plants at the flowering stage showed that pollen development was completely arrested at the microspore stage and grains were never obtained in any of the cross combinations tested. This confirmed that there was probably no allelic variation on S_{10} loci and that gametophytic sterility genes reflecting the indica-japonica differentiation in Asian

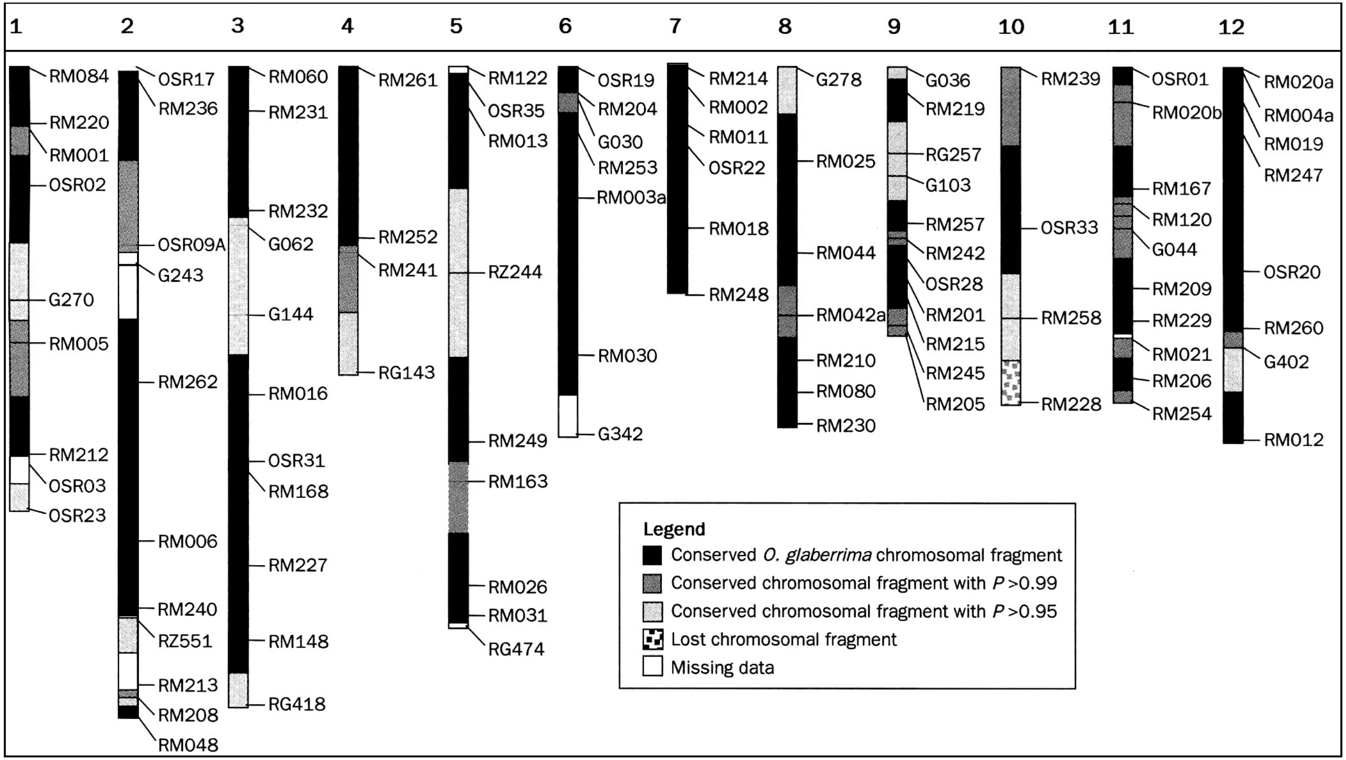


Fig. 2. Conservation of *O. glaberrima* chromosomal fragments in BC_3F_1 and BC_2F_2 genotypes along the rice genome. Only fertile BC_3F_1 and BC_2F_2 genotypes or BC_3F_1 with available BC_4F_1 progenies were considered.

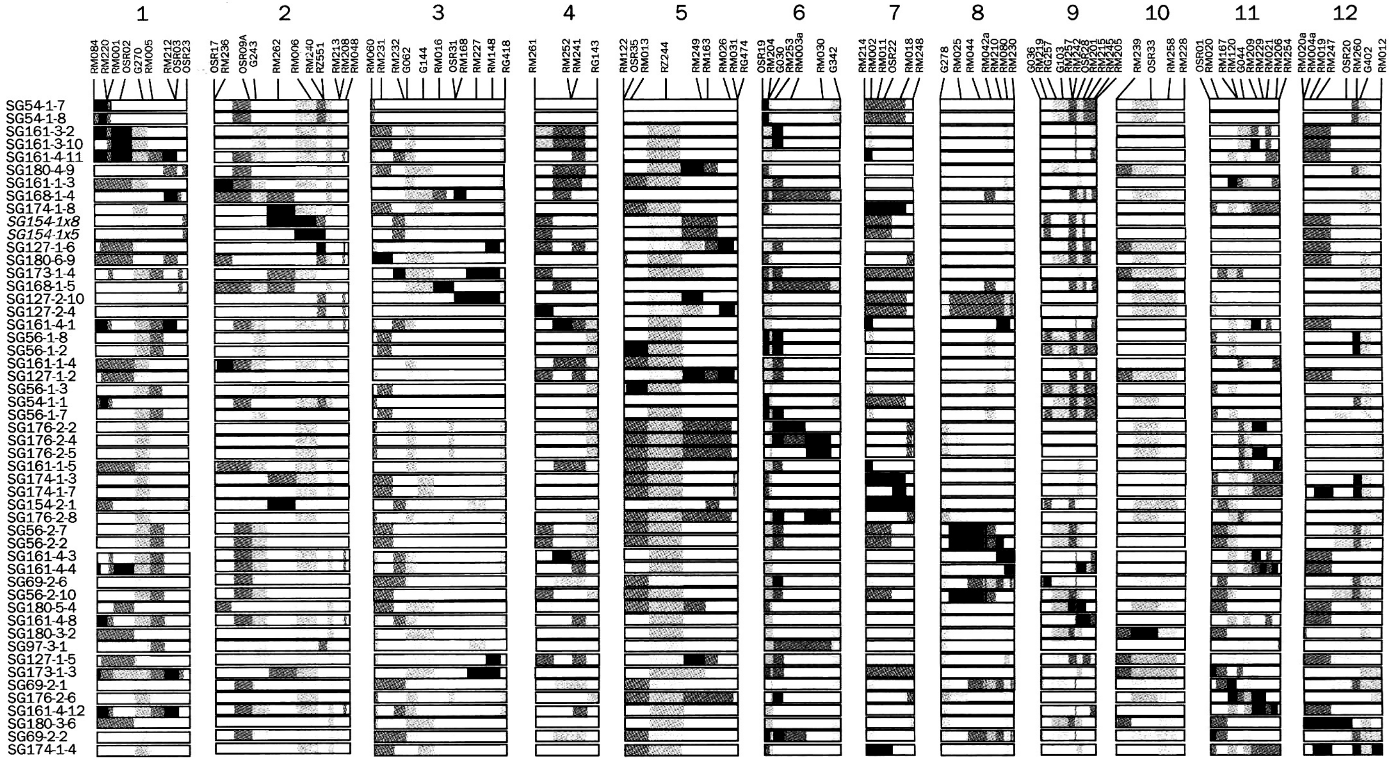


Fig. 3. Graphical genotyping of a series of 49 BC_3F_1 *Oryza sativa* x *O. glaberrima* genotypes that represent the *O. glaberrima* genome in a contiguous pattern of introgreseed fragments. Two BC_2F_2 lines (SG154-1x5 and SG154-1x8, in italics) were also retained to fill a gap on chromosome 2. A fragment of about 17 cM on chromosome 10 was lost. See a summary in Figure 2.

rice were not interacting with S_{10} to improve interspecific F_1 sterility. The recovery of fertility in selfed BC_1 and BC_2 of IR64 × Tog5681 was scored at WARDA (Senegal) at both the spikelet and pollen level. BC_1F_2 (100 plants) and BC_2F_3 showed a segregation for spikelet fertility (>50%:<50%) close to 1:3 (BC_1F_2) and 3:1 (BC_2F_3), respectively. The restoration of fertility is clearly visible in BC_2F_3 progenies, which gave a majority of fertile plants even if progenies were coming from semisterile F_2 plants. One BC_2F_3 progeny was scored for the OSR25 microsatellite marker close to S_{10} and showed a 1:1 segregation corresponding very well to the two classes of spikelet fertility. Semisterile plants developed a majority of pollen at the one cellular microspore stage (MS). The percentage of MS is highly correlated with apparent seed set. In semisterile plants, up to 60% of the pollen was at the MS, whereas this fraction represented only 6% in fertile plants.

Ongoing positional gene cloning project

In the course of developing rice molecular resources, the characterization of interesting traits in *O. glaberrima* offered opportunities to initiate original positional cloning projects. Among them, a gene with resistance to rice yellow mottle virus (RYMV) has focused our interest in recent years. This virus is restricted to the African continent and Madagascar and is responsible for major crop losses in indica rice varieties grown in irrigated conditions such as IR64. Although partial resistance was observed in upland rice varieties and was dependent on a polygenic control (Albar et al 1998), a very high pattern of resistance was observed in only five accessions of *O. glaberrima* (including Tog5681) and in a single *O. sativa* cultivar (Gigante). The complete absence of symptoms and very low virus content in leaves after mechanical inoculation using a large range of representative strains of the virus were two characteristics of these accessions (Ndjiondjop et al 1999). Moreover, protoplasts and cytological studies suggested that this resistance could come from the failure of cell-to-cell movement of the virus (Ndjiondjop et al 2001). Genetic analyses of intra- and interspecific progenies as well as allelism tests showed that the high resistance was determined by the same single recessive gene in both resistant accessions. Therefore, the rarity of this natural resistance as well as genetic determinism and the inferred mechanism of resistance suggested that this resistance could result from the mutation of a host component critical for the accomplishment of the virus cycle. The positional cloning of this gene began by using variety Gigante advantageously as an RYMV resistance donor to derive large convenient IR64 × Azucena and Nipponbare × Gigante F_2 progenies. Fine mapping of the gene allowed us to localize this gene on the long arm of chromosome 4 between microsatellite markers RM273 and RM252 (Albar et al, n.d.). Using data of rice physical mapping and sequencing projects, the resistance gene has been located recently on a contig of a bacterial artificial chromosome of about 600 kb, corresponding to 3.5 cM, almost totally sequenced. Additional convenient markers deduced from sequencing data are currently used to reduce the physical size of the fragment around the gene. Progress in physical mapping and sequence annotation of the target zone will permit the rapid identification of candidate genes and determine allelic variations in resistant varieties of *O. glaberrima* and in other rice germplasm. In parallel, the RYMV resistance gene has been transferred in different very susceptible indica varieties to envisage the deployment of this gene at the field level in West Africa.

Resistance to nematode represents a specific interest since it can indirectly contribute to improving drought tolerance in rainfed conditions (Coyne et al 1999). It is also anticipated that modifications of rice-growing systems to save water reserves in Asia will dramatically amplify the nematode effect in irrigated conditions. *Meloidogyne graminicola* (rice root-knot nematode) is of special concern in many Asian rice-growing countries and no natural resistance has been found in rice germplasm except in the two African rice species *O. longistaminata* and *O. glaberrima* (Soriano et al 1999). *O. glaberrima* accessions show various resistances to nematode species of *Meloidogyne* (*M. incognita, M. javanica,* and *M. graminicola*) and to the cyst nematode *H. sacchari* (G. Reversat, IRD, personal communication). Evaluation of interspecific progenies derived from accession Tog5681 after inoculation by *H. sacchari* and *M. incognita* suggested that different resistance genes were acting since they showed different patterns of resistance heredity. Particularly, a BC_1F_3 progeny gave a fraction of resistant individuals completely free of cyst development and which was according to the presence of a single gene with intermediate dominance. This progeny served to map this gene on chromosome 11. Increasing marker density and physical mapping of the gene are envisaged in the near future.

Conclusions

Genetic mapping and the development of introgression lines now provide a basis for characterizing useful variations in *O. glaberrima.* Additional microsatellite markers will replace STS and will be useful for identifying possible recombination in the initial targeted segment and for deriving isogenic lines with reduced alien fragments. This work will be facilitated by the very large number of available mapped microsatellite markers (Cho et al 1998, Temnykh et al 2000). Selfing of selected lines and control of the genetic background followed by multiplication will give a permanent resource for characterizing and identifying genes coming from *O. glaberrima.* Multiplication of introgression lines and large-scale evaluation of many traits are planned to take place through partnership with international institutions (WARDA, CIAT, and IRRI) and any interested institutions. A pilot experiment already carried out at WARDA (Senegal) evidenced interesting variation for heading date, plant type, and tillering ability on a large panel of BC_3 progenies. There is probably no recombination limitation to successfully introgressing major genes or QTLs from *O. glaberrima.* Using various *O. sativa* lines to improve seed set in F_1 indicated that complete sterility is probably a very general rule in interspecific F_1 hybrids regardless of the content of sterility genes affecting indica-japonica combinations. Nevertheless, while the S_{10} allele from *O. glaberrima* is acting as a “gamete eliminator” on both male and female gametes in F_1, its action is lowered in backcross progenies and was limited to only the pollen fraction. Therefore, a sterility gene at the S_{10} locus may have different effects on male and pollen fractions according to the recovery of the parental genome background and interactions with other sterility genes. For instance, most of the tropical japonica have the wide compatibility allele at the S_5 locus on chromosome 6, which can significantly reduce F_1 sterility in indica crosses (Yanagihara et al 1995). This gene itself did not improve interspecific F_1 fertility but could explain why interspecific DH lines have been obtained at WARDA from BC_2 derived from crosses with varieties with wide compatibility since success with anther culture is related to the ability of microspores to evolve normally.

We expect that rapid development of rice genomics will help to decipher the structure of the African rice genome and to identify original genes of *O. glaberrima.* Special emphasis should be given to analyzing sterility barriers and developing interspecific bridges in the early generation with acceptable fertility and crossability with various *O. sativa* genetic materials since interesting traits of *O. glaberrima* are scattered in different accessions. The use of interspecific bridges will allow for the genetic studies required to establish the genetic basis and mapping of traits coming from *O. glaberrima* and will facilitate a more complete use of this gene pool in rice breeding, particularly in the indica genetic background. Incorporation of selected interspecific lines in existing recurrent populations of *O. sativa* is also another possible way to introduce *O. glaberrima* genes and increase the occurrence of favorable recombinations.

References

Akagi H, Yokoseki Y, Inagaki A, Fujimura T. 1996. Microsatellite DNA markers for rice chromosomes. Theor. Appl. Genet. 93:1071-1077.

Alba L, Lorieux M, Ahmadi N, Rimbault I, Pinel A, Sy AA, Fargette D, Ghesquière A. 1998. Genetic basis and mapping of the resistance to *Rice yellow mottle virus.* I. QTLs identification and relationship between resistance and plant morphology. Theor. Appl. Genet. 97:1145-1154.

Albar L, Ndjiondjop M-N, Esshak Z, Berger A, Pinel A, Fargette A, Ghesquière A. n.d. Fine mapping of a gene required for *Rice yellow mottle* virus cell-to-cell movement in view of positional cloning. Theor. Appl. Genet. (Submitted.)

Bougerol B, Pham J. 1989. Influence of the *Oryza sativa* genotype on the fertility and quantitative traits of F_1 hybrids between the two cultivated rice species *O. sativa* L. and *O. glaberrima* Steud. Genome 32:810-815.

Causse MA, Fulton TM, Cho YG, Ahn SN, Chunwongse J, Wu K, iao J, Yu Z, Ronald PC, Harrington SE, Second G, McCouch SR, Tanksley SD. 1994. Saturated molecular map of the rice genome based on an interspecific backcross population. Genetics 138:1251-1274.

Chen X, Temnykh S, Xu Y, Cho YG, McCouch SR. 1997. Development of a microsatellite framework map providing genome-wide coverage in rice (*Oryza sativa* L.). Theor. Appl. Genet. 95:553-567.

Cho YG, McCouch SR, Kuiper M, Kang MR, Pot J, Groenen JTM, Eun MY. 1998. Integrated map of AFLP, SSLP and RFLP markers using a recombinant inbred population of rice (*Oryza sativa* L.). Theor. Appl. Genet. 97:370-380.

Coyne D, Plowright R, Fofana B. 1999. Observations on the susceptibility of *Oryza sativa* and resistance of *Oryza glaberrima* to the cyst nematode (*Heterodera sacchari*) and the influence of weed management in upland rice in Ivory Coast. Int. J. Pest Manage. 45:255-258.

Dally A, Second G. 1990. Chloroplast DNA diversity in wild and cultivated species of rice (Genus *Oryza* section *Oryza*): cladistic-mutation and genetic-distance analysis. Theor. Appl. Genet. 80:209-222.

Dingkhun M, Johnson D, Jones M. 1997. Physiological basis for developing low-management upland rice types. In: Jones MD, Johnson DE, Fagades SO, editors. Proceedings of the workshop: Africa/Asia Joint Research on Interspecific Hybridization between the African and Asian rice species (*O. glaberrima* and *O. sativa*), 16-18 December 1996. BouakC (Côte d'Ivoire): West Africa Rice Development Association. p 81-102.

Ghesquière A, Séquier J, Second G, Lorieux M. 1997. First steps towards a rational use of African rice, *Oryza glaberrima,* in rice breeding through a 'contig line' concept. Euphytica 96:31-39.

Ikehashi H, Wan J. 1996. Differentiation of alleles at seven loci for hybrid sterility in cultivated rice (*Oryza sativa* L.). In : Khush GS, editor. Rice genetics III. Proceedings of the Third International Rice Genetics Symposium. Manila (Philippines): International Rice Research Institute. p 404-408.

Inoue T, Zhong HS, Miyao A, Ashikawa I, Monna L, Fukuoka S, Miyadera N, Nagamura Y, Kurata N, Sasaki T, Minobe Y. 1994. Sequence-tagged sites (STSs) as standard landmarkers in the rice genome. Theor. Appl. Genet. 89:728-734.

John V, Thottapilly G, Ng N, Allury K, Gibbons J. 1985. Varietal reaction to *Rice yellow mottle virus* resistance. FAO Plant Prot. Bull. 33:109-111.

Jones M, Aluko GK, Semon M. 1997a. Characterization and utilization of *O. glaberrima* Steud. in upland rice improvement. In: Jones MD, Johnson DE, Fagades SO, editors. Proceedings of the workshop: AfricdAsia Joint Research on Interspecific Hybridization between the African and Asian rice species (*O. glaberrima* and *O. sativa*), 16-18 December 1996. Bouakd (Côte d'hoire): West Africa Rice Development Association. p 43-59.

Jones M, Dingkhun M, Aluko GK, Semon M. 1997b. Using backcrossing and doubled haploid breeding to generate weed-competitive rices from *O. sativa* L. x *O. glaberrirna* Steud. genepools. In: Jones MD, Johnson DE, Fagades SO, editors. Proceedings of the workshop: Africa/Asia Joint Research on Interspecific Hybridization between the African and Asian rice species (*O. glaberrirna* and *O. sativa*). 16-18 December 1996. Bouaké (Côte d'Ivoire): West Africa Rice Development Association. p 61-70.

Kurata N, Nagamura Y, Yamamoto K, Harushima Y, Sue N, Wu J, Antonio BA, Shomura A, Shimizu T, Lin S-Y, Inoue T, Fukuda A, Shimano T, Kuboki Y, Toyama T, Miyamoto Y, Kirihara T, Hayasaka K, Miyao A, Monna L, Zhong HS, Tamura Y, Wang Z-X, Momma T, Umehara Y, Yano M, Sasaki T, Minobe Y. 1994. A 300 kilobase interval genetic map of rice including 883 expressed sequences. Nature Genet. 8:365-372.

Lorieux M, Ndjiondjop M-N, Ghesquière A. 2000. A first interspecific *Oryza sativa* x *O. glaberrima* microsatellite-based genetic linkage map. Theor. Appl. Genet. 100:593-601.

McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffman WR, Tanksley SD. 1988. Molecular mapping of rice chromosomes. Theor. Appl. Genet. 76:815-829.

Ndjiondjop M-N, Albar A, Fargette D, Fauquet C, Ghesquière A. 1999. The genetic basis of high resistance to rice yellow mottle virus (RYMV) in cultivars of two cultivated rice species. Plant Dis. 83:931-935.

Ndjiondjop M-N, Brugidou C, Zang S, Fargette D, Ghesquière A, Fauquet C. 2001. High resistance to rice yellow mottle virus in two cultivated rice cultivars is correlated with failure of cell to cell movement. Physiol. Mol. Plant Pathol. 59:309-316.

Ohmido N, Fukui K. 1995. Cytological studies of African cultivated rice, *Oryza glaberrima.* Theor. Appl. Genet. 91:212-217.

Panaud O, Chen X, McCouch SR. 1996. Development of microsatellite markers and characterization of simple sequence length polymorphism (SSLP) in rice (*Oryza sativa* L.). Mol. Gen. Genet. 252:597.

Portkres R. 1950. Vieilles agricultures de l'Afrique intertropicale: centres d'origine et de diversification variétale primaire et berceaux de l'agriculture antérieure au XVIe siècle. Agron. Trop. V 489-507.

Reversat G, Destombes D. 1998. Screening for resistance to *Heterodera sacchari* in the two cultivated rice species, *Oryza sativa* and *O. glaberrima.* Fundam. Appl. Nematol. 21:307-317.

Sano Y. 1985. Sterility barriers between *Oryza sativa* and *O. glaberimma.* In: Rice genetics. Proceedings of the International Rice Genetics Symposium, 27-31 May 1985. Los Baños (Philippines): International Rice Research Institute. p 109-118.

Sano Y. 1990. The genic nature of gamete eliminator in rice. Genetics 125:161-191.

Sano Y, Chu Y, Oka H. 1979. Genetic studies of speciation in cultivated rice. 1. Genic analysis for the F_1 sterility between *Oryza sativa* and *O. glaberrima* Steud. Jpn. J. Genet. 54:121-132.

Sano Y, Sano R, Morishima H. 1984. Neighbour effects between two naturally occurring rice species, *Oryza sativa* and *O. glaberrima.* J. Appl. Ecol. 21:245-254.

Sauphanor B. 1985. Some factors of upland rice tolerance to stem-borers in West Africa. Insect Sci. Appl. 6:429-434.

Second G. 1982. Origin of the genic diversity of cultivated rice (*Oryza* spp.): study of the polymorphism scored at 40 isozyme loci. Jpn. J. Genet. 57:25-57.

Second G, Ghesquière A. 1995. Cartographie des introgressions réciproques entre les sous-espèces *indica* et *japonica* de riz cultivé (*Oryza sativa* L.): In: Techniques et Utilisations des Marqueurs Moléculaires. Montpellier, France, 29-31 March 1995. Les Colloques n° 72. Paris (France): Ed. INRA. p 83-93.

Silue D, Nottkghem J. 1991. Resistance of 99 *Oryza glaberrima* varieties to blast. Int. Rice Res. Newsl. 16:13-14.

Soriano I, Schmitt V, Brar DS, Prot J-C, Reversat G. 1999. Resistance to rice root-knot nematode *Meloidogyne graminicola* identified in *Oryza longistaminata* and *O. glaberrima.* Nematology 14:395-398.

Temnykh S, Park WD, Ayres N, Cartinhour S, Hauck N, Lipovich L, Cho YG, Ishii T, McCouch SR. 2000. Mapping and genome organization of microsatellite sequences in rice (Oryza sativa L.). Theor. Appl. Genet. 100:697-712.

Wang Z, Second G, Tanksley S. 1991. Polymorphism and phylogenetic relationships among species in the genus *Oryza* as determined by analysis of nuclear RFLPs. Theor. Appl. Genet. 83:565-581.

Wu K, Tanksley S. 1993. Abundance, polymorphism and genetic mapping of microsatellites in rice. Mol. Gen. Genet. 241:225-235.

Xu Y, Zhu L, Xiao J, Huang N, McCouch S. 1997. Chromosomal regions associated with segregation distortion of molecular markers in F_2, backcross, doubled haploid, and recombinant inbred populations in rice (*Oryza sativa* L.). Mol. Gen. Genet. 253:535-545.

Yanagihara S, McCouch SR, Ishikawa K, Ogi Y, Maruyama K, Ikehashi H. 1995. Molecular analysis of the inheritance of the S_5 locus conferring wide compatibility in indica/japonica hybrids of rice (*O. sativa* L.). Theor. Appl. Genet. 90:182-188.

Notes

Authors' addresses: A. Ghesquière, M. Lorieux, L. Albar, IRD, BP 64501, 34394 Montpellier cedex 5, France; S. Heuer, K. Miezan, WARDA Sahel Station, Ndiaye, B.P. 9 Saint Louis, Senegal; M-Ndjiondiop, M. Jones, WARDNADRAO, 01 BP 2551, Bouaké, Republic of Côte d'Ivoire.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Developing and evaluating rice chromosome segment substition lines

K. Doi, Sobrizal, K. Ikeda, P.L. Sanchez, T. Kurakazu, Y. Nagai, and A. Yoshimura

Some series of chromosome segment substitution lines (CSSLs) in the background of *Oryza sativa* have been developed. Three A-genome species, *O. glaberrima* (IRGC104038), *O. glumaepatula* (IRGC105668), and *O. meridionalis* (W1625), were used as donor parents and japonica variety Taichung 65 was commonly used as a recurrent parent for backcrossing. CSSLs developed in this study provide good materials for more detailed genetic analysis on naturally occurring variations among A-genome species of rice. So far, more than 20 genes have been mapped on a restriction fragment length polymorphism linkage map. The identified genes include those causing sterility, weakness, shattering, and changes in heading date. Some of these genes are being isolated by map-based cloning. The process of development of the CSSLs, genetic analysis using the CSSLs, and characterization of identified genes are presented in this paper.

Asian cultivated rice, *Oryza sativa* L., is a major food crop in the world and African cultivated rice, *O. glaberrima* Steud., is endemic to West Africa. Both belong to A-genome species in the genus *Oryza. O. sativa* is believed to be differentiated from a wild species, *O. rufipogon* Griff., whereas *O. glaberrima* was domesticated from *O. barthii* A. Chev. Other A-genome wild species, *O. nivara* Sharma et Shastry, *O. longistaminata* Chev. et Roehr., *O. glumaepatula* Steud., and *O. meridionalis* Ng, are known to exist in Asia, Africa, Latin America, and Australia, respectively. Although these A-genome species are a potential source of new and valuable genes and can be easily crossed with *O. sativa,* they have rarely been used for fundamental and practical breeding studies (Oka 1988, Bra and Khush 1997, Xiao et al 1998). However, the recent success of the New Rice for Africa (NERICA, www.warda.cgiar.org/warda/main/Achievements/nerica.htm), derived from an interspecific cross between *O. sativa* and *O. glaberrima,* clearly revealed the genetic potential of exotic germplasm.

Rice breeders are running out of genetic variation in cultivated rice, whose variation has been narrowed through domestication. To exploit the genetic potential of exotic germplasm resources, we developed some series of chromosome segment substitution lines (CSSLs) in the background of *O. sativa.* A CSSL contains marker-defined chromosomal segments from an agriculturally unadapted source in the background of cultivated varieties. Such lines are referred to as introgression lines (Eshed and Zamir 1995), contig lines (Ghesquiére et al 1997), or exotic libraries (Zamir 2001). The essence of this concept, however, is to provide a way to broaden the genetic variation of materials for plant breeding (Tanksley and McCouch 1997, Zamir 2001). CSSL populations are competent for phenotypic evaluation over years and locations because they are genetically fixed lines with a uniform background of cultivated varieties. CSSLs therefore enable precise characterization of hidden useful genes in alien resources. Some genes in wild germplasm were identified as quantitative trait loci (QTLs) and already cloned in tomato (Fridman et al 2000, Frary et al 2000). Here, we present the development of A-genome CSSLs, their usefulness in genetic analysis, and the characteristics of newly identified genes.

Chromosome segment substitution lines

Three different A-genome species, *O. glaberrima* (IRGC 104038), *O. glumaepatula* (IRGC105668), and *O. meridionalis* (W1625), were used as donor parents and japonica variety Taichung 65 (T65) was commonly used as a recurrent parent for backcrossing. To develop *O. glaberrima* CSSLs (glaCSSLs), a framework restriction fragment length polymorphism (RFLP) linkage map was constructed using a BC_1F_1 population (Doi et al 1998b). Based on the RFLP map, plants with desired genotypes were selected from BC_2F_1 and BC_3F_1 generations. Candidate plants for glaCSSLs were selected to carry homozygous introgressed segments from the donor parent (Doi et al 1997). To develop *O. glumaepatula* CSSLs (glumCSSLs) and *O. meridionalis* CSSLs (merCSSLs), F_1 plants obtained through the reciprocal crosses between the donors and T65 were continuously backcrossed with T65 to produce the BC_3F_1 or BC_4F_1 populations. Consequently, glumCSSLs and merCSSLs consist of lines with reciprocal cytoplasm (Sobrizal et al 1999a, Kurakazu et al 2001a). Next, the populations were genotyped using about 100 RFLP markers scattered across the rice genome. The fixation of glumCSSLs and merCSSLs is under way. F_1s of all combinations were completely male sterile, but fertility was gradually restored by backcrossing. All the obtained CSSLs are fertile and can be maintained without crossing.

We successfully developed the CSSLs from three donors. The genotypes of glaCSSLs are shown in Figure 1, and those of other CSSLs were presented in previous reports (Sobrizal et al 1999a, Kurakazu et al 2001 a). We did not encounter any serious problem that would prevent the construction of CSSLs, such as a crossing barrier, hybrid inviability, or reduced recombination. Developed CSSLs are ready for repeated and multilocational evaluation for gene discovery and characterization. Some

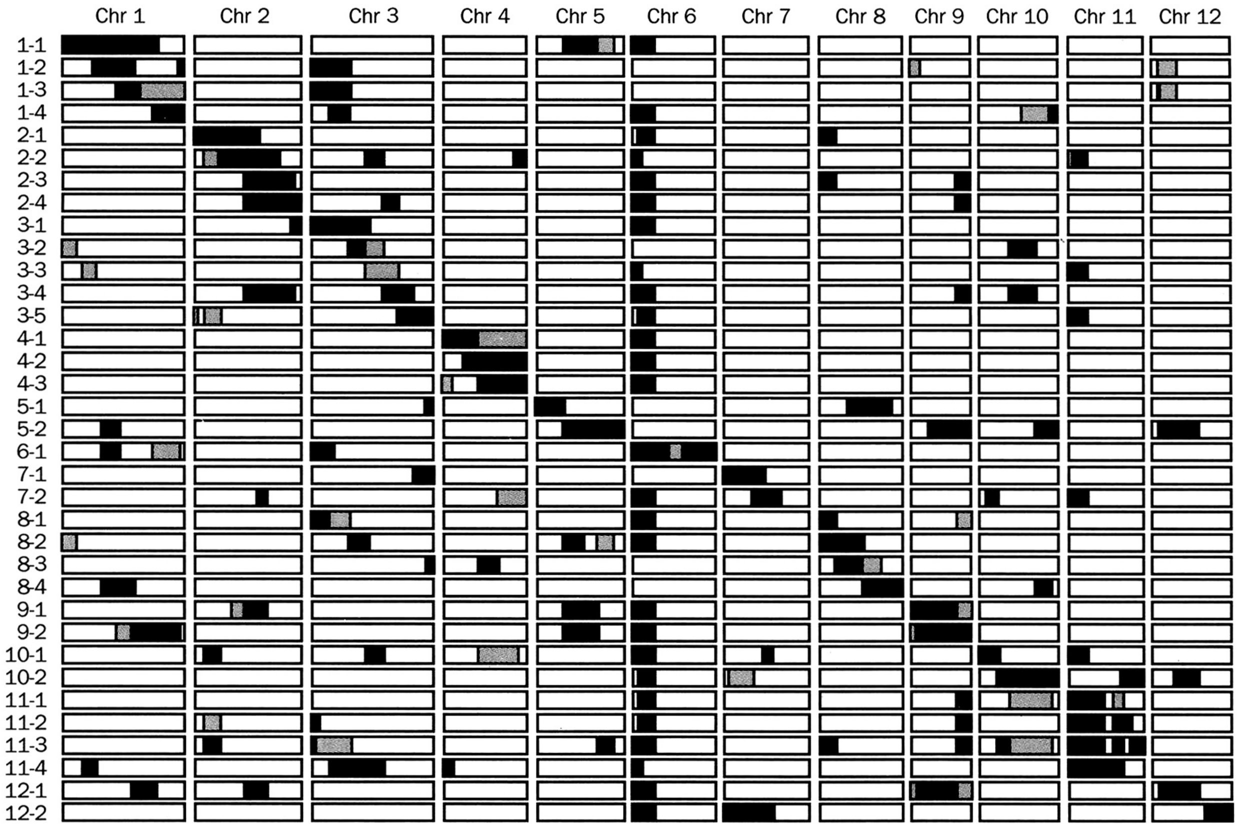


Fig. 1. An ideogram of the glaCSSLs. Linkage groups are drawn to scale. The solid black regions, the white regions, and the shaded regions represent donor, recurrent, and heterozygous segments, respectively.

Table 1. Genes identified using chromosome segment substitution lines (CSSLs).

Gene (chromosome)	Character	Origin (cytoplasm)
Reproductive barriers		
S1 (6), *S18* (10), *S19* (3), *S20* (7), *S21* (7)	F_1 pollen sterility	glaCSSLs
S22 (2), *S23* (7), *S27* (8)	F_1 pollen sterility	glumCSSLs (T65)
hwf1 (4)	F_2 hybrid weakness	glumCSSLs (T65)
Rhw (8)	Restoration for hybrid weakness	glumCSSLs (glum)
Domestication-related traits		
Sh3 (4), *Sh5* (5)	Seed shattering	glumCSSLs (T65)
Sh6 (5)	Seed shattering	merCSSLs (mer)
An7 (5), *An8* (4)	Awnness	merCSSLs
Heading		
Ehd1 = *Ef*(t) (10)	Early heading	glaCSSLs
Ehd1-glum (10)	Early heading	glumCSSLs (T65)
Lhd1 (6), *Lhd2* (7)	Late heading	glumCSSLs (T65)
Morphological trait		
Spr (4)	Spreading panicle	glumCSSLs (T65)

chromosomal regions, however, could not be introgressed because of hybrid sterility or hybrid weakness genes described later.

Identifying genes using CSSLs

CSSLs were useful for identifying new genes. Practically, the materials derived from the process of development were quite useful for the genetic analysis. Table 1 lists identified genes. Currently, our priority is to identify genes related to reproductive barriers and domestication-related traits.

Genes related to reproductive barrier

In glaCSSLs, new hybrid sterility genes, *S18, S19, S20,* and *S21* as well as *S1* (Sano 1986), were identified and located on the linkage map (Doi et al 1998a, 1999, Taguchi et al 1999). It is noteworthy that QTL analysis using the BC_2F_1 population (Doi et al 1998b) provided useful information for the identification of these new loci and the construction of CSSL-derived near-isogenic lines (NILs) using marker-assisted selection. NILs for these genes enabled precise mapping and characterization.

Some genes causing hybrid sterility/weakness were identified in glumCSSLs. *S22* (Sobrizal et al 2000a), *S23* (Sobrizal et al 2000b), and *S27* (Sobrizal et al 2001a) caused F_1 pollen sterility and *hwf1* (Sobrizal et al 2001b) caused F_2 weakness. A unique cytoplasmic weakness gene, *Rhw* (restoration of hybrid weakness), was identified in glumCSSL with *O. glumaepatula* cytoplasm (Ikeda et al 1999). The dominant *Rhw* allele from *O. glumaepatula* can restore the hybrid weakness of plants having *O. glumaepatula* cytoplasm.

Genes for domestication-related traits

Seed shattering is the most important trait in the domestication of rice. A shattering gene, *Sh3,* was identified and mapped on chromosome 4 using glumCSSLs (Sobrizal et al 1999b) as well as a previous study (Eiguchi and Sano 1990). NILs for *Sh3-glum* (*O. glumaepatula*) show a severe level of seed shattering comparable with that of the wild species. *Sh3* was also identified in merCSSLs and in a NIL carrying the *O. rufipogon* allele (Nagai et al 2002b). Therefore, this gene is considered as a key gene for rice domestication and it is being isolated by map-based cloning. Interestingly, *Sh3* was also identified in glaCSSLs, whose donor parent was nonshattering (Nagai et al 2002a). In addition to that, mapping of *Sh3-gla (O. glaberrima)* revealed the presence of *iSh3,* an inhibitor gene for *Sh3* (Nagai et al 2002a). This clearly indicates that loss-of-function of *Sh3* is closely involved in the domestication of *O. sativa,* but is not related to the nonshattering phenotype of *O. glaberrima.* Other shattering genes, *Sh5* and *Sh6,* were also identified in glumCSSLs and merCSSLs, respectively (Sanchez et al 2002). Awnness is a likely target trait during domestication and causal genes were identified (Kurakazu et al 2001b). The distribution and differentiation of these genes in the rice genome and germplasm resources should be of future interest.

Other genes identified in CSSLs

Several genes causing earliness or late heading were identified (Doi and Yoshimura 1998, Sanchez et al 2000). They are considered to be alleles of QTLs found in a japonica/indica cross (Yano et al 2001). This means that genetic analysis using the japonica/indica cross can cover the naturally occurring variation to some degree. However, this would not deny the fact that CSSLs could create broader genetic variation than intraspecific crosses. Other genes causing changes in panicle morphology or endosperm were also identified using CSSLs (data not shown).

Map-based cloning of *Ehd1*

Map-based cloning is already quite feasible in rice. Ehdl (Early heading date I, formerly referred to as *Ef* (t), Doi and Yoshimura 1998) identified in *O. glaberrima* was isolated by map-based cloning. A large mapping population of the BC_3F_4 generation consisting of >2,500 plants was used for high-resolution mapping and the candidate genomic region was narrowed to <20 kb. The function of candidate genes was confirmed by transformation. *Ehdl* encodes a 341-amino-acid protein that has homology to response regulators (data not shown). We believe that *Ehdl* is involved in light-signal transduction because heading of the NIL with *Ehdl-gla (O. glaberrima)* is promoted, especially in short-day conditions, and response regulators are involved in the His-to-Asp phospho-relay signaling (or two-component) system (Hwang et al 2002).

Sequence analysis of four alleles, three functional alleles (*O. glaberrima,* Nipponbare, and Kasalath), and one loss-of-function (T65) revealed that an amino acid change of a highly conserved residue in the DNA-binding domain was unique to T65 (Fig. 2). The gel-mobility-shift assay confirmed that the DNA-binding domain

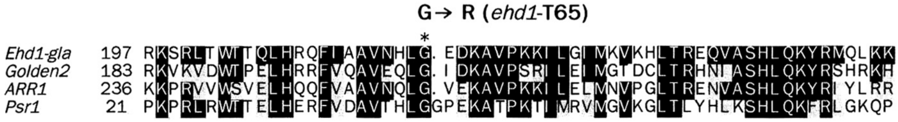


Fig. 2. Alignment of DNA-binding domains of *Ehd1-gla* and related proteins (*Golden2,* AAG32325; *ARR1,* T51246; and *Psr1,* AAD55941). The position of amino-acid variation in T65 (G to R) caused by a nucleotide change is indicated by an asterisk. Residues identical to those in *Ehd1-Kas* are in black boxes; unidentical but similar ones are In shaded boxes.

of the T65 allele has reduced DNA-binding ability (data not shown). This indicated that this nucleotide change is crucial for the reduced function of the T65 allele. We believe that intensive investigation into the nucleotide changes associated with phenotypic changes should be conducted to evaluate and draw out the full potential of naturally occurring variation (Buckler and Thornsberry 2002, Nesbitt and Tanksley 2002).

Conclusions

The primitive and unadapted phenotype of wild species has prevented the rational use of genetic resources. Developed CSSLs are good materials as a starting point to evaluate the useful genes hidden in wild rice. Another limiting factor was reproductive barriers between cultivated rice and alien species and many genes related to this phenomenon were identified. As shown in the examples of analysis of shattering and heading date, CSSLs also provide materials suitable for detailed genetic analysis. However, evaluation of the constructed CSSLs for practical characters has just started and this is more challenging. In spite of the anticipated difficulty at the practical level, the capability of CSSLs is promising.

References

Brar DS, Khush GS. 1997. Alien introgression in rice. Plant Mol. Biol. 35:35-47.

Buckler ES, Thornsbeny JM. 2002. Plant molecular diversity and applications to genomics. Curr. Opin. Plant Biol. 5:107-111.

Doi K, Yoshimura A. 1998. RFLP mapping of a gene for heading date in African rice. Rice Genet. Newsl. 15:148-149.

Doi K, Iwata N, Yoshimura A. 1997. The construction of chromosome substitution lines of African rice (*Oryza glaberrima* Steud.) in the background of Japonica rice (*O. sativa* L.). Rice Genet. Newsl. 14:39-41.

Doi K, Taguchi K, Yoshimura A. 1998a. A new locus affecting high F_1 pollen sterility found in backcross progenies of Japonica rice and African rice. Rice Genet. Newsl. 15:146-148.

Doi K, Yoshimura A, Iwata N. 1998b. RFLP mapping and QTL analysis of heading date and pollen sterility using backcross populations between *Oryza sativa* L. and *O. glaberrima* Steud. Breed. Sci. 48:395-399.

Doi K, Taguchi K, Yoshimura A. 1999. RFLP mapping of *S20* and *S21,* loci for F_1 pollen sterility found in a cross between *Oryza sativa* and *O. glaberrima.* Rice Genet. Newsl. 16:65-68.

Eiguchi M, Sano Y. 1990. A gene complex responsible for seed shattering and panicle spreading found in common wild rices. Rice Genet. Newsl. 7:105-107.

Eshed Y, Zamir D. 1995. An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield-associated QTL. Genetics 141:1147-1162.

Frary A, Nesbitt TC, Frary A, Grandillo S, van der Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert KA, Tanksley SD. 2000. *fw* 2.2: a quantitative trait locus key to the evolution of tomato fruit size. Science 289:85-88.

Fridman E, Pleban T, Zamir D. 2000. A recombination hotspot delimits a wild-species quantitative trait locus for tomato sugar content to 484 bp within an invertase gene. Proc. Natl. Acad. Sci. USA 97:4718-4723.

Ghesquiére A, SCquier J, Second G, Lorieux M. 1997. First steps towards a rational use of African rice, *Oryza glaberrima,* in rice breeding through a ‘contig line’ concept. Euphytica 96:31-39.

Hwang I, Chen HC, Sheen J. 2002. Two-component signal transduction pathways in *Arabidopsis.* Plant Physiol. 129:500-515.

Ikeda K, Sobrizal, Sanchez PL, Yasui H, Yoshimura A. 1999. Hybrid weakness restoration gene (Rhw) for *Oryza glumaepatula* cytoplasm. Rice Genet. Newsl. 16:62-64.

Kurakazu T, Sobrizal, Ikeda K, Sanchez PL, Doi K, Angeles ER, Khush GS, Yoshimura A. 2001a. *Oryza meridionalis* chromosomal segment introgression lines in cultivated rice, *O. sativa* L. Rice Genet. Newsl. 18:81-82.

Kurakazu T, Sobrizal, Yoshimura A. 2001b. RFLP mapping of the genes for awn on chromosomes 4 and 5 in rice using the *Oryza meridionalis* introgression lines. Rice Genet. Newsl. 18:28-30.

Nagai YS, Doi K, Yoshimura A. 2002a. A seed shattering gene, *Sh3,* and its inhibitor gene found in an African cultivated rice, *Oryza glaberrima* Steud. Rice Genet. Newsl. 19. (In press.)

Nagai YS, Sobrizal, Sanchez PL, Kurakazu T, Doi K, Yoshimura A. 2002b. *Sh3,* a gene for seed shattering, commonly found in wild rices. Rice Genet. Newsl. 19. (In press.)

Nesbitt TC, Tanksley SD. 2002. Comparative sequencing in the genus *Lycopersicon:* implications for the evolution of fruit size in the domestication of cultivated tomatoes. Genetics 162:365-379.

Oka HI. 1988. Origin of cultivated rice. Tokyo (Japan): Japanese Science Society Press. 254 p.

Sanchez PL, Sobrizal, Ikeda K, Yasui H, Yoshimura A. 2000. Linkage analysis of late heading genes using *Oryza glumaepatula* introgression lines. Rice Genet. Newsl. 17:46-48.

Sanchez PL, Kurakazu T, Hirata C, Sobrizal, Yoshimura A. 2002. Identification and mapping of seed shattering genes using introgression lines from wild rice species. Rice Genet. Newsl. 19. (In press.)

Sano Y. 1986. Sterility barriers between *Oryza sativa* and *O. glaberrima.* In: Rice genetics. Proceedings of the International Rice Genetic Symposium, 27-31 May 1985, Los Baños, Philippines. Manila (Philippines): International Rice Research Institute. p 109-118.

Sobrizal, Ikeda K, Sanchez PL, Doi K, Angeles ER, Khush GS, Yoshimura A. 1999a. Development of *Oryza glumaepatula* introgression lines in rice, *Oryza sativa* L. Rice Genet. Newsl. 16:107-108.

Sobrizal, Ikeda K, Sanchez PL, Yoshimura A. 1999b. RFLP mapping of seed shattering gene on chromosome 4 in rice. Rice Genet. Newsl. 16:74-75.

Sobrizal, Matsuzaki Y, Sanchez PL, Ikeda K, Yoshimura A. 2000a. Identification of a gene for male gamete abortion in backcross progeny of *Oryza sativa* and *Oryza glumaepatula.* Rice Genet. Newsl. 17:59-61.

Sobrizal, Matsuzaki Y, Sanchez PL, Ikeda K, Yoshimura A. 2000b. Mapping of F_1 pollen semi-sterility gene found in backcross progeny of *Oryza sativa* L. and *Oryza glumaepatula* Steud. Rice Genet. Newsl. 17:61-63.

Sobrizal, Matsuzaki Y, Yoshimura A. 2001a. Mapping of a gene for pollen semi-sterility on chromosome 8 of rice. Rice Genet. Newsl. 1859-61.

Sobrizal, Tanaka C, Yasui H, Yoshimura A. 2001b. Mapping of a gene for F_2 weakness on chromosome 4 of rice. Rice Genet. Newsl. 18:61-63.

Taguchi K, Doi K, Yoshimura A. 1999. RFLP mapping of *S19,* a gene for F_1 pollen sterility found in backcross progeny of *Oryza sativa* and *O. glaberrima.* Rice Genet. Newsl. 16:70-71.

Tanksley SD, McCouch SR. 1997. Seed banks and genetic maps: unlocking genetic potential from the wild. Science 277:1063-1066.

Xiao J, Li J, Grandillo S, Ahn SN, Yuan L, Tanksley SD, McCouch SR. 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon.* Genetics 150:899-909.

Yano M, Kojima S, Takahashi Y, Lin HX, Sasaki T. 2001. Genetic control of flowering time in rice, a short-day plant. Plant Physiol. 127:1425-1429.

Zamir D. 2001. Improving plant breeding with exotic genetic libraries. Nature Rev. Genet. 2:983-989.

Notes

Authors' addresses: K. Doi, Sobrizal, Plant Breeding Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan. Current address: Plant Breeding Laboratory, National Atomic Energy Agency, PO Box 7002 JKSKL, Jakarta 12070, Indonesia; K. Ikeda, P.L. Sanchez, T. Kurakazu, Y. Nagai, and A. Yoshimura, current address: Toyota Biotechnology & Afforestation Laboratory, 1099 Marune, Kurozasa, Miyoshi, Aichi 470-0201, Japan.

Acknowledgments: The authors thank Drs. G.S. Khush and E.R. Angeles for providing convenience in planting. We are also grateful to Drs. M. Yano and T. Izawa and the members of their group for the cloning and characterization of *Ehd1*.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Biology of developmental and physiological traits

A genetic program for shoot development in rice

J.-I. Itoh, N. Satoh, and Y. Nagato

To elucidate how shoot architecture is developmentally established in rice, we have analyzed several mutants associated with the initiation and maintenance of the shoot apical meristem (SAM). Recessive alleles for three *SHOOTLESS* loci *(SHL1, SHL2,* and *SHL4)* fail to initiate the SAM in the embryo, but form a normal radicle. Expression analysis of a rice homeobox gene, *OSH1,* a marker of domain for SAM initiation in the globular embryo, reveals that the *shl1, shl2,* and *shl4* embryos have a smaller domain of *OSH1* expression than the wild-type embryo. Thus, the *SHL* genes are involved in the acquisition of indeterminate cells for the SAM. The *shoot organization (sho)* mutants produce thread-like leaves with an aberrant phyllotaxy and short plastochron in the early vegetative phase. The SAM of *sho* seedlings is geometrically abnormal. Reduced expression of *OSH1* in the SAM suggests that an indeterminate cell population in *sho* SAMs is reduced. Accordingly, *SHL* genes are required for SAM initiation and *SHO* genes are essential for proper SAM organization.

Shoot architecture is elaborated by the activities of the shoot apical meristem (SAM) because the SAM is not only a source of aboveground organs; it also determines a spatial and temporal arrangement of lateral organs. Thus, if the activities of the SAM are modified, drastic changes in shoot architecture could occur. To understand how the shoot architecture is established in rice, we have characterized several mutants showing abnormal development of the embryo and shoot (Hong et al 1995). In this paper, we focus on two classes of mutants that are defective in the initiation and/or maintenance of the SAM. In *Arabidopsis,* several mutants associated with SAM initiation and/or maintenance have been reported, such as *shoot meristemless (stm), wuschel, pinhead/zwille,* and *cup-shaped cotyledon* (Aida et al 1999, Endrizzi et al 1996, Laux et al 1996, Lynn et al 1999, Mayer et al 1998, Moussian et al 1998). Genetic and molecular analyses of these genes have given us a better understanding of the establishment and maintenance of the SAM. One of these mutants, *stm* encoding the KNOTTED class of homeodomain protein, fails to produce the SAM during embryogenesis (Long et al 1996). Analyses of weak *stm* alleles indicate that *stm* is required for both the initiation and maintenance of the SAM (Endrizzi et al 1996). In monocots, however, a genetic program for shoot development, especially SAM formation and maintenance, is not well understood.

In this paper, we present recent advances in genetic analyses for shoot development in rice, describing two classes of mutants that are defective in shoot initiation and maintenance.

shootless mutants

We have identified several *shootless* mutants characterized by the lack of shoot (coleoptile, three embryonic leaves, and SAM) in the mature embryo (Hong et al 1995, Satoh et al 1999) (Fig. 1). The *shootless* mutants were derived from four independent loci *(SHL1–SHL4).* In all the *sh1* embryos, except for *shl3,* the radicle and scutellum were formed normally. The scutellum of these mutants is considered to be functionally normal because *RAmylA,* a major α-amylase gene, was expressed normally in the epithelium of the scutellum. To elucidate the developmental events taking place in the early *shl* embryos, we observed the expression pattern of the rice homeobox gene, *OSH1,* an ortholog of *knotted1* in maize (Matsuoka et al 1993). The *OSH1* expression in the wild-type globular embryo is restricted to a region where the SAM is formed later (Sato et al 1996). Thus, *OSH1* is a useful molecular marker of the SAM-related domain. Some *in situ* hybridization experiments showed that the domain expressing *OSH1* was greatly reduced in the early embryo of *shl1, shl2,* and *shl4* (Fig. 2), indicating that *shl1, shl2,* and *shl4* embryos do not have enough domain to initiate the SAM. Accordingly, *SHL1, SHL2,* and *SHLA* genes are required for the recruitment of the SAM initiation domain. On the other hand, the expression domain of *OSH1* in *shl3* was relatively normal. These results indicate that *SHLI, SHL2,* and *SHL4* genes act upstream of *OSH1* and that the *SHL3* gene acts downstream or independently of *OSH1.* We carried out regeneration experiments from the scutellum-derived calli to examine whether *SHL* genes were also associated with adventitious SAM formation. However, no adventitious shoots were regenerated in any *shl* calli. This indicates that *SHL* genes are necessary for both embryonic and adventitious SAM formation.

Recently, we identified weak alleles of the *SHL2* gene. These weak alleles could provide us with further information on *SHL2* functions. The weak *shl2* mutants formed a SAM at 5–6 days after pollination and produced one or two leaf primordia. The SAM was not detected, however, in the mature embryo. This indicates that the SAM was consumed in the course of embryo development. The expression domain of *OSH1* just before SAM initiation in the weak alleles was larger than that in the strong alleles, but was smaller than that in the wild type. Thus, SAM formation depends on the number of alleles and is correlated with the size of the *OSH1* expression domain. Accordingly, the *SHL2* gene is indispensable for both SAM formation and maintenance, and one of the functions is to develop enough indeterminate cells for SAM initiation and maintenance.

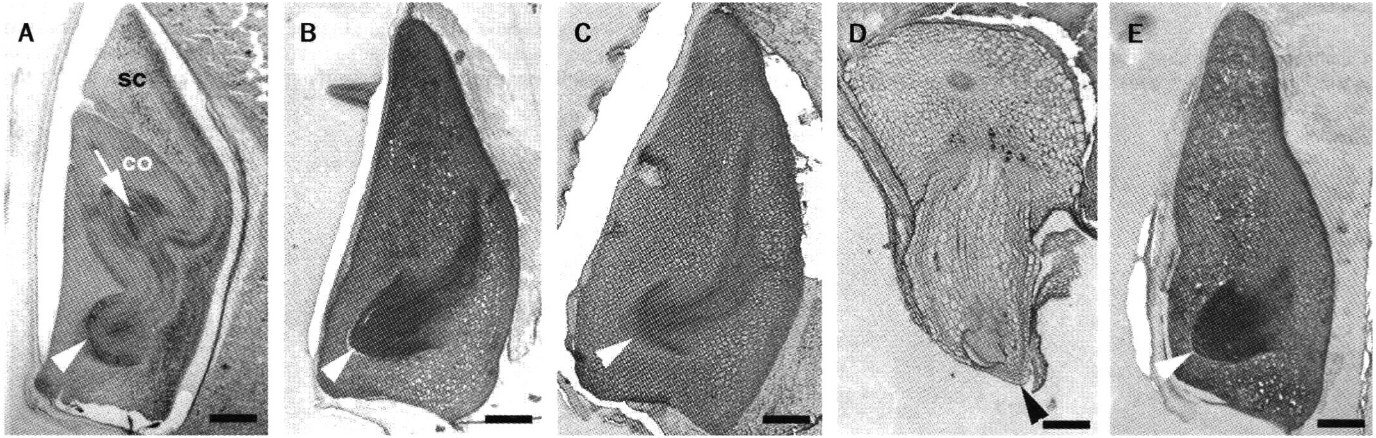


Fig. 1. Phenotype of mature embryos in *shootless* mutants. (A) Wild type with shoot apical meristem (arrow), radicle (arrowhead), coleoptile (co), and scutellum (sc). (6) *shl1*-1, (C) *shl2*-1, (D) *shl3,* and (E) *shl4.* In each mutant embryo, the shoot apical meristem and coleoptile are lost, but the radicle (arrowhead) is normally differentiated. Bars = 0.2 mm.

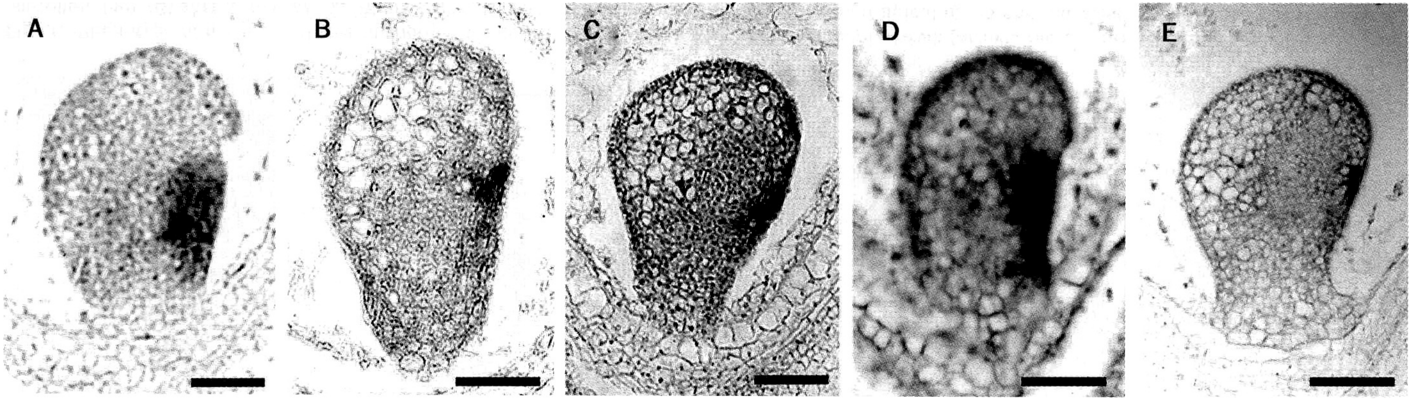


Fig. 2. Expression of *OSH1* in *shootless* embryos. (A) Wild-type embryo at 4 days after pollination. (B), (C), (D), and (E), *shl1-1, shl2-1, shl3,* and *shl4* embryos, respectively, at 5 d after pollination. *OSH1* expression in *shl1, shl2,* and *shl4* embryos is restricted to a narrow region. In *shl3* embryos, the expression pattern is similar to that in the wild-type embryo. Bars = 0.56 mm.

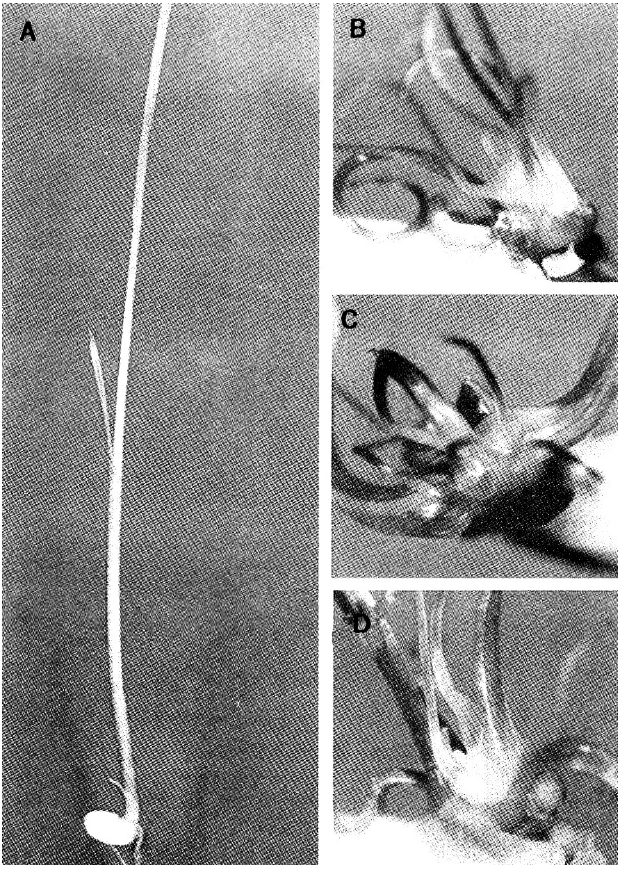


Fig. 3. Seedlings of wild-type and *sho* mutants at 1 wk after germination. (A) Wild type. (B) *sho1-1.* (c) *sho2.* (D) *sho3.* In *sho* seedlings, many thread-like leaves are produced with an aberrant phyllotaxy.

shoot organization mutants

We identified several *shoot organization* (*sho*) mutants derived from three loci, *SHO1, SHO2,* and *SHO3,* exhibiting extremely abnormal shoots in the early vegetative phase (Itoh et al 2000, Tamura et al 1992). The mutant seedlings showed an aberrant phyllotaxy, short plastochron, and thread-like leaves (Fig. 3). It is easy to suppose that these abnormalities are caused by defects in the SAM organization. To elucidate how aberrant leaf production in *sho* mutants is related to the SAM, we observed the SAM structure. In the sho mutants, SAMs were relatively flat-shaped, although their shape and size were highly variable among plants of the same genotype. In addition, rapid leaf production in irregular phyllotaxy was correlated with the frequent and

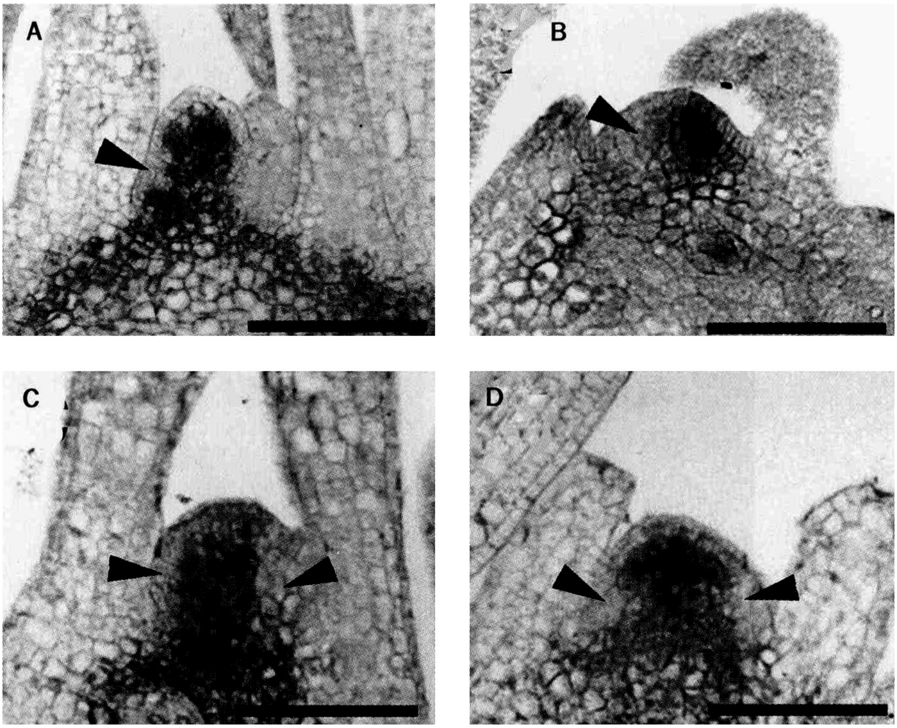


Fig. 4. ***OSH1*** **expression in wild-type and** ***sho*** **meristems at 1 wk after germination. (A) Wild type. The signal is detected in the SAM except for the L1 layer and leaf founder cells (arrowhead). (B)** ***sho1-1.*** **(C)** ***sho2.*** **(D)** ***sho3.*** **The domain for** ***OSH1*** **expression in** ***sho*** **SAMs is reduced. Bars = 0.1 mm.**

disorganized cell divisions in the SAM. Next, we examined *OSH1* expression in *sho* SAMs. *OSH1* in the wild type is expressed in the SAM but is down-regulated in the L1 layer and leaf founder cells (Matsuoka et al 1993, Sato et al 1996). In *sho* mutants, *OSH1* was expressed in a smaller domain than in the wild type (Fig. 4). This abnormal *OSH1* expression indicates that *sho* mutants have fewer indeterminate cells than the wild type and that many cells are competent for leaf founder cells, resulting in rapid and random leaf initiation. Thus, the *SHO* genes have an important role in maintaining the proper organization of the SAM, which is essential for the normal initiation of leaf primordia.

Embryo development was also disrupted in *sho* mutants. The *sho* embryos fail to form a coleoptile, suggesting that coleoptile initiation depends on the presence of the normal SAM.

Conclusions

Our main interest is to understand how shoot architecture in rice is genetically established and what regulatory processes operate in shoot development. To do this, we have followed a genetic approach using developmental mutants involved in SAM initiation and maintenance. Our analyses show that both *shl* and *sho* genes are important for shoot development in rice. *SHL* genes are required for SAM initiation and maintenance and *SHO* genes are indispensable for proper SAM organization. Although a major difference exists between *shl* and *sho* in that the SAM is deleted only in *shl* mutants, they share several phenotypes. Both mutants are defective in coleoptile formation and show a reduced *OSH1* expression domain (indeterminate cell population) in the SAM. In addition, weak *shl2* alleles produce seedlings similar to those of *sho*. Therefore, *SHL* and *SHO* genes are likely to be associated with the same developmental process. Our analyses of *SHL* and *SHO* mutants lead us to important insights into shoot formation in rice:

1. At least four genes are hierarchically involved in SAM formation in rice.
2. Some *SHL* genes are required for both initiation and maintenance of SAM.
3. Shoot architecture (plastochron and phyllotaxy) is tightly linked with SAM organization and activities.
4. *SHO* genes and some *SHL* genes are important for regulating the size of the indeterminate cell population in the SAM.

References

Aida M, Ishida T, Tasaka M. 1999. Shoot apical meristem and cotyledon formation during *Arabidopsis* embryogenesis: interaction among the *CUP-SHAPED COTYLEDON* and *SHOOT MERISTEMLESS* genes. Development 126:1563-1570.

Endrizzi K, Moussian B, Heacker A, Levin JZ, Laux T. 1996. The *SHOOT MERISTEMLESS* gene is required for maintenance of undifferentiated cells in *Arabidopsis* shoot and floral meristems and acts at a different regulatory level than the meristem genes *WUSCHEL* and *ZWILLE.* Plant J. 10:967-979.

Hong SK, Aoki T, Kitano H, Satoh H, Nagato Y. 1995. Phenotypic diversity of 188 rice embryo mutants. Dev. Genet. 16:298-310.

Itoh JI, Kitano H, Matsuoka M, Nagato Y. 2000. *SHOOT ORGANIZATION* genes regulate shoot apical meristem organization and pattern of leaf initiation in rice. Plant Cell 12:2161 - 2174.

Laux T, Mayer KFX, Berger J, Jurgens G. 1996. The *WUSCHEL* gene is required for shoot and floral meristem identity in *Arabidopsis.* Development 12297-96.

Long JA, Moan EI, Medford JI, Barton MK. 1996. A member of the KNOTTED class of homeodomain proteins encoded by the *STM* gene of *Arabidopsis.* Nature 379:66-69.

Lynn K, Fernandez A, Aida M, Sedbrook J, Tasaka M, Masson P, Barton MK. 1999. The *PINHEAD/ZWILLE* gene acts pleiotropically in *Arabidopsis* development and has overlapping functions with the *ARGONAUTEI* gene. Development 126:469-481.

Matsuoka M, Ichikawa H, Saito A, Tada Y, Fujimura T, Kano-Murakami Y. 1993. Expression of a rice homeobox gene causes altered morphology of transgenic plants. Plant Cell 5: 1039-1048.

Mayer KFX, Schoof H, Haecker A, Lenhard M, Juergens G. Laux T. 1998. Role of *WUSCHEL* in regulating stem cell fate in the *Arabidopsis* shoot meristem. Cell 95:805-815.

Moussian B, Schoof H, Haecker A, Juergens G, Laux T. 1998. Role of the *ZWILLE* gene in the regulation of central shoot meristem cell fate during *Arabidopsis* embryogenesis. EMBO J. 17:1799-1809.

Sato Y, Hong S, Tagiri A, Kitano H, Yamamoto N, Nagato Y, Matsuoka M. 1996. A rice homeobox gene, *OSH1,* is expressed before organ differentiation in a specific region during early embryogenesis. Proc. Natl. Acad. Sci. USA 93:8117-8122.

Satoh N, Hong SK, Nishimura A, Matsuoka M, Kitano H. Nagato Y. 1999. Initiation of shoot apical meristem in rice: characterization of four *SHOOTLESS* genes. Development 126:3629-3636.

Tamura Y, Kitano H, Satoh H, Nagato Y. 1992. A gene profoundly affecting shoot organization in the early phase of rice development. Plant Sci. 82:91-99.

Notes

Authors' address: Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo 113-8657, Japan. E-mail: ajunito@mail.ecc.u-tokyo.ac.jp.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Genetic analysis of root elongation in higher plants

M. Ichii and S.-G. Yao

Root length has been proven to be one of the most important parameters closely related to the ability of a plant in acquiring nutrients and water, lodging and drought tolerance, and productivity. Thus, to uncover the mechanisms controlling root elongation will be of outstanding agronomic importance, especially in cereal plants. Root elongation is determined by two coordinated processes of cell division and cell elongation, and extensive mutational analysis has identified many genes relating to these processes. In this paper, three aspects are analyzed in describing the recent progress in the understanding of the mechanisms underlying root elongation: (1) genes involved in embryonic and postembryonic root cell division, showing how the mutations that occurred at each root developmental stage inhibit root formation or root elongation by affecting root cell division; (2) genes involved in root cell expansion, showing how the mutations affect the extent and direction of cell expansion by inducing abnormal cell wall formation: and (3) hormonal regulation of root elongation. Since phytohormones are central regulators of almost all aspects of cell behavior, including cell division and cell expansion, we describe briefly how the genes involved in hormone biosynthesis or hormone response affect root elongation by altering root cell division and/or cell expansion.

Root systems of plants function in various ways, especially for nutrient and water uptake (Osaki et al 1997, Jeschke and Hartung 2000). Because the supplies of nutrients and water in the soil are always limited, local, and variable, the spatial distribution of the root system, that is, the root architecture, in large measure determines the ability of a plant to exploit these resources (Lynch 1995). The root architecture is defined by several parameters such as length, number, and dimension, and root length is considered to be related to various important characters such as nutrient uptake (Teo et al 1995), lodging tolerance (Terashima et al 1994), drought tolerance (Nemoto et al 1998, Azhiri-Sigari et al 2000), and yield (Morita et al 1988, Kang et al 1994).

Thus, to uncover the mechanisms controlling root elongation will be of outstanding agronomic importance, especially in improving the sustainability and productivity of cereal plants.

Root elongation is governed by two successive processes of cell division and cell expansion, and extensive mutational analysis has identified many genes involved in these two processes. In this review, we take the dicotyledonous plant *Arabidopsis* and the monocotyledonous plant rice as examples to describe how the mutations that occurred at the embryonic and postembryonic root developmental stage affect root elongation by altering cell division and/or cell expansion.

Genes involved in root cell division

Embryonic root cell division regulation

The primary root development of higher plants consists of embryonic and postembryonic stages. In *Arabidopsis,* embryonic development starts from fertilization: the zygote divides asymmetrically, giving two daughter cells: a smaller apical cell and a larger basal cell. The smaller cell forms most of the embryo proper, whereas the larger one contributes to the root of the embryo but principally gives rise to the suspensor (Fig. 1; Laux and Jurgens 1997). The primary root meristem in *Arabidopsis* originates from the hypophyseal cell and an adjoining cell tier by a stereotyped set of cell divisions, and becomes active in the heart-shaped embryo. Since the embryonic pattern is reiterated through the meristem during postembryonic development, defects in the construction of primary root primordia often cause altered embryonic root formation and postembryonic root elongation.

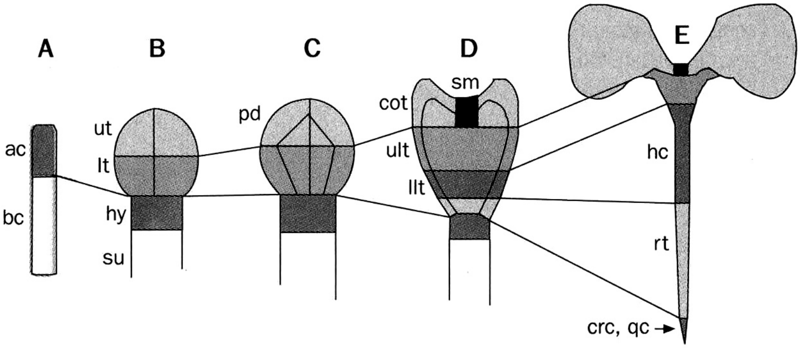


Fig. 1. Pattern formation of *Arabidopsis* plant body (after Laux and Jurgens 1997). (A) Two-cell stage. ac = apical cell, bc = basal cell. (B) Octant stage. ut = upper tler, lt = lower tier, hy = hypophysis, su = suspensor. (C) Dermatogen stage. pd = protoderm. (D) Heart stage. cot = cotyledon, ult = upper-lower tier, llt = lower-lower tler, sm = shoot meristem. (E) Seedling stage. hc = hypocotyl, rt = root, crc = central root cap, qc = quiescent center.

Several genes that are required for correct root morphogenesis in *Arabidopsis* are expressed during early embryogenesis. In the mutant *gnom,* asymmetric division of the zygote is altered by producing two nearly equal-sized cells, and the uppermost derivative of the basal cell fails to become the hypophysis. As a result, seedlings derived from this mutation all lack primary roots (Mayer et al 1993). *EMB30,* an allele of *GNOM,* is also involved in apical-basal pattern formation in the *Arabidopsis* embryos (Shevell et al 1994). Mutations in this locus produce mutants with no roots and true hypocotyls. Molecular study indicates that the gene encodes a protein that has similarity to the yeast Sec7 protein, and affects cell division, cell expansion, and cell adhesion throughout plant development. In contrast, the *HOBBIT (HBT)* gene is required for root meristem formation (Willemsen et al 1998). The *hbt* mutant phenotype shows abnormal development of the basal region from the quadrant stage onward, which normally gives rise to the hypophysis. Strong *hbt* mutants give rise to seedlings that lack a mitotically active root meristem and have extremely short primary roots. *MONOPTEROS* (MP) is a gene required specifically for the initiation of the hypocotyl/root axis (Berleth and Jurgens 1993). Mutation in this gene results in abnormal cell division in the hypophysis, producing seedlings that lack a primary root and a hypocotyl, although postembryonic crown root formation is unaffected. Molecular analysis indicates that the *MP* gene encodes an auxin-response transcription factor (Hardtke and Berleth 1998). Mutation in the *HYDRA1* gene, however, affects the establishment of the protoderm (Topping et al 1997). The *hydra1* embryo appears to develop normally to the octant stage but lacks bilateral symmetry, resulting in seedlings characterized by a variable number of cotyledons, short and wide hypocotyl, and much reduced root system. Moreover, dark-grown *hydra1* seedlings have evident etiolation but no evidence of hypocotyl elongation compared with that under light conditions, suggesting that the *HYDRA1* gene might be required for proper cell elongation.

Arabidopsis roots are particularly consistent in their cellular organization (Fig. 2; Dolan et al 1993). In the mature region of the root, single layers of epidermis, cortex, endodermis, and pericycle surround a small number of vascular cells. Clonal analysis revealed that the meristematic root can be traced back to initial cells originating from a single tier of cells in the heart-stage embryo (Scheres et al 1994), and cell division in the embryonic axis generally determines the radial organization of the seedling root. Thus, alterations in radial organization of the embryonic axis will result in radial pattern defects in seedling roots, which usually result in root growth retardation. For example, mutations in the genes of *WOODEN LEG (WOL), GOLLUM (GLM), PINOCCHIO (PIC), SCARECROW (SCR), SHORTROOT (SHR),* and *FASS (FS)* all result in seedlings characterized by greatly reduced primary root length (Benfey et al 1993, Scheres et al 1995). Histological observation reveals that all these mutants have altered radial organization of the root, which is caused by altered cell division in the embryonic axis. Roots of *fs* seedlings show alteration in almost all cell types except the endodermis. In contrast, roots in *glm* seedlings lack vascular tissue and the pericycle layer, while roots of *wol* seedlings contain vascular tissue with fewer cells compared with the wild type. In contrast, roots contained in seedlings of *shr, scr,* and *pic* mutants show a similar defect in cortex/endodermis

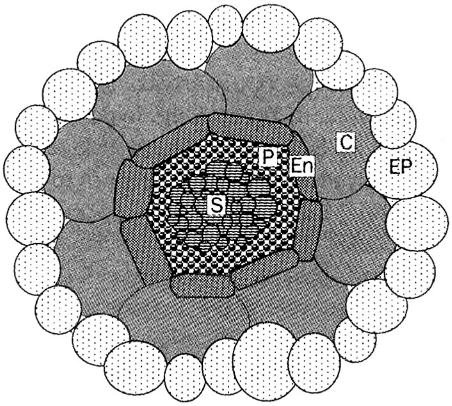


Fig. 2. Transversal section of *Arabidopsis* root tip (after Dolan et al 1993). EP = epidermis, C = cortex, En = endodermis, P = perlcycle, S = stele.

formation. Moreover, tissue-specific markers reveal that *SCR* is expressed in the cortex/endodermal initial cells and in the endodermal cell lineage, suggesting that SCR, a putative transcription factor, plays a key role in the regulation of the asymmetric cell division of the cortex/endodermis initial (Laurenzio et al 1996). In contrast, two endodermis-specific markers are all absent from the *shr* mutant layer (Benfey et al 1993), suggesting that, apart from controlling asymmetric cell division that is responsible for the formation of cortex/endodermis tissues, the *SHR* gene may also be involved in the specification of endodermis cell identity (Helariutta et al 2000). Molecular cloning indicates that the *SHR* gene encodes a putative transcription factor with homology to SCR. In addition, detailed analysis of the double mutant *shrscr* using RNA blot analysis indicates that *SHR* functions upstream of SCR. Furthermore, RNA *in situ* hybridization reveals that *SHR* mRNA is found exclusively in the stele cells, but *SHR* protein localizes not only in the stele but also in all cells of immediately adjacent layers, suggesting the action of *SHR* protein as a signal from the stele and the non-cell-autonomous function of *SHR* required for root radial patterning (Nakajima et al 2001).

Postembryonic root cell division regulation

Postembryonic root development starts from the mature embryo in the desiccated seed. After imbibition and germination, cell division is activated in the root apical cells, thus producing the root meristem. These apical meristem cells can maintain themselves in the cell cycle to produce new cells that enter the elongation zone behind the apical meristem. The *Arabidopsis* root meristemless mutants *rml1* and *rml2,* for example, produce normal embryonic roots. However, cell division in the root apical cells is inhibited after germination, resulting in seedlings characterized by greatly reduced root length and lack of root meristem (Cheng et al 1995). Detailed analysis of cell division activity in the embryo, shoot, and callus cells indicates that the *RML* gene functions specifically in activating the cell division cycle in the root apical cells. Molecular cloning of the *RML* gene reveals that it encodes the first enzyme of glutathione (GSH) biosynthesis, which is required for the G_1 to S phase transition (Vernoux et al 2000). These results suggest that the existence of a GSH-dependent pathway is essential for the initiation and maintenance of cell division during postembryonic root development.

Several mutants with reduced root length were also identified in rice. The *srt5* mutant, for example, is characterized by a compact system (Yao et al 2002). Root elongation of the mutant at the seedling stage is greatly inhibited immediately after germination, with a root length of about 5% of that of the wild type. Cyto-histological observation shows that the radicle of the mutant develops normally; however, the mature cortical cell length of the mutant is significantly shorter than that of the wild type. Moreover, cell division activity estimation indicates that cellochron for the mutant is about 6 times longer than that for the wild type, suggesting that the *srt5* gene inhibits postembryonic root elongation by inhibiting both cell expansion and cell division. Among other short-root mutants identified in rice so far, *rt* (Kitano and Futsuhara 1989), *srt1* (Ichii and Ishikawa 1997), *srt4* (Ichii and Liang 1997), and *rr12* (Inukai et al 2001) also inhibit cell division during postembryonic root elongation, whereas *crl2* was reported to promote the maintenance of the root apical meristem (Inukai et al 2001). These results suggest that at least six genes are involved in the regulation of root cell division, and the interactions between these genes determine the extent of root elongation in rice.

Genes involved in root cell expansion

The final shape of a plant organ is a consequence of cell division and cell expansion. In root meristematic tissue, cell division is followed by cell expansion, which determines the shape of individual cells and thus root length and root shape. Conversely, cell expansion is determined by two principal parameters: extent and direction.

1. Cell expansion extent regulation

The growth rate of plant cells is controlled by the extensibility of the cell wall and the turgor pressure inside the cell. Two types of cell walls can usually be distinguished: a thinner primary wall and a thicker secondary wall. The primary wall is synthesized during cell expansion and is capable of yielding to turgor pressure (Cosgrove 1993); the secondary wall deposits in the fully expanded cell between the primary wall and the plasma membrane, and provides mechanical strength and rigidity to support aerial structures and hydrophobicity for transport functions. Root growth mutants resulting from defective cell wall formation have been identified in *Arabidopsis*. For example, the *ectopic lignification 1 (eli1)* mutant shows a primary root about 3 times shorter with a reduced elongation zone, shortened cell length, and disorganized xylem strands compared with its wild type (Cano-Delgado et al 2000). Phloroglucinol staining reveals that the primary root of *eli1* has an abnormal lignification pattern, at which the lignification occurs not only in the xylem cells but also in other vascular, pericycle, cortical, and endodermal cells. Furthermore, calcofluor staining indicates that *eli1* has an altered distribution of cellulosic materials in the secondary cell walls. Concomitant observations of other root expansion mutants such as *lit* (Benfey et al 1993, Hauser et al 1995), *wol* (Scheres et al 1995), or *kor1* (Nicol et al 1998) further demonstrate the existence of a linkage between cell expansion and the initiation of secondary cell wall formation and subsequent lignification. *EMB30* has been identified as a gene involved in embryogenesis and pattern formation; mutation in this locus gives seedlings that all lack a root (Shevell et al 1994). Callus observation reveals that cells in *emb30* tissue are disorganized, abnormally shaped, and often do not adhere to each other. Chemical staining of seedling tissues indicates that in wild-type tissues, cells secrete substances only into the *corner* junctions between cells (cell *corners*), and most of the interstitial space between the wild-type cells remains clear. In *emb30* tissues, however, the entire interstitial space, as well as the cell *corners,* often contains secreted material. In addition, pectin, an important component for cell adhesion, is also abnormally localized in the mutant plants (Shevell et al 2000). These results suggest that *EMB30* is essential for normal cell adhesion and polar cell growth during seedling development.

Several genes are also involved in the regulation of cell expansion extent in rice (Kitano and Futsuhara 1989, Inukai et al 2001, Yao et al 200 1,2002), *srt2,* for example, is a mutant with greatly inhibited root elongation rate immediately after germination (Liang and Ichii 1996). Microscopic study indicates that the meristematic region and cell and tissue structure in the mutant are normal, but mature cortical cell length is only about 50% of that in the wild type. Moreover, the radicle of *srt2* is smaller than that of the wild type. Root growth of *srt2* can be greatly promoted when exposed to light, whereas light usually has an inhibitory effect on wild-type root growth. This suggests that the *srt2* gene is expressed as early as the embryonic root development stage, and the effect of the *SRT2* gene might be related to the phytochrome in the regulation of cell expansion in rice.

2. Cell expansion direction regulation

The direction of root cell expansion is controlled by the cellulose microfibrils in the cell wall, and these molecules are arranged transverse to the direction of root growth. The orientation of the cellulose is controlled by cortical microtubules, which are aligned in the same direction as the cellulose microfibrils. Any disruption of the microtubules will cause abnormal cellulose microfibril formation, and thus abnormal cell expansion. For example, mutation at the *PROCUSTE1* (*PRC1*) locus shows greatly reduced lengths of hypocotyl and root with strong radially expanded cells in the epidermis, cortex, and endodermis (Fagard et al 2000). Chemical staining and FTIR microspectroscopic observation of cell walls of *prc1* seedlings show that a major deficiency in crystalline cellulose should be mainly responsible for the mutant phenotype, suggesting the requirement of *PRC1* expression in the cellulose synthesis for normal cell wall formation. Map-based cloning reveals that *PRC1* encodes a novel member of the cellulose synthase catalytic subunit family, CesA6. In contrast, mutation in the gene *BOTERO1 (BOT1)* results in seedlings of short and thick roots and hypocotyls (Bichet et al 2001). Microscopic observation of the root epidermis reveals that fully expanded cells in the mutant are broader and shorter compared with the wild type, which is caused by continued radial expansion after the cessation of mitosis, Investigation by FITC-labeled antibodies shows that all cortical microtubules become organized in transverse arrays after cessation of cell division in the wild type. However, in the *bot1* mutant, these molecules fail to reorient and remain disordered throughout the elongation zone. These results suggest that *BOT1* is required for organizing cortical microtubules into transverse arrays in interphase cells.

srt6 is a mutant derived from *Oryza sativa* cultivar Oochikara seeds mutagenized with NaN_3 (Yao et al 2001). Aside from significantly shortened root length, the root diameter of the mutant is also greatly reduced. Cyto-histological observation shows that both the extent and direction of cell expansion are altered in the mutant. Although root length in *srt6* gradually recovers to that of the wild type with the advance in growth, root diameter remains thin in the mutant all over the growth stages (unpublished data), suggesting that the *SRT6* (the wild-type allele) gene might be required specifically for correct cell expansion along the longitudinal direction.

3. Control of cell expansion in elongating and dividing cells

The expansion rate of plant organs is regulated by cell expansion and cell division. However, it is not always appreciated that cells seldom only divide, producing ever-smaller cells; instead, most dividing cells undergo a slow but steady expansion, which tends to keep the average size of cells in a dividing population constant. Thus, here emerges the question of whether expansion in these two regions requires different mechanisms, and the identification of the gene *STUNTED PLANT 1 (STP 1)* gives us an answer to the question to some extent. The *stp1* mutant is characterized by a reduced root elongation rate immediately after germination (Baskin et al 1992). Microscopic observation indicates that the inhibited root elongation in the mutant is due to a reduced dividing cell number and cell expansion rate (Baskin et al 1995). However, elongation of dividing cells is not affected since the *stp1* callus grows at a rate identical to that in the wild type, suggesting the existence of distinct mechanisms for the control of dividing and nondividing cells.

Hormonal regulation of root elongation

Plant hormones, including auxin, gibberellin (GA), ethylene, cytokinin, and abscisic acid (ABA), together with the steroid hormone brassinosteriod (BR), are central regulators of many aspects of plant growth and development (Kende and Zeevaart 1997, Toyama 2000). They act by binding to specific receptors on the target cell surface (for BR, inside the target cell) and thus initiate a series of intracellular reactions that regulate nearly all aspects of cell behavior, including cell division, cell elongation, cell differentiation, and cellular patterning.

The homozygous *axr6* mutant, for example, arrests growth soon after germination, resulting in seedlings lacking a root and hypocotyl (Hobbie et al 2000). Microscopic observation of embryos at different developmental stages reveals that the hypophyseal cell in the mutant is not produced as a result of abnormal cell division that occurred in the suspensor. However, the *axr6* homozygous callus can develop morphologically normal roots when cultured on NPA (an auxin transport inhibitor), whereas the wild-type tissue remains as a callus under identical conditions. Moreover, the *axr6* heterozygous seedlings show strong resistance to 2,4-D, NAA, and IAA, suggesting that the *AXR6* gene is involved in auxin response and early embryonic development. In contrast, mutation in the *BODENLOS (BDL)* gene results in seedlings lacking hypocotyl, root, and primary root meristem. However, postembryonic root development is unaffected in *bdl* seedlings (Hamann et al 1999). Observation of developing ovules from heterozygous *bdl/BDL* plants reveals that the embryogenic alteration occurs as early as the two-cell stage, at which the apical daughter cell of the zygote divides horizontally instead of vertically. Phenotypic similarity and genetic interaction with other auxin-response mutants suggest that *BDL* is required for auxin-mediated processes of apical-basal patterning in the *Arabidopsis* embryo.

The *AUXIN TRANSPORT INHIBITOR3 (TIR3)* gene is recovered by screening seedlings with increased root elongation on phytotropin, which changes the distribution of endogenous auxin within the organ (Ruegger et al 1997). Mutation in this locus results in seedlings characterized by a reduction in the length of all elongating organs and the near absence of lateral roots. Microscopic observation indicates that the reduced root length in the mutant is due to reduced cell division because epidermal cell length of the mutant is similar to that of the wild type. Biochemical analysis indicates that *tir3* plants have a reduced number of NPA binding sites, suggesting that the *TIR3* gene may encode the NPA binding protein (NBP), or be required for expression, localization, or stabilization of the NBP. However, comparison of root growth in *stp1* (Baskin et al 1995) and the wild type treated with exogenous cytokinin and auxin reveals that auxin lowers root elongation by narrowing the elongation zone and reducing the time spent by a cell in this zone, but does not decrease the maximal strain rate. In addition, auxin increases the length of the meristem. In contrast, cytokinin reduces root elongation by lowering the maximal strain rate, but does not change the time spent by a cell within the elongation zone. Moreover, cytokinin blocks the increase in length and cell number of the meristem and elongation zone (Beemster and Baskin 2000).

Much evidence indicates that hormonal interaction usually controls root growth (Cary et al 1995, Clouse et al 1996, Ephiritikhine et al 1999, Tian and Reed 1999). For example, the recessive mutant *hyl1* has pleiotropic effects on various characters, including a decreased rate of root growth (Lu and Fedoroff 2000). Exogenous application of plant hormones shows that *hyl1* seedlings are hypersensitive to ABA and less sensitive to auxin and cytokinin, suggesting that the pleiotropic developmental phenotype of the mutation is due to the defective ability to perceive or transmit hormonal information. Molecular analysis indicates that the *HYL1* gene is ABA-regulated and encodes a nuclear dsRNA binding protein, which may serve as a regulatory protein functioning at the transcriptional or posttranscriptional level.

Despite the great importance of phytohormones for root elongation, few root-growth mutants that show an altered phytohormone synthesis or response have been reported in rice so far. *srt5* might be the first mutant that shows multiple phytohormone responses (Yao et al 2002). As described above, root elongation of *srt5* at the seedling stage is extremely inhibited, which is caused by inhibited cell division and cell expansion. Exogenous phytohormone application reveals that the inhibited root growth in the mutant can be partially rescued by ABA, and the mutant also shows concomitantly high resistances to 2,4-D, GA_3, and KIN. However, the resistances to the three hormones disappear when these are concomitantly applied with ABA. The finding that root morphology in the mutant recovers to its wild type completely at later growth stages suggests that the gene *srt5* affects early root elongation by altering phytohormone homeostasis, in which ABA might play a central role in the different signaling pathways represented by the other three hormones. In contrast, *srt6* shows a normal response to all the other hormones tested, except for ABA, to which root growth of the mutant is insensitive (unpublished data). The mutant also responds normally to fluridone, an ABA biosynthesis inhibitor, indicating that the short-root phenotype of *srt6* is related to the abnormality in the ABA signal transduction pathway. The two short-root genes, characterized by their pleiotropic morphological effects and phase-specific expression, but different phytohormone, especially ABA, response, are valuable materials in the understanding of the genetic and physiological mechanisms underlying root elongation in rice.

Conclusions

The growth and development of roots in higher plants can be considered to be characterized by the execution of cell division, cell expansion, and cell differentiation along two axes: the apical-basal axis and the radial axis, during the embryonic and postembryonic stages. The extensive mutational analysis in the model plant *Arabidopsis* has resulted in the identification of many genes involved in direct mediation of root elongation, and many of these genes have also been fine-mapped or cloned. The challenge will be to determine their functions.

However, the monocotyledonous root system, such as that of rice, is organized fundamentally different from that in the dicotyledonous plants such as *Arabidopsis*. For example, their embryos do not display regular cell division patterns, and cellular organization in these monocots is much more complicated. Although some developmental mechanisms may be well conserved between monocot and dicot plants (Sato et al 2001), to what extent we can extrapolate from *Arabidopsis* to distantly related monocots should be considered seriously because genes with very high similarity may have different functions in different species. Orthologs of any genes implicated in *Arabidopsis* root elongation need to be studied carefully in the rice root system to judge how generally these genes are used.

The number of root-growth mutants in monocots such as rice is much lower than in *Arabidopsis.* This is unfortunate because isolation of root mutants in different species may reveal critical features, for example, salt tolerance, that may not be apparent in *Arabidopsis* (Maggio et al 2001). Several short-root mutants have been isolated and genetically characterized in rice, but much more work will be necessary before the genes controlling root elongation are fully understood. Some of the essential tools, such as stable transformation techniques, transposon-tagged mutant libraries, and map-based cloning systems with fine-map information and numerous molecular markers, have been developed for molecular studies in rice (Izawa and Shimamoto 1996). These tools, combined with hydroponic cultures that allow direct investigation of the root system, will greatly facilitate the cloning of the genes responsible for the identified phenotype, and thus gene function.

References

Azhiri-Sigari T, Yamauchi A, Kamoshita A, Wade LJ. 2000. Genotypic variation in response of rainfed lowland rice to drought and rewatering. Plant Prod. Sci. 3:180-188.

Baskin TI, Betzner AS, Hoggart R, Cork A, Williamson RE. 1992. Root morphology mutants in *Arabidopsis thaliana.* Aust. J. Plant Physiol. 19:427-437.

Baskin TI, Cork A, Williamson RE, Gorst JR. 1995. *STUNTED PLANT1,* a gene required for expansion in rapidly elongating but not in dividing cells and mediating root growth response to applied cytokinin. Plant Physiol. 107:233-243.

Benfey PN, Linstead PJ, Roberts K, Schiefelbein JW, Hauser M-T, Aeschbacher RA. 1993. Root development in *Arabidopsis:* four mutants with dramatically altered root morphogenesis. Development 119:57-70.

Berleth T, Jurgens G. 1993. The role of the monopteros gene in organising the basal body region of the *Arabidopsis* embryo. Development 118:575-587.

Bichet A, Desnos T, Turner S, Grandjean O, Hafte H. 2001. *BOTERO1* is required for normal orientation of cortical microtubules and anisotropic cell expansion in *Arabidopsis.* Plant J. 25:137-148.

Cano-Delgado AL, Metzlaff K, Bevan MW. 2000. The *eli1* mutation reveals a link between cell expansion and secondary cell wall formation in *Arabidopsis thaliana.* Development 127:3395-3405.

Cary AJ, Liu W, Howell SH. 1995. Cytokinin action is coupled to ethylene in its effects on the inhibition of root and hypocotyl elongation in *Arabidopsis thaliana* seedlings. Plant Physiol. 107:1075-1082.

Cheng J-C, Seeley KA, Sung ZR. 1995. *RML1* and *RML2, Arabidopsis* genes required for cell proliferation at the root tip. Plant Physiol. 107:365-376.

Clouse SD, Langford M, McMorris TC. 1996. A brassinosteroid-insensitive mutant in *Arabidopsis thaliana* exhibits multiple defects in growth and development. Plant Physiol. 111:671-678.

Cosgrove DJ. 1993. How do plant cell walls extend? Plant Physiol. 102:l-6.

Dolan L, Janmaat K, Willemsen V, Linstead P, Poethig S, Roberts K, Scheres B. 1993. Cellular organization of the *Arabidopsis thaliana* root. Development 119:71-84.

Ephritikhine G, Fellner M, Vannini C, Lapous D, Barbier-Brygoo H. 1999. The *sax1* dwarf mutant of *Arabidopsis thaliana* shows altered sensitivity of growth responses to abscisic acid, auxin, gibberellins and ethylene and is partially rescued by exogenous brassinosteroid. Plant J. 18:303-314.

Fagard M, Desnos T, Desprez T, Goubet F, Refregier G, Mouille G, McCann M, Rayon C, Vernhettes S, Hofte H. 2000. *PROCUSTE1* encodes a cellulose synthase required for normal cell elongation specifically in roots and dark-grown hypocotyls of *Arabidopsis.* Plant Cell 12:2409-2424.

Hamann T, Mayer U, Jurgens G. 1999. The auxin-insensitive *bodenlosmutation* affects primary root formation and apical-basal patterning in the *Arabidopsis* embryo. Development 126:1387-1395.

Hardtke CS, Berleth T. 1998. The *Arabidopsis* gene *MONOPTEROS* encodes a transcription factor mediating embryo axis formation and vascular development. EMBO J. 17:1405-1411.

Hauser M-T, Morikami A, Benfey PN. 1995. Conditional root expansion mutants of *Arabidopsis.* Development 121:1237-1252.

Helariutta Y, Fukaki H, Wysocka-Diller J, Nakajima K. Jung J, Sena G, Hauser M-T, Benfey PN. 2000. The *SHORT-ROOT* gene controls radial patterning of the *Arabidopsis* root through radial signaling. Cell 101:555-567.

Hobbie L, McGovern M, Hurwitz LR, Pierro A, Liu NY, Bandyopadhyay A, Estelle M. 2000. The *axr6* mutants of *Arabidopsis thaliana* define a gene involved in auxin response and early development. Development 127:23-32.

Ichii M, Ishikawa M. 1997. Genetic analysis of newly induced short-root mutants in rice (*Oryza sativa* L.). Breed. Sci. 47:121-125.

Ichii M, Liang ZW. 1997. Morphological characteristics and its inheritance of a short-root mutant RMI0 in rice. Breed. Sci. 47(Suppl. 1):310. (In Japanese.)

Inukai Y, Miwa W, Nagato Y, Kitano H, Yamauchi A. 2001. *RRLl, RRL2* and *CRL2* loci regulating root elongation in rice. Breed. Sci. 51:231-239.

Izawa T, Shimamoto K. 1996. Becoming a model plant: the importance of rice to plant science. Trends Plant Sci. I:95-99.

Jeschke WD, Hartung W. 2000. Root-shoot interactions in mineral nutrition. Plant Soil 226:57-69.

Kang SY, Morita S, Yamazaki K. 1994. Root growth and distribution in some Japonica-Indica hybrid and Japonica-type rice cultivars under field conditions. Jpn. J. Crop Sci. 63: 118-124.

Kende H, Zeevaart JAD. 1997. The five “classical” plant hormones. Plant Cell 9:1197-1210.

Kitano H, Futsuhara Y. 1989 Inheritance and gene expression of a root-growth inhibiting mutant in rice *(Oryza sativa* L.). Proceedings of the 6th International Congress. SABRAO. p 349-352.

Laurenzio LD, Wysocka-Diller J, Malamy JE, Pysh L, Helariutta Y, Freshour G, Hahn MG, Feldmann KA, Benfey PN. 1996. The *SCARECROW* gene regulates an asymmetric cell division that is essential for generating the radial organization of the *Arabidopsis* root. Cell 86:423-433.

Laux T, Jurgens G. 1997. Embryogenesis: a new start in life. Plant Cell 9:989-1000.

Liang ZW, Ichii M. 1996. Genetic analysis of a short-root mutant LMI0 induced from rice (*Oryza sativa* L.) cultivar IR8. Breed. Sci. 46:373-377. (In Japanese with English summary.)

Lu C, Fedoroff N. 2000. A mutation in the *Arabidopsis BYLl* gene encoding a dsRNA binding protein affects responses to abscisic acid, auxin, and cytokinin. Plant Cell 12:2351-2365.

Lynch J. 1995. Root architecture and plant productivity. Plant Physiol. 109:7-13.

Maggio A, Hasegawa PM, Bressan RA, Consiglio MF, Joly RJ. 2001. Unravelling the functional relationship between root anatomy and stress tolerance. Aust. J. Plant Physiol. 28:999-1004.

Mayer U, Buttner G, Jurgens G. 1993. Apical-basal pattern formation in the *Arabidopsis* embryo: studies on the role of the *gnom* gene. Development 117:149-162.

Morita S, Suga T, Yamazaki K. 1988. The relationship between root length density and yield in rice plants. J. Crop Sci. 57:438-443.

Nakajima K, Sena G, Nawy T, Benfey PN. 2001. Intercellular movement of the putative transcription factor SHR in root patterning. Nature 413:307-311.

Nemoto H, Suga R, Ishihara M, Okutsu Y. 1998. Deep-rooted rice varieties detected through the observation of root characteristics using the trench method. Breed. Sci. 48:321-324.

Nicol F, His I, Jauneau A, Vernhettes S, Canut H, Hofte H. 1998. A plasma membrane-bound putative endo-1,4-ß3-D-glucanase is required for normal wall assembly and cell elongation in *Arabidopsis*. EMBO J. 17(19):5563-5576.

Osaki M, Shinano T, Matsumoto M, Zheng T, Tadano T. 1997. A root-shoot interaction hypothesis for high productivity of field crops. Soil Sci. Plant Nutr. 43:1079-1084.

Ruegger M, Dewey E, Hobbie L, Brown D, Bernascoli P, Tuener J, Muday G, Estelle M. 1997. Reduced naphthylphthalamic acid binding in the *tir3* mutant of *Arabidopsis* is associated with a reduction in polar auxin transport and diverse morphological defects. Plant Cell 9:745-757.

Sato Y, Nishimura A, Ito M, Ashikari M, Hirano H-K, Matsuoka M. 2001. Auxin response factor family in rice. Genes Genet. Syst. 76:373-380.

Scheres B, Wolkenfelt H, Willemsen V, Terlouw M, Lawson E, Dean C, Weisbeek P. 1994. Embryonic origin of the *Arabidopsis* primary root and root meristem initials. Development 120:2475-2487.

Scheres B, Laurenzio LD, Willemsen V, Hauser M-T, Janmaat K, Weisbeek P, Benfey PN. 1995. Mutations affecting the radial organization of the *Arabidopsis* root display specific defects throughout the embryonic axis. Development 121:53-62.

Shevell DE, Leu W-M, Gillmor CS, Xia G. Feldmann KA, Chua N-H. 1994. *EMB30* is essential for normal cell division, cell expansion, and cell adhesion in *Arabidopsis* and encodes a protein that has similarity to Sec7. Cell 77:1051-1062.

Shevell DE, Kunkel T, Chua N-H. 2000. Cell wall alterations in the *Arabidopsis emb30* mutant. Plant Cell 12:2047-2059.

Teo YH, Beyrouty CA, Norman RJ, Gbur EE. 1995. Nutrient uptake relationship to root characteristics of rice. Plant Soil 171:297-302.

Terashima K, Ogata T, Akita S. 1994. Eco-physiological characteristics related with lodging tolerance of rice in direct sowing cultivation. Jpn. J. Crop Sci. 63:34-41.

Tian Q, Reed JW. 1999. Control of auxin-regulated root development by the *Arabidopsis thaliana SHY3/IAA3* gene. Development 126:711-721.

Topping JF, May VJ, Muskett PR, Lindsey K. 1997. Mutations in the *HYDRAl* gene of *Arabidopsis* perturb cell shape and disrupt embryonic and seedling morphogenesis. Development 124:4415-4424.

Toyama S. 2000. Recent studies on brassinosteroids: with special regard to the growth physiology of crop plants. Jpn. J. Crop Sci. 69:453-463.

Vernoux T, Wilson RC, Seeley KA, Reichheld J-P, Muroy S, Brown S, Maughan SC, Cobbett CS, Montagu MV, Inzé D, May MJ, Sung ZR. 2000. The *ROOT MERISTEMLESSl/ CADMIUM SENSITIVE2* gene defines a glutathione-dependent pathway involved in initiation and maintenance of cell division during postembryonic root development. Plant Cell 12:97-110.

Willemsen V, Wolkenfelt H, Vrieze GD, Weisbeek P, Scheres B. 1998. The *HOBBIT* gene is required for formation of the root meristem in the *Arabidopsis* embryo. Development 125:521-531.

Yao S-G, Taketa S, Ichii M. 2001. Isolation and characterization of four short-root mutants in rice *(Oryza sativa* L.). Proceedings of the 6th Symposium of the International Society of Root Research. p 210-211.

Yao S-G, Taketa S, Ichii M. 2002. A novel short-root gene that affects specifically early root development in rice *(Oryza sativa* L.). Plant Sci. 163:207-215.

Notes

Authors' address: Faculty of Agriculture, Kagawa University, Japan. E-mail: ichii@ag.kagawa-u.ac.jp.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Embryonic cell growth control of the rice high-oil mutant gene, *GIANT EMBRYO*

N. Nagasawa, S.-K. Hong, and H. Sakai

Oil is a key agricultural product that supports our nutrition and health. Oil produced from cereals also provides better feed quality with its high energy source. To understand the high-oil trait at the molecular level, we analyzed rice *giant embryo* mutants that have a high accumulation of seed oil. The oil localization in mutant seeds indicates that the larger embryonic structure is the primary base of the high-oil trait. To examine the possible correlation between the embryo phenotype and cell proliferation, the pattern of histone H4 RNA accumulation was analyzed in the *ge* mutant and wild type. We found that the apical region of the scutellum shows higher cell division activity in *ge* than the wild type at the first-leaf stage. Furthermore, the basal epithelial region of the scutellum in the mutant has cells active in division into the late embryogenesis stages at around 9 days after pollination. By analyzing cell morphology, we conclude that the rice *GIANT EMBRYO* gene regulates not only cell size but also cell division activity during seed development.

Seeds generally produce three forms of storage macromolecules: starch, proteins, and oil. These molecules, which serve as a reservoir of energy and nutrients for germinating plants, are also important components of our nutrition. Of those three forms, oil serves as an excellent source of food oil directly consumed by humans. High-oil crop seeds are also in high demand as feed for their rich energy source. Because of these attributes, the creation of high-oil cultivars has been the focus of a number of breeding programs in the past. For instance, recurrent selections in maize over many generations enabled oil accumulation to reach a level more than three times that of the wild type (Miševiae and Alexander 1989). Despite the interest in the high-oil trait, the genetic base of the trait remains mostly unknown. One reason appears to be associated with the complex genetic interactions underlying the trait. Quantitative trait loci (QTLs) are shown to be responsible for maize high-oil phenotypes (Sughroue and Rocheford 1994).

In rice, one cultivar, Haiminori, was recently registered as a high-oil variety. Also, high-oil mutants have been isolated through mutagenesis using N-nitroso-N-methylurea. The *giant embryo (ge)* mutant was shown to accumulate 40% more oil than the wild type (Satoh and Omura 1981). It has further been reported that the large embryo size of *ge* mutants was caused by enlargement of the scutellum, whereas the total number of embryonic cells remains the same (Hong et al 1996). Here, we analyzed *ge* mutants in detail, focusing on cell proliferation, cell size, cell structures, and oil accumulation. Our findings indicate that tissue-specific cell division and cell size control are the bases of the high-oil trait of ge mutants.

Materials and methods

Morphological analysis

Mature seeds were imbibed in water at 4 °C for 3 days and fixed with 4% paraformaldehyde (Electron Microscopy Sciences, PA) in PBS (pH 7.0) for 1 wk at 4 °C. For plastic sections, fixed samples were cut in half and dehydrated through the acetone series. The samples were then transferred into Technovit:acetone = 1:1 solution and subsequently into Technovit 100%. Specimens were infiltrated for 2-4 weeks at 4 °C and embedded in Technovit 8100 (Heraeus Kulzer GmbH & Co.) as instructed. Samples were sectioned at 2–3-µmthickness and mounted on slides.

For hand sectioning, fixed samples were washed with PBS for 30 min and sectioned with a razor blade. Sections were then stained with 0.5% oil red in 60% triethylphosphate.

Prepared sections were analyzed under the Eclipse E800 microscope (Nikon, Tokyo, Japan). Images were captured by a 3 CCD Camera (Toshiba, Tokyo, Japan) and cell size was measured manually using Image-Pro Plus version 4.0 (Media Cybernetics LP).

In situ hybridization

Developing seed tissues were fixed in 4% paraformaldehyde in PBS for 16 h at 4 °C. They were dehydrated through the buthanol series, embedded in Paraplast, and sectioned at 8-µm thickness by a rotary microtome. A DIG-labeled RNA probe was synthesized from the clone containing a full sequence of histone H4 coding region using the DIG RNA labeling kit (Roche Molecular Biochemicals). Hybridization and immunological detection with alkaline phosphatase were performed according to the method described by Kouchi and Hata (1993).

Measurement of endosperm and embryo volumes

Mutant and wild-type seeds without hulls were imbibed in water at 4 °C overnight. A 5-mL plastic pipette was cut in half and the bottom end was sealed. About 2 mL of water was poured into the pipette. Thirty seeds were submerged in water. The seed volume was calculated by the difference in water volume with and without seeds. To measure the embryo volume, we measured the volume of endosperm without embryo and subtracted it from the seed volume. The average volume per seed was obtained from three measurements of 30 seeds.

Table 1. Volume of endosperm and embryo per seed.

	Seed volume[a]	Endosperm volume[a]	Embryo volume[a]	Embryo ratio[b]
T65	1.86 (21)	1.80 (20)	0.06 (0.7)	3.2
ge-2	1.63 (18)	1.35 (15)	0.28 (3)	17.2
ge-3	1.83 (20)	1.51 (17)	0.32 (4)	17.5
ge-7	1.87 (21)	1.59 (18)	0.28 (3)	15.0

[a] Unit is mL. The numbers in parentheses are the volumes of one seed in μL.
[b] Embryo ratio was calculated by dividing the embryo volume by the seed volume and shown as percent.

Results

Seed and embryo volumes of *ge* mutants

We measured the volume of seed and embryos of *ge-2, ge-3, ge-7,* and the corresponding wild type (Taichung 65). The average volume of wild-type seed was 21 μL. The seed volume of *ge-3* and *ge-7* did not differ significantly from that of the wild type, whereas *ge-2* showed a slightly smaller seed volume than the wild type. The embryo size of *ge* mutants varied from 3 to 4 μL, whereas the wild-type embryo was 0.7 μL (Table 1). The ratio of embryo volume to seed volume was 3%, 17%, 18%, and 15% in the wild type, *ge-2, ge-3,* and *ge-7,* respectively. These data showed that *ge* mutants produced five times more embryonic tissue than the wild type without changing the whole seed size.

Localization of seed oil

In most plants, oil is synthesized as triacylglycerol in the endoplasmic reticulum and stored in the oil body formed within cells (Lacy and Hills 1996, Wanner et al 1981). To investigate whether there is any aberrant localization of seed oil in ge mutants, we visualized lipids by staining with oil red. In wild-type seeds, oil-red staining was observed in most of the embryonic tissues—in the shoot, radicle, and vascular bundles to a lesser extent—and aleurone layer but was not detected in the endosperm. In ge-2, the embryo was stained in a similar manner as the wild type. However, the middle of the scutellum tissues, especially in highly vacuolated cells, showed lesser oil accumulation than the wild type (Fig. 1B).

Morphological analysis

The embryo size difference between the mutants and wild type was previously shown to be related to cell size rather than to cell number (Hong et al 1996). To investigate detailed alterations of cell and tissue structures in the mutant embryo, we performed cytological analyses of *ge-2* and wild-type embryos at the maturation stage.

The most distinctive abnormality of the mutant embryo was the enlargement of cells (Fig. 2). Enlarged cells in *ge-2* showed an area-size twice as large as wild-type cells; especially, the internal tissues of the scutellum and other organs exhibited significant cell enlargement (Table 2). Accordingly, the scutellum size was also

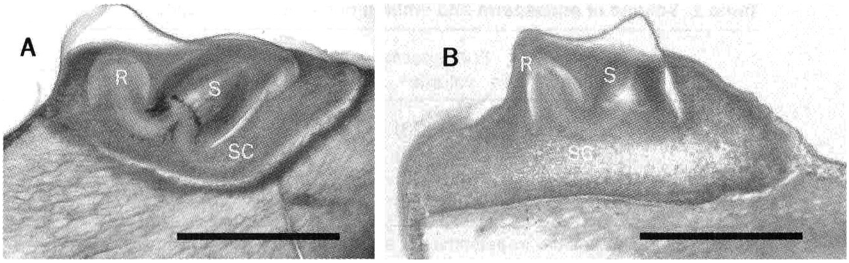


Fig. 1. Oil localization in mature rice seed. (A) A wild-type embryo. Oil stains are detected in the embryo, aleurone layer, and pericarp. (B) A *ge-2* embryo. Oil stains are detected like those in the wild type, except that the central region of the scutellum gave weaker signals. S = shoot, R = radicle, SC = scutellum. Bar = 1 mm.

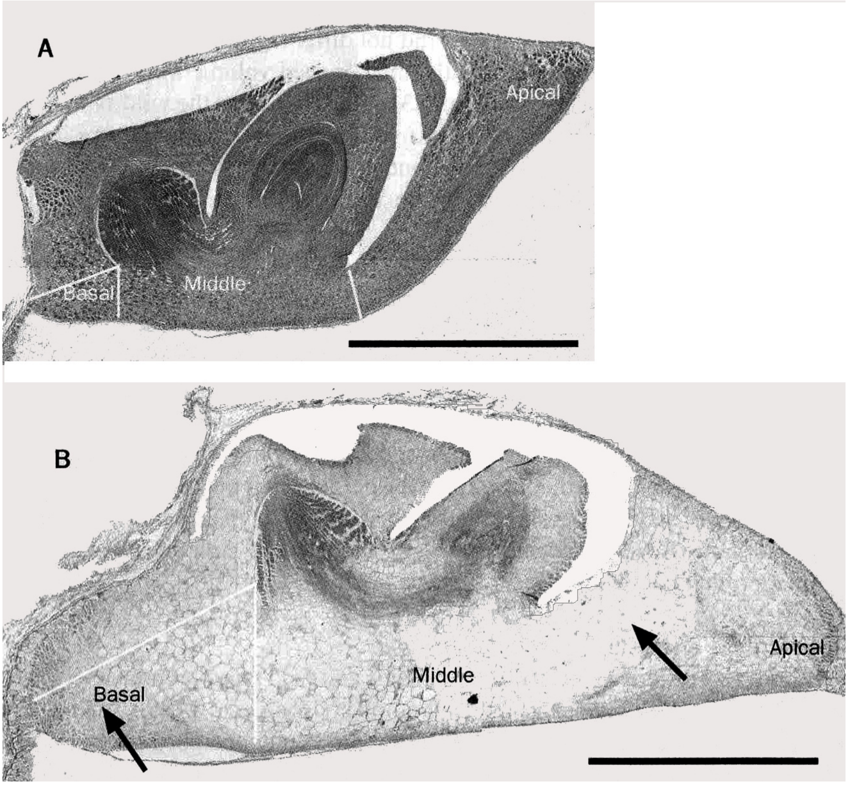


Fig. 2. Morphology of *ge-2* and wild-type mature embryos. (A) Longitudinal section of a wild-type embryo. (B) Longitudinal section of a *ge-2* mature embryo. Expanded basal and apical regions of the scutellum are indicated by arrowheads. White lines show the areas where cell numbers were examined in Table 3. Bar = 1 mm.

Table 2. Cell size of various embryonic tissues of *ge* and wild type. [a]

	Scutellum (apical part)	Scutellum (middle part)	Scutellum (basal part)	Bud scale	Second leaf
Wild type	2.519 ± 930	1,882 ± 515	2,466 ± 991	1,344 ± 285	479 ± 100
ge-2	5,065 ± 1,481	3,785 ± 1,875	4,152 ± 1.669	2,971 ± 973	1.063 ± 306
Ratio (*ge/wild* type)	2.0	2.0	1.7	2.2	2.2

[a] Unit is the pixel number found in the area of corresponding tissues observed under the same magnifications. Data were collected from three individual embryos for each genetic background. Twenty cells were counted on each section.

enlarged. However, there was no obvious difference in the overall shoot and radicle structure of *ge-2* and the wild type although the size of the *ge-2* shoot and radicle cells was twice as large as the wild type on average.

Besides cell size, the *ge-2* embryo showed other abnormalities in structures of the scutellum. In addition to the overall enlargement of the scutellum because of the cell size, the basal region was formed by producing extra cells. The number of cells across the scutellum between its basal edge and the radicle base was 1.5 times larger in *ge-2* than in the wild type (Fig. 2, Table 3). Another abnormality was seen in the shape of the epithelial scutellum cells. In the wild type, elongated epithelium cells were evident in the apical, abaxial part of the scutellum (Fig. 3, Table 4). As shown by the increasing ratios of the anticlinal to the periclinal cell length, the epithelium cells gradually became elongated from the basal to the apical part in the wild type (Table 4, Fig. 3A,B,C). In the apical region, elongated epithelium cells appeared to form two layers occasionally. In contrast, no epidermal cell of the apical scutellum facing the pericarp showed an elongated shape (Fig. 3C). However, the *ge-2* mutant formed an elongated shape of epithelium cells in the basal region and not in the apical region of the scutellum (Table 4, Fig. 3). This abnormality was correlated with two distinct patterns of cell elongation: mutant cells in the apical and middle epithelial regions were more enlarged in the periclinal direction, and cells in the basal region were enlarged in the anticlinal direction. This resulted in forming apical cells more spherical and basal cells more elongated in the mutant. Also, the size of the mutant epithelium cells of the basal region changed to almost twice the size of those of the apical region. This further enhanced the effect of cell elongation in the basal region.

Expression patterns of histone H4 in wild-type and *ge-2* embryos

To investigate possible effects of *ge* mutations on cell proliferation, we examined cell division activity in developing embryos. For the purpose, we examined histone H4 mRNA accumulation, which is specific to cells at the S phase, by means of *in situ* hybridization.

In the wild type, histone H4 expression was detected uniformly at the globular stage, corresponding to 1-2 DAP (days after pollination) (Fig. 4A). At 3-4 DAP, when the coleoptile started to differentiate, dividing cells were seen more frequently in the longitudinal half of the embryo that contained the coleoptile than in the other half that contained the incipient scutellum (Fig. 4B). The cells in the scutellum region were already distinct from the others because of their slightly enlarged shape at this early stage. Shortly later, when the coleoptile became elongated, the region where the shoot and radicle were being formed between the coleoptile and suspensor showed the highest cell division activity (Fig. 4C). When the first leaf started to be formed in the embryo at 4-5 DAP, dividing cells were frequently observed in the developing leaf primordium, coleoptile, radicle, bud scale, and vascular bundles that connected the radicle, shoot, and apical region of the scutellum (Fig. 4D). At 5-6 DAP, while these tissues continued to show relatively high cell division activity, the cells from other regions of the embryo, especially the epithelium cells of the scutellum, also

Table 3. Cell number and length of scutellum tissues:

	From basal edge to radicle base		From radicle base to closest point of scutellum epithelium	
	Length	Number of cells	Length	Number of cells
Wild type	24.3 ± 0.4	20 ± 0	12.3 ± 0.4	17.0 ± 0
ge-2	59.2 ± 2.7	31 ± 3.6	31.7 ± 1.6	23.3 ± 1.5

[a] Length was determined by printed images of sections in an identical magnification. Unit is cm. The data originated in four embryos in the wild type and three embryos in *ge-2*.

Table 4. The size of epthelium cells.[a]

	Apical				
	Anticlinal	Periclinal	Ratio	Area	Area ratio
Wild type	69.2 ± 8.9	15.6 ± 1.4	4.4	1,080	1.4
ge-2	54.8 ± 11.5	28.2 ± 6.3	1.9	1,545	
	Middle				
	Anticlinal	Periclinal	Ratio	Area	Area ratio
Wild type	31.1 ± 2.4	14.5 ± 2.1	2.1	451	2.5
ge-2	39.5 ± 5.6	28.2 ± 6.3	1.4	1,114	
	Basal				
	Anticlinal	Periclinal	Ratio	Area	Area ratio
Wild type	30.1 ± 5.8	23.5 ± 5.8	1.3	707	2.6
ge-2	81.0 ± 13.1	23.0 ± 6.7	3.5	1,863	

[a] Unit is the number of pixels found in the image of tissues under an identical magnification. Area was calculated by multiplying the anticlinal pixel number by the periclinal pixel number. Ratio shows anticlinal length/periclinal length.

divided frequently (Fig. 4E). When the third leaf was formed (7–8 DAP), most of the embryonic cells, except the young leaf primordia, showed no activity of cell division (Fig. 4F).

The overall expression pattern of histone H4 in *ge-2* was similar to that seen in the wild type. However, morphological differences between *ge-2* and wild-type embryos were already visible at the very early coleoptile stage: the mutant embryo produced more cells in the apical region and the area of the scutellum region facing the endosperm became enlarged (Fig. 5A,B). When the embryo formed the first leaf

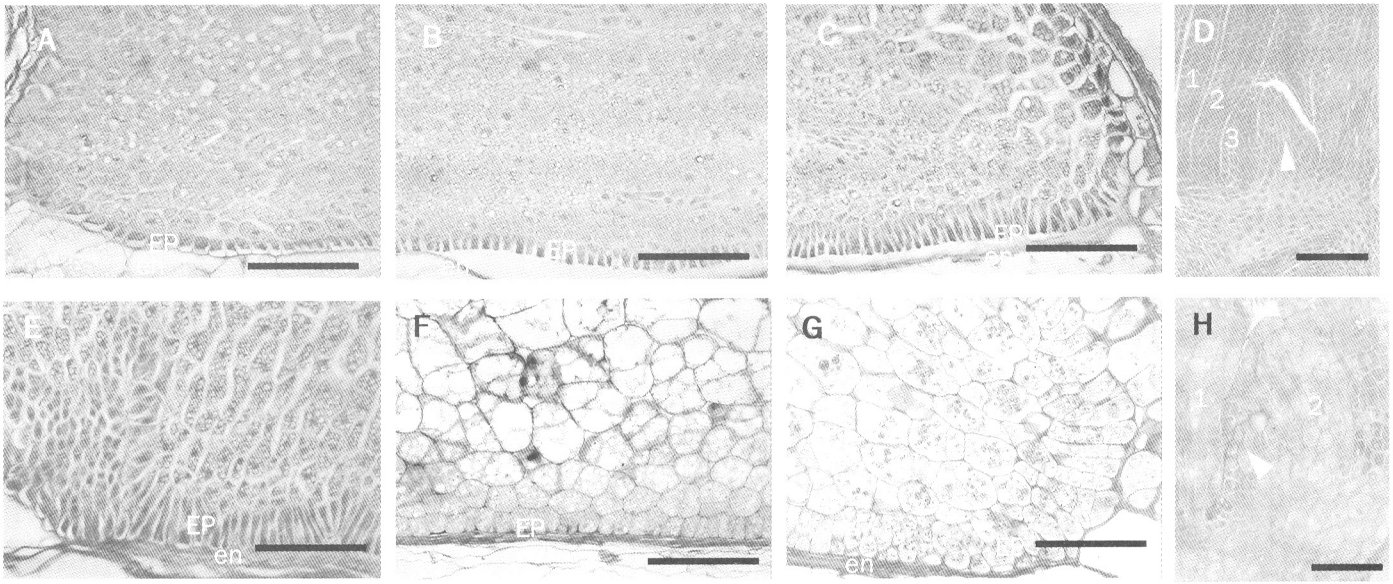


Fig. 3. Detailed scutellum morphology of *ge-2* and wild-type embryos: (A-D) wild type, (E-H) *ge-2.* (A, E) the basal region of the scutellum, (B, F) the middle region of the scutellum, (C, G) the apical region of the scutellum, (D, H) shoot meristem and young leaf primordia. EP = epithelium cell layer, en = endosperm. The numbers in D and H indicate primordia of the first, second, and third leaves, respectively. Arrows show shoot apical meristems. Bar = 100 µm.

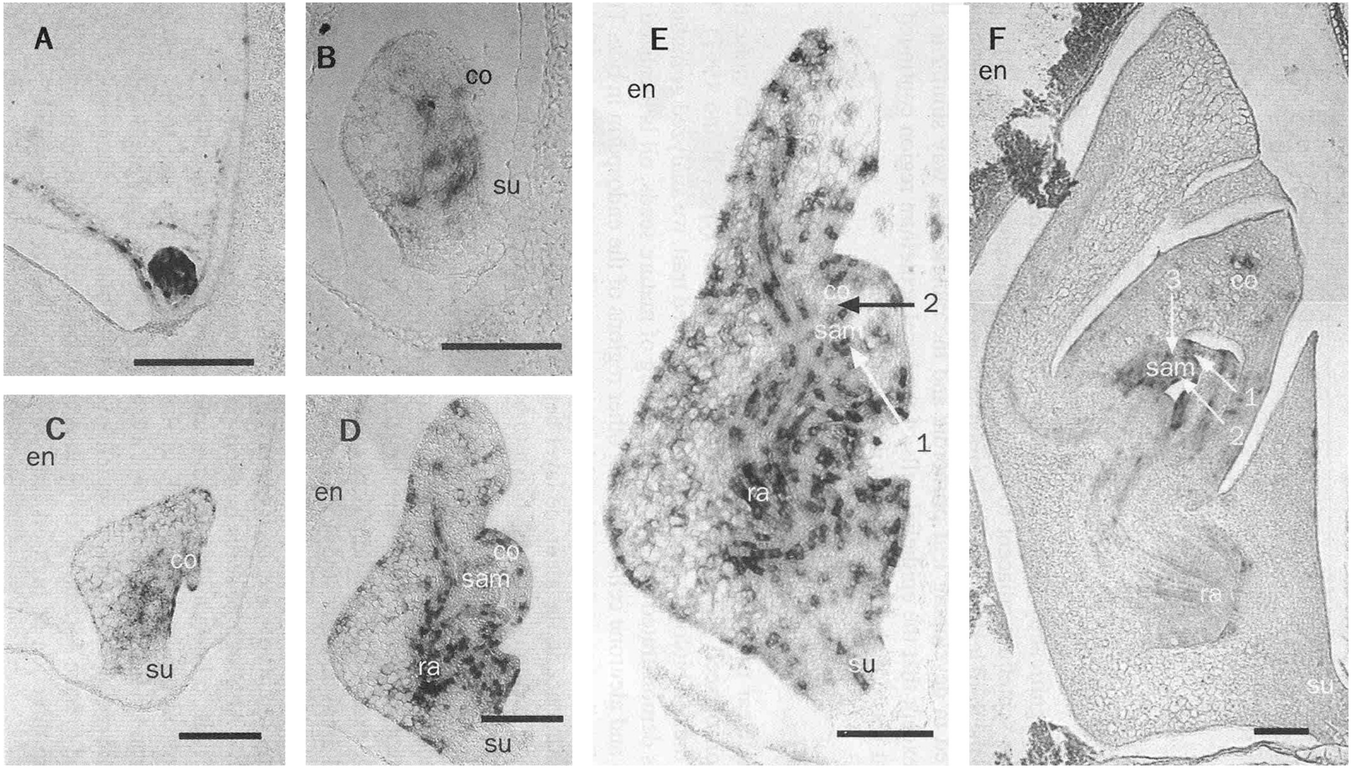


Fig 4. Histone H4 expression in wild-type developing embryos. (A) Globular stage, 1-2 DAP (days after pollination); (B) coleoptile stage, 3 DAP (C) an embryo producing the shoot apical meristem, 3-4 DAP (D) first-leaf stage, 5-6 DAP (E) an embryo producing the second-leaf primordium, 7 DAP (F) an embryo producing the third-leaf primordium, 10 DAP. co = coleoptiles, su = suspensor, en = endosperm, sam = shoot apical meristem, ra = radicle. The numbers indicate primordia of first, second, and third leaves, respectively. Bar = 100 µm.

Table 5. The number of histone H4 signals in scutellum tissue at 5-6 days after planting.

	Scutellum on coleoptile side [a]	Scutellum on endosperm side [a]
Wild type	12.3 ± 1.7 (23.7)	39.7 ± 6.2 (76.2)
ge-2	27.8 ± 7.2 (45.3)	33.5 ± 5.0 (54.7)

[a] The percentage of the number of cells that gave histone H4 expression in the total number of cells in the corresponding area.

primordium, significantly higher cell division activity was observed in the apical region of the scutellum adjacent to the coleoptile primordium (Fig. 5C, Table 5). Later, when the third leaf primordium started to form, cell division was only occasionally observed in developing leaf primordia and the radicle in a way similar to the wild type, except that the epithelial cells of the basal scutellum region continued to divide, what was not observed in the wild type (Fig. SF).

Discussion

Recessive nuclear mutations in the *giant embryo* locus were known to cause the accumulation of seed oil about 40% more than the wild type (Okuno 1997). To understand the cell biology involved in the high-oil seed trait, we analyzed *ge* mutants in detail. As demonstrated by the oil-red staining of mature seeds, oil is localized in the embryo and aleurone cells but not in other regions of the endosperm in rice. The overall oil distribution was not altered in the mutants. Since there was no obvious structural difference in the aleurone layer between mutant and wild-type seeds, the increase in oil accumulation was shown to be directly correlated with the enlarged embryo of the ge mutants.

By measuring the volume of embryos by subtracting the whole-seed volume from the endosperm volume, we showed that *ge* mutants have an embryo five times larger than that of the wild type. The enlargement of the embryo was primarily caused by the altered size of the scutellum tissue rather than by the shoot and radicle structures (Hong et al 1996 and this study). Taking into account that the aleurone cells also produce oil and make up about 54% of a mature seed, the *ge* has about 20% seed tissue in total (embryo + aleurone tissues) that can accumulate oil, while the wild type has 10%. Although *ge* seeds have oil-producing tissues twice as large as those of the wild type, oil accumulation in the mutant increased by only 40%. This low efficiency of oil production per cell in the mutant could be due to the altered metabolism and biology of the scutellum tissues. The low intensity of oil-red staining in the internal region of the mutant scutellum revealed that highly vacuolated cells in the area tend to have a weaker activity in accumulating oil. This finding might lead to the future direction of high-oil seed breeding in the *ge* background, in which

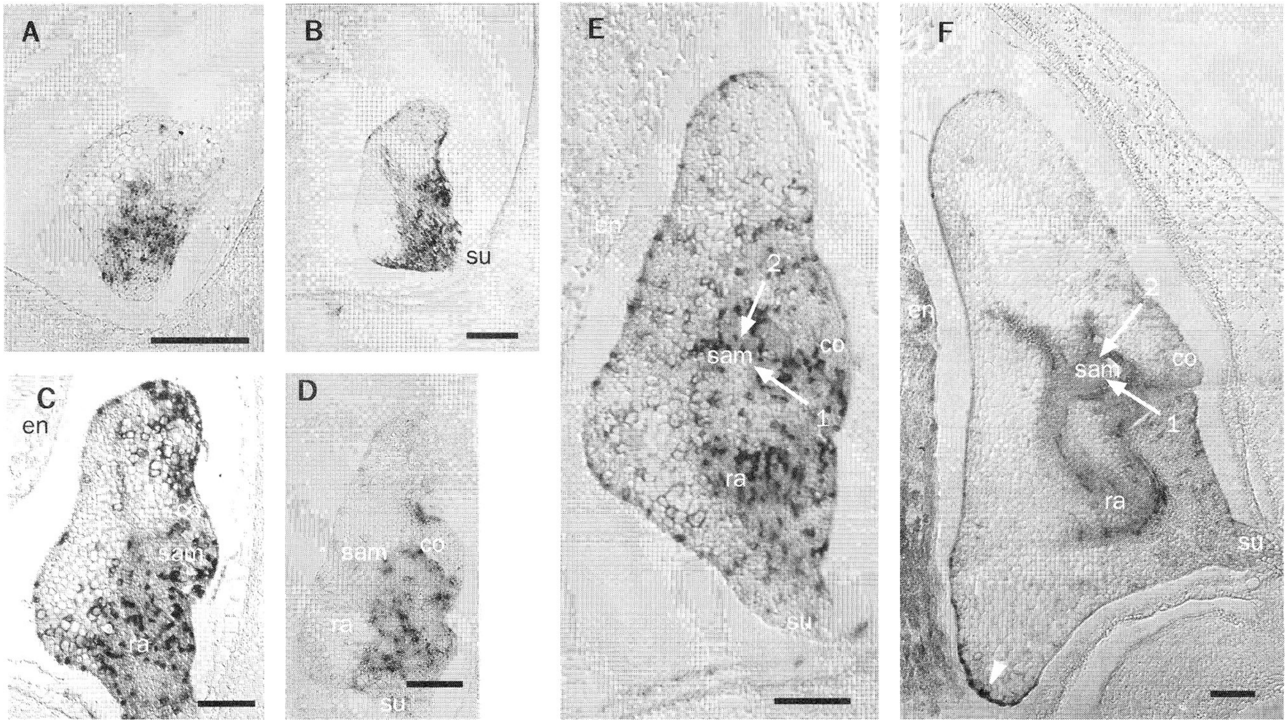


Fig. 5. Histone H4 expression in ge-2 developing embryos. (A) Coleoptile stage, 3 DAP; (B) an embryo producing the coleoptile, 3-4 DAP; (C, D) first-leaf stage, 5-6 DAP; (E) an embryo producing the second leaf primordium, 9 DAP. Arrowhead indicates the epithelium region that shows ectopic cell division activity. co = coleoptiles, su = suspensor, en = endosperm, sam = shoot apical meristem, ra = radicle. The numbers indicate primordia of first and second leaves, respectively. Bar = 100 μm.

improved oil accumulation can be further achieved by increasing oil production in the internal scutellum region.

According to Hong et al (1996), the number of cells in the embryo is roughly the same between *ge* mutants and the wild type. By analyzing cells in various embryonic tissues, we showed that mutants did not have equally enlarged cells across the entire embryo. Rather, some regions tended to have cells with more pronounced enlargement than other regions, and some parts of the embryonic tissues produced more cells than the wild type. For cell size, a significant difference was seen in the epithelium cells of the scutellum. The area of cells in the basal region was enlarged 2.6 times in *ge-2,* whereas that of cells in the apical region was enlarged 1.4 times. Besides cell size, cell shape was also altered in a distinct way. Cells in the basal region were elongated in the anticlinal direction, whereas cells in the apical region were elongated in the periclinal direction. We also found that the correlation between cell size and organ size change varies among different embryonic tissues. In the mutant, cells in shoot and radicle tissues have an area-size twice as large as the corresponding wild-type cells. However, the overall size of the shoot and radicle is not altered in the mutants. In the mutant embryo, shoot and radicle structures are thus formed with half as many cells. This suggests that the organ size of these tissues is not determined by cell number and cell size, but rather by their overall structures. Such an uncoupled link between cell and organ size was not detected in the other part of the embryo, including the scutellum. Cell enlargement and ectopic cell proliferation of some parts of the scutellum result in an overall large scutellum structure in the mutant. By analyzing histone H4 expression, we showed that aberrant cell division activity in the mutant occurs at certain stages of embryogenesis. The apical scutellum region in *ge* was significantly prolific at the coleoptile stage. The basal epithelium cells showed prolonged cell division activity at the late embryonic stages.

Based on the data from our analyses of *ge* mutants, the *GE* gene has functions to control cell size as well as proliferation during embryogenesis. Investigation of *GE* functions at the molecular level would shed further light on the genetic circuits controlling the high-oil seed trait associated with large embryo structures.

References

Hong SK, Kitano H, Satoh H, Nagato Y. 1996. How is embryo size genetically regulated in rice? Development 122:2051-2058.

Kouchi H, Hata S. 1993. Isolation and characterization of novel nodulin cDNA representing genes expressed at early stages of soybean nodule development. Mol. Gen. Genet. 238: 106-119.

Lacy DJ, Hills MJ. 1996. Heterogeneity of the endoplasmic reticulum with respect to lipid synthesis in developing seeds of *Brassica nupus* L. Planta 199:545-551.

Miševiae D, Alexander DE. 1989. Twenty-four cycles of phenotypic recurrent selection for percent oil in maize. I. Per se and test-cross performance. Crop Sci. 29:320-324.

Okuno K. 1997. Lipids, vitamins and components of aroma. In: Takane M, Futsuhara Y, Kikuchi F, Yamaguchi H, editors. Science of the rice plant. Vol. III. Tokyo (Japan): Food and Agriculture Policy Research Center. p 430-437.

Satoh H, Omura T. 1981. New endosperm mutations in rice, *Oryza sativa* L., induced by chemical mutagens. Jpn. J. Breed. 31:316-326.

Sughroue JR, Rocheford TR. 1994. Restriction fragment length polymorphism differences among Illinois long-term selection oil strains. Theor. Appl. Genet. 87:916-924.

Wanner G, Formanek H, Theimer PR. 1981. The ontogeny of lipid bodies (spherosomes) in plant cells: ultrastructural evidence. Planta 151: 109-123.

Notes

Authors' addresses: N. Nasagawa, S.-K. Hong, H. Sakai, DuPont Company, Agriculture and Nutrition, Delaware Technology Park 200 and Innovation Way, Newark, Delaware 19711, USA; S.-K Hong and H. Sakai, Department of Plant and Soil Sciences, 152 Townsend Hall, University of Delaware, Newark, Delaware 19716, USA. Phone: (302) 631-2651, fax: (302) 63 1-2607, E-mail: Hajime.Sakai@usa.dupont.com.

Acknowledgment: We thank Dr. Yasuo Nagato for his kind gift of *ge* mutants.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Mutation in a gibberellin biosynthetic gene, GA20 oxidase, contributed to the rice Green Revolution

M. Ashikari and M. Matsuoka

In the 1960s, an impending global food crisis was a major concern because the world population was expanding rapidly and it was predicted that demand for food would exceed production. Recognizing the problem, the International Rice Research Institute (IRRI) developed a semidwarf rice variety, IR8, known as "miracle rice." Widespread adoption of IR8 led to major increases in rice production and, as a result, the feared food shortages were averted in Asia. This was the so-called rice Green Revolution. The short stature of IR8 was derived from a semidwarf gene, *sd1.* We show that the *sd1* gene encodes a gibberellin (GA) biosynthetic enzyme, GA20 oxidase, which catalyzes the steps from GA_{53} to GA_{20}. The rice genome carries at least two GA20 oxidase genes *(GA20ox-1* and *GA20ox-2)* and *sd1* corresponds to *GA20ox-2,* which is expressed in various organs, with higher expression in the leaf, stem, and unopened flower, whereas *GA20ox-1* is preferentially expressed in the unopened flower. The reduced plant height associated with the *sd1* alleles is due to the low amount of active GA in leaves and stems, which is caused by a mutation of the *GA20ox-2* gene.

Rice (*Oryza sativa* L.) is one of the most important staple foods for humans and it has been estimated that 50% of humans depend on it as their main source of nutrition (White 1994). Rice is particularly important for people living in the monsoonal areas of Asia, where it has a long history of cultivation; consequently, it is deeply ingrained in the daily lives of Asian people.

In the 1960s, the rapid acceleration of the world population growth rate and the dramatic decrease in cultivated lands raised fears that food production would not meet the growing demand, leading to a global food crisis. To attempt to solve the problem, in 1966 the International Rice Research Institute (IRRI) bred a semidwarf and high-yielding variety, IR8 (Fig. 1A), well known as "miracle rice," by crossing Taiwanese native semidwarf variety Dee-geo-woo-gen, which carries the semi dwarf *1 (sd1)* gene, and the Indonesian good-tasting variety Peta (Hargrove and Cabanilla

1979, Dalrymple 1986, Khush 1999). The yield improvement of IR8 mainly resulted from a reduction in plant height caused by the *sd1* allele. In general, nitrogen fertilization is essential to increasing grain production, but it also induces culm elongation, resulting in an overall increase in the height of crop plants. Such tall crop plants are easily damaged by wind and rain and, consequently, yield losses occur. The IR8 semidwarf rice variety dramatically resolved this problem because it responded to fertilizer inputs to produce increased yield without culm elongation. The widespread adoption of IR8 led to major increases in rice grain production and a famine was averted. This was the so-called rice "Green Revolution," Like IR8, the high-yielding varieties Taichung Native 1 in Taiwan Province of China and Tongil in Korea, which also contained the *sdl* allele from Dee-geo-woo-gen, contributed to food security in those countries (Aquino and Jennings 1966, Suh and Heu 1978). Similarly, Japanese native semidwarf variety Jikkoku (Kikuchi et al 1985) and X-ray-induced variety Reimei in Japan (Futsuhara et al 1967) and X-ray-induced variety Calrose 76 in the United States (Foster and Rutger 1978) also carried different *sdl* alleles and were widely used in the rice breeding programs in those countries (Fig. 1A). The fact that such different *sdl* alleles have been used as parents in hybridization and contributed to numerous rice breeding programs for both indica and japonica species demonstrates that the *sdl* locus is the most suitable for controlling the height of the rice plant. The *sdl* mutants have been analyzed using various approaches and these studies have been applied in rice breeding programs (Futsuhara et al 1967, Suge 1975, Kikuchi et al 1985).

Materials and methods

Plant materials

Figure 1 shows the *sd1* mutants that we used in our experiments. Three *sdl* mutants and their corresponding wild-type cultivars were compared: Dee-geo-woo-gen *(sd1)* and Woo-gen (wild-type), Calrose76 *(sd1)* and Calrose (wild-type), and Reimei *(sd1)* and Fujiminori (wild-type). Since Jikkoku is a native variety (japonica), its corresponding wild-type strain has not been identified and therefore we used Taichung 65 (japonica) as a wild-type comparison for Jikkoku in this study. IR8 *(sd1)* was also used in the sequence analysis for *sdl.* Seed materials (Woo-gen, Dee-geo-woo-gen, Calrose, and Calrose76) were kindly provided by the National Institute of Agrobiological Resources and Aichi Prefectural Agricultural Research Center. Seed materials Jikkoku, Reimei, and Fujiminori were stored at Nagoya University.

Analysis of GA response

Ten rice seeds were placed on agar containing various concentrations of GA_3 and incubated at 30 °C under continuous light. After 5 days of incubation, the length of the second leaf sheath was measured. The quantitative analysis of the endogenous GAs was performed by gas chromatography-selected ion monitoring (Kobayashi et al 1995).

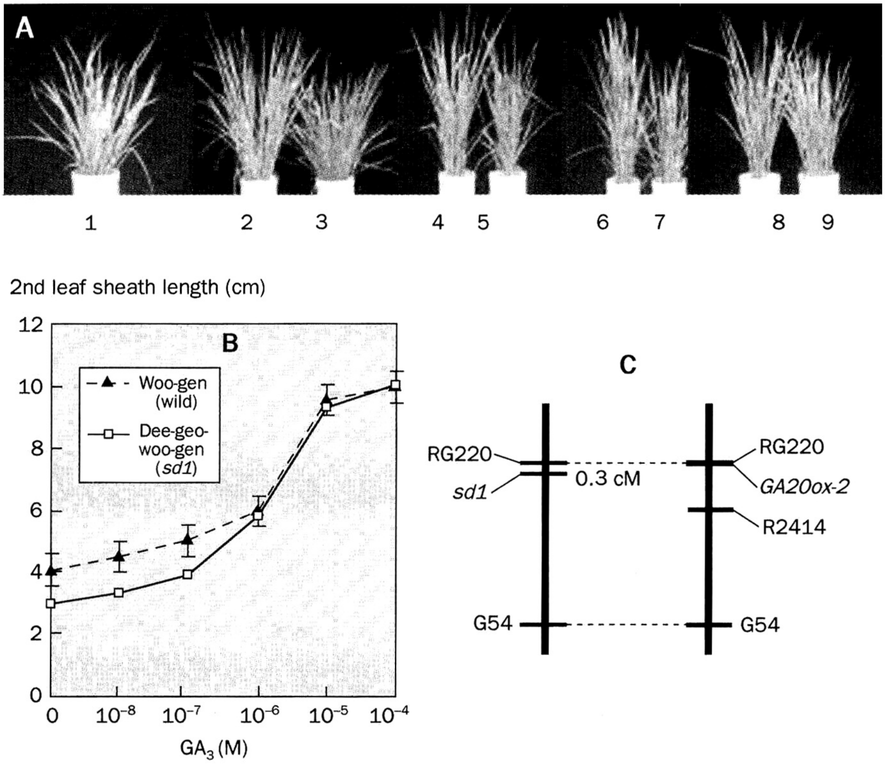


Fig. 1. Plant morphology, response to GA in the *sd1* mutant, map position, and structural features of the *sd1* gene. (A) Plant morphology of various alleles of *sd1* mutants. 1, IR8 *(sd1);* 2, Woo-gen (wild); 3, Dee-geo-woo-gen *(sd1);* 4, Calm (wild); 5, Calrose 76 *(sd1);* 6, Fujiminori (wild), 7; Relmei *(sd1);* 8, Taichung 65 (wild), 9 Jikkoku *(sd1).* (B) Effect of exogenous GA treatment on elongation of the second leaf sheath. (C) Linkage between GA20ox-2 and *sd1* on the rice genome. Left, the chromosomal location of the *GA20ox-2* gene. *GA20ox-2* was cosegregated to RG220 on chromosome 1. Right, the map position of *sd1.* The *sd1* was tightly linked to RG220 on chromosome 1 (Maeda et al 1997). (Continued on next page.)

Molecular cloning, DNA sequencing, and mapping

Primers were designed from the consensus sequences of the rice *GA20* oxidase gene *(GA20ox)* (Toyomasu et al 1997) and *Arabidopsis (GA5)* (Xu et al 1995) (sense: 5'YTNCCNTGGAAYGARACNYT3' and antisense: 5'GTNGGRTCRCARTGNGG3'). The DNA fragment was amplified by polymerase chain reaction (PCR) with the genomic DNA from a japonica line, TC65. Using the amplified DNA as a probe, genomic DNA and cDNA clones were identified from the genomic and cDNA libraries. The genomic and cDNA clones from the wild and *sdl* alleles were sequenced. To map the *GA2Oox-2* gene on the rice genome, linkage analysis was done using a population of backcross inbred lines derived from the

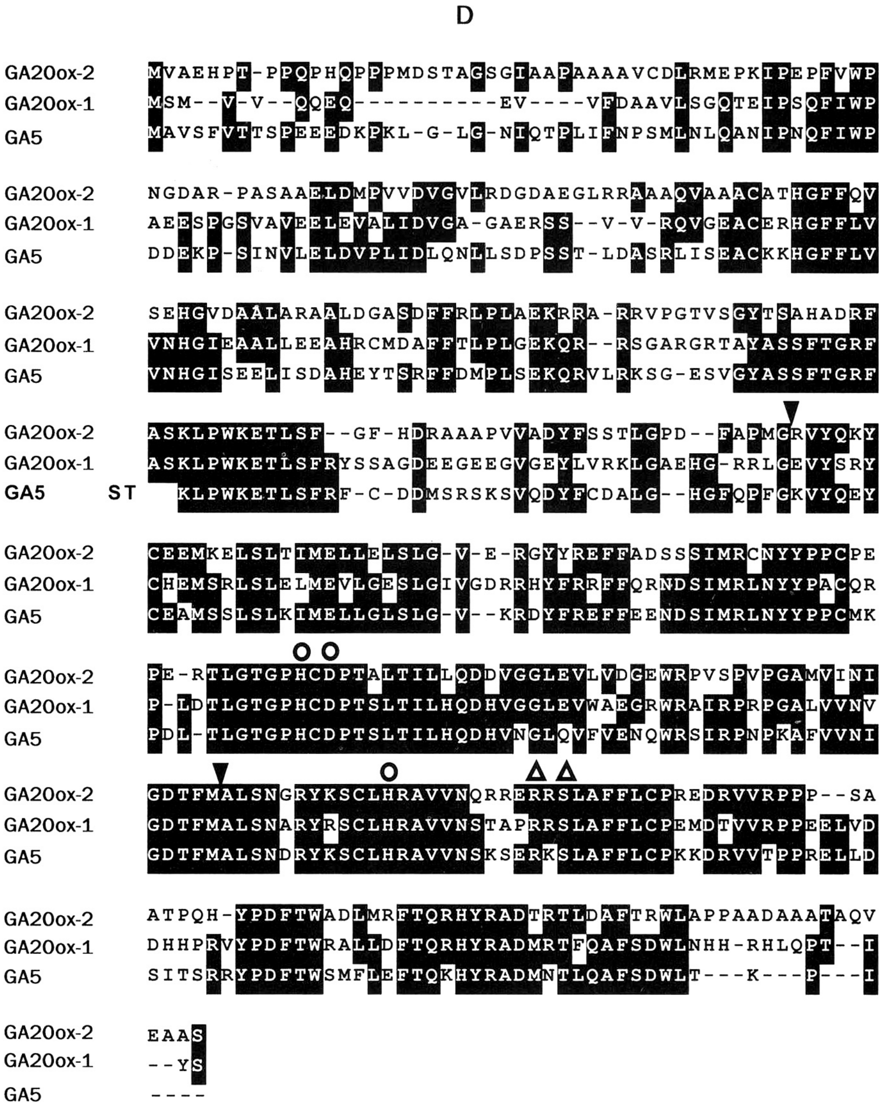


Fig. 1. Continued. (D) Alignment of the deduced amino acid sequences of GA20ox, rice GA20ox-2, GA20ox-1, and *Arabidopsis* GA5. Two of three identical amino acids among the three enzymes are indicated by the box in black. Positions of the intron are marked by arrowheads. Residues that bind the active-Fe are indicated by an open circle. Residues that interact with the 5-carboxylate of 2-oxoglutarate are indicated by an open triangle.

cross between Nipponbare (japonica) and Kasalath (indica) (Lin et al 1998). The linkage was calculated by the MAPMAKER program (Lander et al 1987).

Complementation analysis

A genomic *GA20ox-2* clone from the TC65 line (wild-type), including the entire coding region and the 5' and 3' flanking regions, was inserted into the binary vector pBI101-Hm2 (Sato et al 1998). The construct was introduced into the Jikkoku *sd1* allele by an *Agrobacterium* -mediated transformation (Hiei et al 1994).

In vitro functional assay

The full-length cDNA was excited and inserted in the sense orientation as a translational fusion into the pMAL-c2 expression vector to express in *Escherichia coli* strain JM109. GA catalyzing activity of recombinant protein was measured by full-scan gas chromatography/mass spectrometry (GCMS) (Kobayashi et al 1996).

Expression analysis

Total RNAs were extracted from various organs in rice. Semiquantitative reverse transcriptase (RT)-PCR was done by the following method. The amplified products were electrophoresed in agarose gel and transferred to a Hybond N^+ membrane. The DNA gel blot analysis was done with the coding sequence of a *GA20ox-2* as a probe. For analysis of feedback repression, total RNAs were extracted from seedlings treated with ± 10^{-4} M GA, or ± 10^{-6} M uniconazole (inhibitor of GA biosynthesis) and an RNA gel blot analysis was done.

Results and discussion

There are various reasons for the dwarf phenotype in plants, but one of the most important factors for determining plant height is gibberellins (GAs), known as one of the plant hormones. GAs are a large family of tetracyclic diterpenoids and are associated with several plant growth and developmental processes such as seed germination, stem elongation, flowering, and fruit development (Reid 1993, Hooley 1994, Ross et al 1997). To date, we have studied several rice GA-related mutants and isolated the genes involved in GA biosynthesis and signal transduction in the rice plant (Ashikari et al 1999, Ueguchi-Tanaka et al 2000, Ikeda et al 2001, Itoh et al 2001, 2002). Through these studies on rice GA-related mutants, we recognized that the plant morphology of the *sd1* mutants is similar to that of GA-deficient mutants with a weak allele. To investigate the possibility that the *SD1* gene is related to GA, we examined the GA response in the *sd1* mutant. As a first step, we compared the second leaf sheath elongation in the *sd1* and wild-type plants in response to various amounts of GA_3 treatments. The *sd1* seedlings responded better than the wild type and the sheath length of *sd1* was similar to that of the wild type at 10^{-6} M of GA_3 (Fig. 1B). This result suggests that *sdl* may be GA-deficient.

In *Arabidopsis,* six enzymes (CPS, KS, EKO, EKAO, GA20ox, and GA3ox) have been identified as GA-biosynthetic enzymes (Hedden and Phillips 2000). Recent

Table 1. Endogenous levels of various GAs in the wild and *sd1* plants. GA levels of the wild type (Woo-gen) and *sd1* (Dee-geo-woo-gen) were measured by gas chromatography-mass spectrometry analysis in nanograms per gram fresh weight.

	GA_{53}	GA_{44}	GA_{19}	GA_{20}	GA_1	GA_8	GA_{29}
Wild type	1.5	3.8	17	1.5	0.6	1.9	0.6
Sdl	2.8	3.9	17	0.5	0.2	0.4	nd

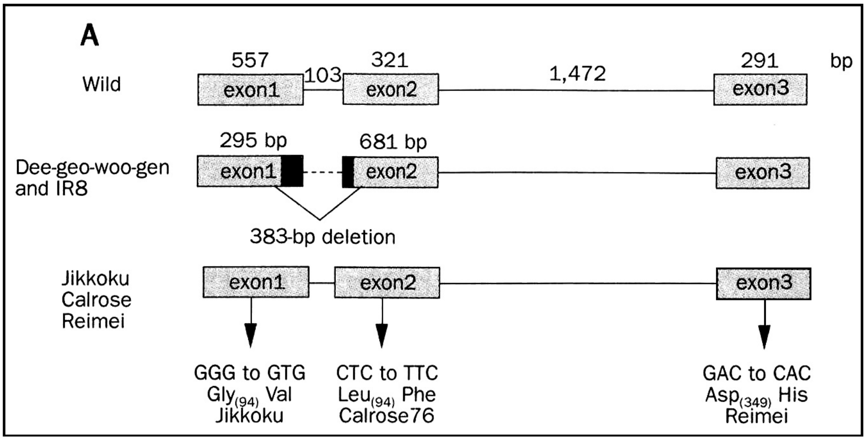
progress in the rice genome project (Sasaki 1998) allows us to easily identify and isolate genes homologous to interesting genes that have been isolated in other plant species such as *Arabidopsis* and maize. Using this information and tools for the rice genome, we have identified five GA-biosynthetic enzymes from rice (CPS, KS, EKO, EKAO, and GA3ox) and cloned their corresponding genomic clones. A mapping analysis of these genomic clones on the rice chromosome revealed that all of these genes do not correspond to the *sd1* gene. Our research team and Hirochika's group in the RGP (Rice Genome Research Program in Japan) have also isolated knockout mutants for these GA-biosynthetic enzymes, all of which show a much stronger dwarf phenotype than that of *sd1* (unpublished data). These mutants with severe dwarfism also support the theory that the *sd1* gene does not encode these enzymes, but encodes the remaining enzyme in the GA-biosynthetic pathway. To identify which enzyme the *sd1* gene encodes, we directly examined the intermediate GA levels in the *sd1* mutant (Table 1). The amounts of GA_{20}, GA_1, GA_8, and GA_{29} in the *sd1* mutants were lower than that of the wild-type plants, whereas the amounts of GA_{44} and GA_{19} in the mutants were equal to those of the wild type. Because GA_1 is mainly used as active GA in rice, these results suggest that the activity of GA 20 oxidase (GA20ox), which catalyzes the three steps from GA_{53}-GA_{44}-GA_{19} to GA_{20} is weaker in the mutants than in the wild type, and therefore the *sd1* gene may encode GA20ox.

So far, one gene encoding a GA20ox *(GA20ox-1)* has been isolated from the rice plant (Toyomasu et al 1997), but it does not correspond to the *SD1* gene since *GA20ox-1* was mapped on chromosome 3 of the rice genome, whereas *sd1* was mapped on the long arm of chromosome 1 (Maeda et al 1997). With this in mind, we suspected that *SD1* may encode another GA20ox since the *Arabidopsis* genome carries three *GA20 oxidase* genes and the products function in a redundant manner (Xu et al 1995). To isolate novel *GA20ox* genes in rice, we designed degenerated primers based on the conserved domain between the rice and *Arabidopsis GA20ox* genes (Toyomasu et al 1997, Xu et al 1995). Two amplified DNA fragments were obtained from the rice genome (japonica cultivar Taichung 65): one corresponds to the previously identified *GA20ox-1* and the other is a novel *GA20ox* gene *(GA20ox-2).* (The accession number of *GA20ox-2* is AB077025.) *GA20ox-2* was located on the long arm of chromosome 1, tightly linked to the *sd1* locus (Fig. 1C). We isolated the full length of the *GA20ox-2* gene and the cDNA clones. The deduced amino acid sequence of *GA20ox-2* showed 47.8% or 49.5% identity to that of *GA20ox-1* or *Arabidopsis GA5,* respectively (Fig. ID). We cloned and sequenced the *GA20ox-2* gene from four *sd1* mutants and found that one *sd1* allele contained a 383-bp deletion (Dee-geo-woo-gen) and that the other three *sd1* alleles had single nucleotide exchanges to induce amino acid exchange respectively (Jikkoku, Reimei, and Calrose 76) (Fig. 2A). Various mutations in the *sd1* gene strongly indicate that *sd1* encodes GA20ox-2. The introduction of the *GA20ox-2* gene from the wild-type plant rescued the dwarf phenotype of *sd1,* confirming that *sd1* encodes GA20ox-2 (Fig. 2B). To demonstrate that *GA20ox-2* encodes an active GA20ox, we subcloned the coding region in an expression vector and expressed its product in *E. coli.* The recombinant protein catalyzed the conversion of GA_{53} to GA_{20}. These results show that *GA20ox-2* encodes an active GA20ox. We also examined whether *GA20ox-2* is regulated by active GAs in a feedback manner because the expression of some *GA20ox* genes is repressed by active GAs (Xu et al 1999). We used germinating seeds for this experiment in the presence of either GA_3 or the GA biosynthetic inhibitor, uniconazole. The expression of *GA20ox-2* was down-regulated by GA_3 in ± uniconazole conditions, indicating that the *GA20ox-2* gene is regulated by active GA.

We also examined the expression pattern of *GA20ox-1* and *GA20ox-2* in different organs by RT-Southern blot analysis. Expression of *GA20ox-2* was observed in all of the organs that we tested, with higher levels in the leaf, stem, rachis, unopened flower, and shoot apex and lower levels in the leaf sheath and root. In contrast, *GA20ox-1* was preferentially expressed in the unopened flower and occurred at a much lower level in the other organs. The higher expression of *GA20ox-2* in the leaf blade and stem corresponds well to the dwarf phenotype of the *sd1* mutants. Although *sd1* mutants show dwarfism because of the reduction in leaves and stems, they do not show any deficiency in flower formation or fertilization, even though active GAs are important for such biological events. The other GA20ox encoded by *GA20ox-1,* which is preferentially expressed in the reproductive organs, may enable the normal development and fertilization of flowers in *sd1.* The presence of redundant enzymes in the flower should be important for the use of the *sd1* allele in rice breeding, since the loss-of-function of *SD1* would severely affect flower development and fertilization if *SD1* were the sole gene encoding GA20ox in rice.

Recently, the wheat Green Revolution gene, *Rht,* was identified and revealed that it encodes a transcriptional factor that works as a negative regulator of GA signaling (Peng et al 1999). As wheat has a hexaploid genome, recessive alleles such as *sd1* in rice are not available for producing a semidwarf strain of wheat. Actually, the *Rht* gene was a gain-of-function allele caused by an N-terminal truncated product that is located in a specific region related to the perception of GA signaling (Peng et al 1999). Even though the genetic and biochemical functions of the rice *sd1* gene and wheat RHT proteins are completely different, the products of both genes are related to GA. The fact that both Green Revolution genes are related to GA may not be a coincidence, but may be a natural consequence. Consequently, manipulation of GA biosynthesis or perception may be a good target for regulation of crop height.

The rate of world population growth has now once again exceeded the rate of growth in food-grain production (Khush 1999), and prompt measures and action for



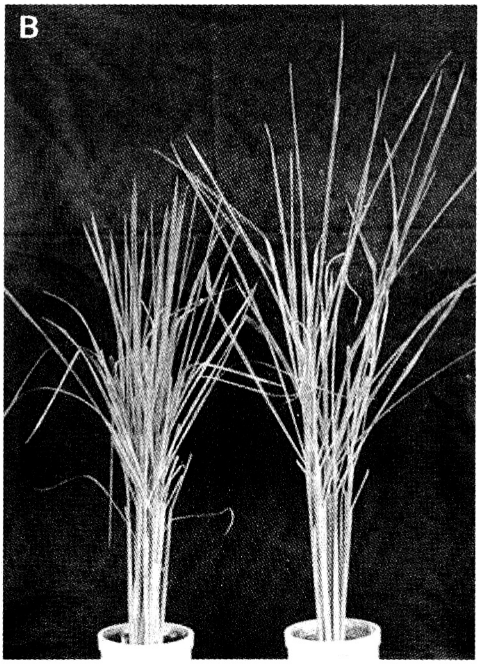


Fig. 2. Structural features of the *sd1* gene and complementation analysis, and biochemical and expression characterization of *GA20ox-2.* (A) The mutation sites of the four *sd1* alleles. The *GA20ox-2* gene consists of three exons and two introns. The mutation for each allele is indicated by an arrow for one-base exchanges or broken lines for an internal deletion. (B) Complementation test of *sd1* with the wild *GA20ox-2* allele. Right, the transgenic plant containing the wild-type *GA20ox-2* gene showed the normal phenotype. Left, a control transgenic plant with the vector DNA.

a second Green Revolution have been called for to avoid widespread food scarcity in the future. As our study revealed that modulating active GA levels during the vegetative stage can produce a suitable plant architecture for high crop yield, the genetic manipulation of GA biosynthesis using a molecular biological approach may provide us with an opportunity to overcome food security concerns, as was the case with the previous Green Revolution.

References

Aquino RC, Jennings PR. 1966. Inheritance and significance of dwarfism in an indica rice variety. Crop Sci. 6:551-554.

Ashikari M, Wu J, Yano M, Sasaki T, Yoshimura A. 1999 Rice gibberellin-insensitive dwarf mutant gene *Dwarf 1* encodes the α subunit of GTP-binding protein. Proc. Natl. Acad. Sci. USA 96:10284-10289.

Ashikari M, Sasaki A, Ueguchi-Tanaka M, Itoh H, Nishimura A, Datta SK, Ishiyama K, Saito T, Kobayashi M, Khush GS, Kitano H, Matsuoka M. 2002. Loss-of-function of a rice gibberellin biosynthetic gene, GA20 oxidase *(GA20ox-2),* led to the rice green revolution. Breed. Sci. 52:143-150.

Dalrymple DG. 1986. Development and spread of high-yielding rice varieties in developing countries. Bureau of Science and Technology, Agency for International Development, Washington, D.C., USA.

Foster KW, Rutger JN. 1978. Inheritance of semi-dwarfism in rice, *Oryza sativa* L. Genetics 88:559-574.

Futsuhara Y, Toriyama K, Tsunoda K. 1967. Breeding of a new rice variety "Reimei" by gamma-ray irradiation. Jpn. J. Breed. 17:85-90.

Hargrove TR, Cabanilla VL. 1979. The impact of semi-dwarf varieties on Asian rice-breeding programs. Bioscience 29:731-735.

Hedden P, Phillips AL. 2000. Gibberellin metabolism: new insights revealed by the genes. Trends Plant Sci. 12:523-530.

Hiei Y, Ohta S, Komai T, Kumashiro T. 1994. Efficient transformation of rice *(Oryza sativa* L.) mediated by *Agrobacterium* and sequence analysis of the boundaries of the T-DNA. Plant J. 6:271-282.

Hooley R. 1994. Gibberellin: perception, transduction and responses. Plant Mol. Biol. 26:1529-1555.

Ikeda A, Ueguchi-Tanaka M, Sonoda Y, Kitano H, Koshioka M, Futsuhara Y, Matsuoka M, Yamaguchi J. 2001. *Slender* rice, a constitutive gibberellin response mutant, is caused by a null mutation of the *SLR1* gene, an ortholog of the height-regulating gene *GAI/RGA/RHT/D8.* Plant Cell 13:999-1010.

Itoh H, Ueguchi-Tanaka M, Sentoku N, Kitano H, Matsuoka M, Kobayashi M. 2001. Cloning and functional analysis of two gibberellin 3ß-hydroxylase genes that are differently expressed during the growth of rice. Proc. Natl. Acad. Sci. USA 98:8909-8914.

Itoh H, Ueguchi-Tanaka M, Sato Y, Ashikari M, Matsuoka M. 2002. The gibberellin signaling pathway is regulated by the appearance and disappearance of *SLENDER RICE1* in nuclei. Plant Cell 14:1-16.

Khush GS. 1999. Green revolution: preparing for the 21st century. Genome 42:646-655.

Kikuchi F, Itakura N, Ikehashi H, Yokoo M, Nakane A, Maruyama K. 1985. Genetic analysis of semi-dwarfism in high-yielding rice varieties in Japan. Bull. Natl. Inst. Agric. Sci., Ser. D 36:125-145.

Kobayashi M, Gomi M, Agematsu J, Asami T, Yoshida S, Sakurai A. 1995. Fluctuation of endogenous gibberellin and abscisic acid levels in the germinating seeds of barley. Biosci. Biotech. Biochem. 59: 1969-1970.

Kobayashi M, Yoshizawa K, Sakurai A, Nakamura T. 1996. Analysis of endogenous gibberellins and abscisic acid in vegetative shoots of normal and weeping Japanese cherry *(Prunus spachiana)*. Biosci. Biotech. Biochem. 60: 159- 160.

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L. 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174-181.

Lin SY, Sasaki T, Yano M. 1998. Mapping quantitative trait loci controlling seed dormancy and heading date in rice, *Oryza sativa* L., using backcross inbred lines. Theor. Appl. Genet. 96:997-1003.

Maeda H, Ishii T, Mori H, Kuroda, Horimoto M, Takamura I, Kinoshita T, Kamijima O. 1997. High density molecular map of semi-dwarfing gene, *sd-1,* in rice *(Oryza sativa* L.). Breed. Sci. 47:317-320.

Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Worland AJ, Pelica F, Sudhakar D, Christou P, Snape JW, Gale MD, Harberd NP. 1999. 'Green Revolution' genes encode mutant gibberellin response modulators. Nature 400:256-261.

Reid JB. 1993. Plant hormone mutants. J. Plant Growth Regul. 12:207-226.

Ross JJ, Murfet IC, Reid JB. 1997. Gibberellin mutants. Physiol. Plant. 100:550-560.

Sasaki T. 1998. The rice genome project in Japan. Proc. Natl. Acad. Sci. USA 95:2027-2028.

Sasaki A, Ashikari M, Ueguchi-Tanaka M, Itoh H. Nishimura A, Datta SK, Ishiyama K, Saito T, Kobayashi M, Khush GS, Kitano H, Matsuoka M. 2002. A mutant of gibberellin-synthesis gene in rice. Nature 416:701-702.

Sato Y, Sentoku N, Nagato Y, Matsuoka M. 1998. Isolation and characterization of a rice homeobox gene, *OSH15*. Plant Mol. Biol. 38:983-998.

Suge H. 1975. Complementary genes for height inheritance in relation to gibberellin production in rice plants. Jpn. J. Genet. 50:121-131.

Suh HS, Heu HM. 1978. The segregation mode of plant height in the cross of rice varieties. II. Linkage analysis of the semi-dwarfness of rice variety "Tongil". Korean J. Breed. 10:1-6.

Toyomasu T, Kawaide H, Sekimoto H, Numers CV, Phillips AL, Hedden P, Kamiya Y. 1997. Cloning and characterization of a cDNA encoding gibberellin 20-oxidase from rice (Oryza sativa) seedlings. Physiol. Plant. 99: 1 1 1-118.

Ueguchi-Tanaka M, Fujisawa Y, Kobayashi M, Ashikari M, Iwasaki Y, Kitano H, Matsuoka M. 2000. Rice dwarf mutant *d1,* which is defective in the α subunit of the heterotrimeric G protein, affects gibberellin signal transduction. Proc. Natl. Acad. Sci. USA 97:11638-11643.

White PT. 1994. Rice: the essential harvest. Natl. Geogr. 185:48-79.

Xu Y-L, Li L, Wu K, Peeters AJM, Gage DA, Zeevaart ADJ. 1995. The *GA5* locus of *Arabidopsis thaliana* encodes a multifunctional gibberellin 20-oxidase: molecular cloning and functional expression. Proc. Natl. Acad. Sci. USA 92:6640-6644.

Xu Y-L, Li L, Gage DA, Zeevaart AD. 1999. Feedback regulation of *GA5* expression and metabolic engineering of gibberellin levels in *Arabidopsis.* Plant Cell 11:927-935.

Notes

Authors' address: Bioscience Center, Nagoya University, Furouchou, Chikusa, Nagoya, Aichi 464-8601, Japan.

Citation: Mew TW, Bra DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Manipulating starch and storage protein biosynthesis during endosperm development to increase rice yield

C. Sakulsingharoj, Sang-Bong Choi, M. Ogawa, S. Singh, J. Bork, C.R. Meyer,
G.E. Edwards, J. Preiss, and T.W. Okita

Rice yields are dependent on the quantity and weight of seeds. The bulk of the seed weight is contributed by the starchy endosperm, which provides a substantial portion of food for many Asian countries. A second important but rather minor component of the starchy endosperm is protein. Despite the distinct biochemical processes, starch and storage protein syntheses display parallel responses in rice and other cereals, indicating that they are interrelated processes. The basis for this pleiotropic relationship remains unknown. In this article, we describe current findings to understand the molecular and cellular basis of starch and storage protein biosynthesis, which will provide insights into their relationship. Starch synthesis in cereal endosperm is controlled by the key regulatory enzyme ADP-glucose pyrophosphorylase (AGPase), which is present in two forms, one located in the cytoplasm and the other in the amyloplast. Using a transgenic approach, we manipulated the cytoplasmic and amyloplast AGPase enzyme activity levels during rice seed development. Based on the effects on starch biosynthesis, the cytoplasmic AGPase plays a dominant role in starch synthesis, whereas the plastid form plays only a minor role. We also describe the mechanism of storage protein synthesis in rice as a model for cereals. The results indicate the involvement of storage protein mRNA localization in protein targeting and accumulation in endosperm cells.

Cereal seed formation is a product of a double fertilization event that leads to the formation of the diploid embryo and triploid endosperm. In the latter, multiple rounds of mitoses occur after the fusion of the two haploid egg nuclei and one haploid sperm nucleus, followed by cellularization and cell division. Maturation of the endosperm commences where starch and proteins are synthesized and accumulated.

Rice is valued as a crop in large measure because of its starchy endosperm. Although its protein content is much lower, rice may be the dominant source of essential amino acids for some Asian populations. In view of this food value, considerable effort has been made to increase rice yields and the quality of starch and protein.

Although starch synthesis and storage protein synthesis appear to be distinct biochemical processes, genetic and molecular studies have demonstrated that these two processes are closely interrelated. This relationship is readily evident in various cereal mutants, which are genetically defective in seed development (Nelson 1982). High-lysine maize and barley mutants that contain less protein are invariably lower in seed weight than the parental variety from which they were derived. Likewise, seed mutants defective in starch biosynthesis show a reduction in protein content (although higher percentage of lysine content). This relationship is also readily evident in transgenic plants that have reduced or increased starch content. A reduction in tuber starch by antisense suppression of ADP-glucose pyrophosphorylase, an essential enzyme for starch biosynthesis, results in almost a total abolishment of starch (Muller-Rober et al 1992). Interestingly, protein content is also reduced. An increase in starch content in potato tubers (Stark et al 1992) and maize seeds (Giroux et al 1996) results in no changes in net protein composition, indicating that protein levels increased at a corresponding percentage relative to starch. The basis for this interaction between starch and protein is not understood. Despite this deficiency in our knowledge, this relationship can be exploited to increase rice yields where increases in starch content will result in increases in protein content and vice versa. Studies on these two processes will provide insight into photoassimilate use and will be useful for improving plant yield as well as the quantity and quality of seed storage proteins. Before we describe our efforts to increase starch and protein content and, in turn, seed weight, some discussion on the processes that limit rice productivity and yield is warranted.

Rice productivity is dependent on source-sink relationships

The genetic yield potential of crop plants is dependent on source-sink relationships (Ho 1988, Turgeon 1989). Source leaves capture light energy and fix carbon dioxide to produce sugars and other metabolites that are exported to developing sink tissues, which use these basic precursors for growth and development (e.g., young leaves) or for the production of storage reserves (e.g., developing seeds). The interaction of source and sink tissues in affecting productivity was first shown using chimeric plants of spinach beet shoots grafted onto sugar beet roots, which have a higher sink capacity than spinach beet roots (Thorne and Evans 1964). The grafted shoots had a much higher photosynthetic rate than control plants, suggesting that the larger sink capacity of sugar beet roots stimulated photosynthesis (Thorne 1964). Likewise, several studies have shown that the removal of sink organs can decrease photosynthesis because of feedback. One general form of feedback occurs through changes in the levels of metabolites, especially the buildup of organic phosphates, which limits the availability of inorganic phosphate required for photosynthesis (Sharkey et al 1986, Stitt et al 1987, Woodrow and Berry 1988, Schaffer and Zamski 1996). During rice grain filling, sucrose and amino acids are transported from photosynthetic tissues (flag leaf and glumes) or remobilized from vegetative storage reserves to the developing seed.

Sucrose is hydrolyzed into UDP-glucose and fructose, whereupon the bulk of these hexose sugars is converted into starch. Amino acids are mainly used for protein synthesis, especially the storage proteins. The rate by which these carbon and nitrogen building blocks can be converted into these reserves is an important factor that controls seed yields. This sink capacity also affects photosynthetic capacity when the rate of photosynthesis is adjusted to a level at which sinks can use photoassimilates efficiently.

Limitations in photosynthetic capacity via sink capacity

During photosynthesis, the bulk of the triose-P is converted mainly into sucrose, which is then transported to sink tissues. When the rate of sucrose synthesis exceeds the rate by which it can be transported and used by sink tissues, sucrose levels and, in turn, triose-P levels build up. The latter prevents the recycling of Pi, which is required for photosynthesis and results in feedback. Photosynthetic feedback is very apparent in our studies with rice grown under ambient levels of CO_2, moderate temperature, and high light as evidenced by the insensitivity of CO_2 fixation to decreased O_2 or increased CO_2 (Winder et al 1998, Sun et al 1999). This feedback, which is readily evident during all stages of rice development, is probably due to the limited capacity of sinks to use sucrose as suggested by the response of rice under CO_2 enrichment. Rowland-Bamford et al (1990) and Chen et al (1994) showed that rice plants exposed to increasing CO_2 concentrations had elevated photosynthetic rates and either increased levels in the total nonstructural carbohydrate in the vegetative parts of the plants (Rowland-Bamford et al 1990) or increased sucrose levels in peduncle exudates (Chen et al 1994). The enhancement in photosynthesis and photosynthate under higher levels of CO_2 in rice, however, did not result in higher grain weight because of the inability of developing seeds to uptake and use this photosynthate (Chen et al 1994). In turn, because of the inability of sinks to use additional photosynthate, a strong acclimation and feedback effect on source activity was observed, resulting in a large linear decline in Rubisco content (Rowland-Bamford et al 1991).

Factors limiting conversion of sucrose into starch

Sucrose is the principal sugar transported into developing rice grain, where it is hydrolyzed by sucrose synthase (SuSy) to yield UDP-glucose and fructose, which can be converted into hexose monophosphates (Fig. 1). Transport studies with intact cereal amyloplasts showed that hexose phosphates were the most efficient precursors of newly synthesized starch (Neuhaus and Emes 2000). Within the amyloplast compartment, hexose monophosphates in the form of glucose 1-phosphate can be used by ADP-glucose pyrophosphorylase (AGPase) to form ADP-glucose, the substrate for starch synthase.

More recent developments have demonstrated the existence of a second AGPase pathway involving a cytoplasmic form. In rice, maize, and barley endosperm, the predominant AGPase activity is located extra-plastidial, presumably in the cytoplasm (Denyer et al 1996, Thorbjornsen et al 1996, Sikka et al 2001). The formation of ADP-glucose in the cytoplasm would require a transporter for this sugar nucleotide,

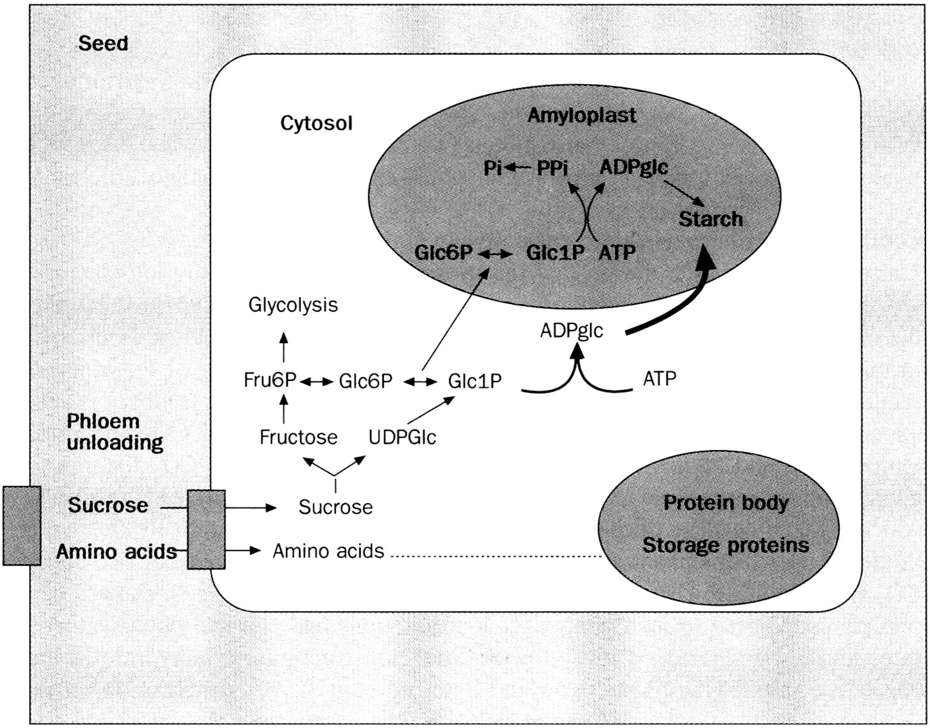


Fig. 1. Metabolic pathway of starch and storage protein syntheses in developing seeds. Sucrose and amino acids are unloaded from the phloem and transported into the endosperm cells. ADP-glucose, the precursor for starch biosynthesis, can be made in the cytoplasm (major pathway) or amyloplasts (minor pathway).

whose existence (maize *Bt1*) is supported by both biochemical and genetic data (Sullivan and Kaneko 1995, Shannon et al 1998). Despite the brevity of the description on the pathways of carbon into starch, processes that could limit starch synthesis are sucrose hydrolysis, the transport of metabolites between the amyloplast and cytoplasmic compartments, and the formation and use of ADP-glucose. Although all of these processes will likely affect starch synthesis, the formation of ADP-glucose is most critical, as described below.

The allosteric properties of AGPase limit seed starch synthesis

The catalytic activity of both the rice leaf and seed AGPases is subject to allosteric control by the activator 3-phosphoglyceric acid (PGA) and by the inhibitor Pi. During photosynthesis, when the 3-PGA/Pi ratio is low, the enzyme is down-regulated in catalytic activity so that little of the sugars is routed into starch. When sucrose synthesis becomes saturated, the effector ratio is high, resulting in activation of AGPase activity and starch synthesis. This allosteric regulation of AGPase by the ratio of these effectors is essential for normal partitioning of carbon between sucrose and starch.

Unlike the situation in leaf tissue, where starch synthesis must be tightly controlled, the ideal condition in the starchy endosperm is to maximize carbon flow into starch since starch metabolism is required only in the biosynthetic direction. Since the levels of 3-PGA and Pi are not likely to oscillate in developing endosperm tissue, as observed in leaves, the allosteric regulation of endosperm AGPases may be an evolutionary carryover and may not be necessary for carbon metabolism in developing cereal seeds. Giroux et al (1996) showed that a maize AGPase revertant enzyme, Rev6, displayed altered sensitivity to Pi inhibition. Plants expressing the Rev6 AGPase had a higher seed weight (higher starch levels). This evidence supports the view that the inhibitory effect of Pi on the AGPase activity restricts the flow of carbon into starch. Although the plant produces high levels of AGPase during seed development to compensate for this Pi inhibition of the AGPase activity, starch synthesis has probably not reached its maximum potential in sink tissues (Okita et al 1993, Nakata and Okita 1994). To increase sink strength, manipulation of AGPase enzyme activity by the introduction of a modified enzyme with increased sensitivity to 3-PGA activation andor increased resistance toward Pi inhibition may be successful. Indeed, research studies in potato (Stark et al 1992), in maize (Giroux et al 1996), and in wheat (Smidansky et al 2002) have shown that the introduction of the allosteric regulatory mutants of AGPase can increase starch production in these plants.

The introduction of allosteric mutant ADP-glucose pyrophosphorylase increases rice yield

Of the various AGPase mutants at our disposal, we selected the *E. coli glgC*-TM gene, which encodes an enzyme that differs from the normal enzyme in containing three amino acid replacements, R67K, P295D, and G336D. Each of the individual changes alters the allosteric properties of the enzyme. When the amino acid replacements are pyramided together, the TM enzyme shows 90% activity of the fully activated wild-type enzyme in the absence of any activator and is highly resistant to Pi inhibition. Sikka et al (2001) showed that the rice AGPase is present in two isoforms: a major form located in the cytoplasm and a minor one present in the amyloplast. The TM enzyme was targeted to the amyloplast or cytoplasm to determine whether the intracellular location of the bacterial enzyme has an effect on starch synthesis.

Transgenic rice plants expressing the TM enzyme into two different compartments in endosperm cells were produced. pT0125 plants contained the *glgC*-TM gene fused with the *Bt*1-transit peptide (*Bt*-TP) sequence (Sullivan et al 1991) to target the TM enzyme into the amyloplast. pCS8 plants contained the bacterial mutant gene without the TP sequence; hence, the TM enzyme was retained in the cytoplasm. Immunoblot results revealed that the TM enzyme was expressed in the cytoplasm (pCS8) and amyloplast (pT0125) of transgenic rice seeds (Sakulsingharoj et al 2002). pT0125 plants showed multiple polypeptides immunoreacting with anti-TM (Sakulsingharoj et al 2002). The band of 48-kDa polypeptide was consistent with the mature TM polypeptide, suggesting that the transit peptide was removed during translocation of the TM enzyme into the amyloplast. The band of 50 kDa was the product of the cleavage at the alternative cleavage site proposed by Shannon et al (1998). The largest band of 52 kDa corresponded to a precursor polypeptide containing the intact BT1-TP sequence.

Expression of the TM enzyme to either the cytoplasm (pCS8) or amyloplast (pTO125) resulted in about a 3-4-fold increase in AGPase activity in rice endosperm (Sakulsingharoj 2002). The effect of increased AGPase activity on starch synthesis was studied by ^{14}C sucrose-labeling experiments. Panicles were fed ^{14}C sucrose through the cut stem and then incubated up to 16 h in the light. Seed samples were collected at 8 and 16 h and the amount of ^{14}C radioactivity incorporated into starch and soluble fractions was measured. Plants containing the cytoplasmic TM (pCS8) showed a significant increase in ^{14}C-sucrose incorporation into starch in developing seeds (Fig. 2). Consistent with the higher ^{14}C sucrose incorporation into starch, pCS8 plants produced seeds of individual weights up to 10% higher than those from wild-type plants. Hence, expression of the TM AGPase in the cytoplasm resulted in a positive correlation of increased cytoplasmic AGPase activity, starch synthesis, and seed weight (Fig. 2). In contrast, pT0125 plants displaying an increase in amyloplast-localized AGPase activity showed varying ^{14}C labeling rates in starch and variable seed weight (Fig. 2). The results suggested that the intracellular location of AGPase plays an important role in starch synthesis and that the cytoplasmic-localized AGPase is the predominant form responsible for ADP-glucose formation and, in turn, starch synthesis.

The variation in ^{14}C-incorporation rate and seed weight among pTO125 plants was dependent on the plant line analyzed. Some lines showed small to moderate increases in ^{14}C-labeling in starch and in seed weight. Other pTO125 lines showed small to moderate increases in ^{14}C-incorporation rate but produced seeds that were lower in weight than wild-type seeds. This reduced seed weight phenotype cosegregated with the *glgC* -TM gene, indicating that the expression of the bacterial gene was the cause of the seed phenotype (results not shown). The basis of this reduced seed weight phenotype is not known but it may be due to the activation of starch degradation, which would lead to a futile cycle of synthesis and degradation. This variability in ^{14}C-incorporation rate and seed weight among pTO125 lines is reminiscent of the conditions observed in potato, in which expression of an allosteric mutant *glg* C16 resulted in an increase in tuber starch (Stark et al 1992) or no change in tuber starch (Sweetlove et al 1996).

The effects of elevated CO_2 on seed starch synthesis

Studies of rice plants grown under elevated CO_2 conditions suggested the limitation of developing seeds in the conversion of photoassimilate into starch (Rowland-Bamford et al 1990, Chen et al 1994). Transgenic plants expressing amyloplast TM (pTO125) and cytoplasmic TM (pCS8) were grown under enriched CO_2 (800 ppm) to determine whether expression of TM resulted in enhanced capacity to use the excess photoassimilate. Surprisingly, both transgenic plant types displayed responses

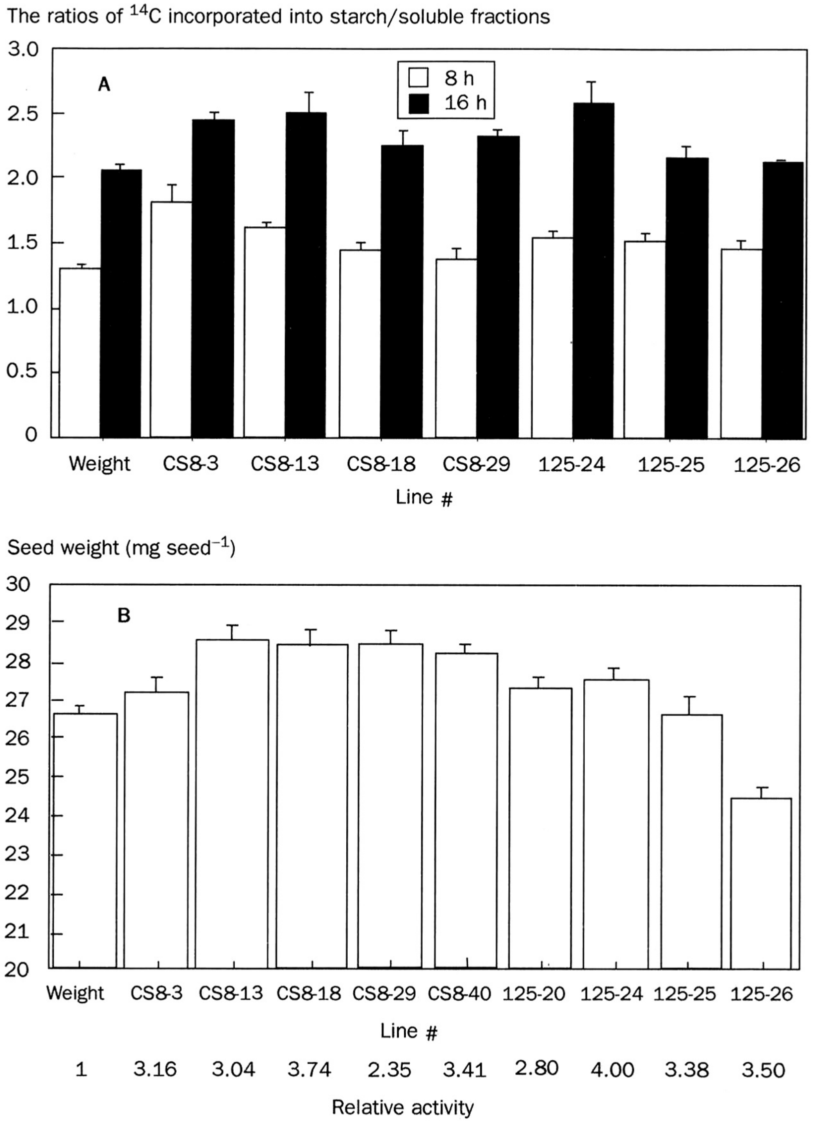


Fig. 2. Analysis of transgenic plants expressing cytoplasmic TM enzyme (pCS8) and amyloplast TM enzyme (pTO125) grown at ambient CO_2 conditions. A positive correlation of increased cytoplasmic AGPase activity (relative activity), ^{14}C-labeling into starch, and seed weight was observed among several lines of pCS8 plants. In contrast, pTO125 plants showed a variable response of ^{14}C-Incorporation rates and seed weight although these plants exhibited increased AGPase activity.

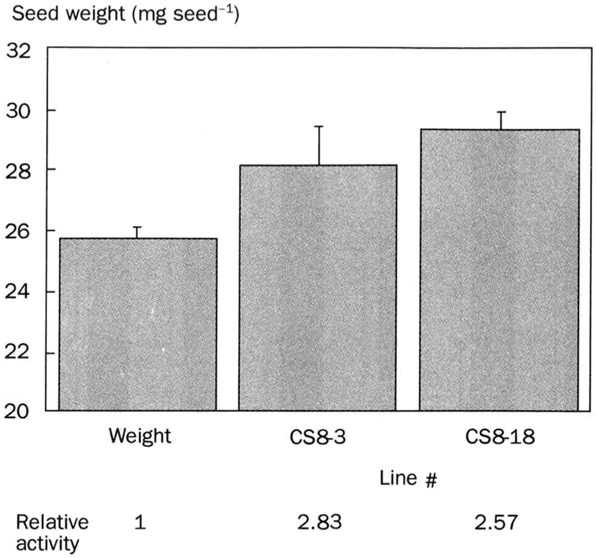


Fig. 3. Analysis of pCS8 plants (cytoplasmic TM enzyme) grown under elevated CO_2 conditions. These plants showed increased AGPase activity in developing seeds. The seed weight was greater than that in wild-type plants. However, the extent of increased seed weight in pCS8 plants was similar to that observed In the plants grown under normal CO_2 conditions.

similar to those observed under ambient conditions. pT0125 plants showed increased AGPase activity in developing seeds but reduced seed weight compared with wild-type plants, supporting the view that amyloplast AGPase is a minor form responsible for starch synthesis. pCS8 plants showed higher AGPase activity (2.5- to 3-fold) and bore seeds of higher weight than wild-type plants (Fig. 3). The extent of increase in seed weight from pCS8 plants grown under elevated CO_2 was no different from that of pCS8 plants grown under ambient conditions. These observations indicate that increasing the cytoplasmic AGPase activity results in higher starch content and, in turn, higher seed weight but only to a certain limit. This inability to mobilize excess photoassimilate into starch under elevated CO_2 conditions may indicate that the AGPase reaction remains limiting. Alternatively, carbon flux into starch may be limited because of some other reaction step in the pathway (see Fig. 1).

Manipulation of storage protein synthesis

Rice accumulates storage proteins, which serve as a reservoir of carbon, nitrogen, and sulfur for the postgerminating seedling. The major seed storage proteins of rice are the glutelins, which make up about 60% of the total seed protein. Despite their general insolubility in aqueous and alcoholic solutions, the glutelins are structurally homologous to the 11S globulins, the storage protein accumulated by dicotyledonous plants. Rice also accumulates the alcoholic-soluble prolamines, the storage protein typically found in the endosperm of cereal seeds. The rice prolamines are present at levels about equimolar to those of the glutelins but, because of their much smaller size, constitute only about 15-20% of the total seed protein on a weight basis (Li et al 1993).

Seed storage protein trafficking

Both prolamines and glutelins are synthesized on the endoplasmic reticulum (ER) membrane and translocated into the ER lumen. Within this region of the endomembrane system, the proteins are then packaged into separate compartments to form distinct protein bodies (PBs). As viewed by electron microscopy, the prolamine PBs are intracisternal inclusion granules formed within the ER lumen. They are spherical in shape and about 1-2 µm in diameter (PB-I) and are electron-lucent. Glutelin PBs are storage vacuoles. They are larger in size (usually >2 µm in diameter) than the prolamine PBs, are more irregularly shaped, and are electron-dense in appearance (PB-II) (Tanaka et al 1980, Krishnan et al 1986, Ogawa et al 1987). The transport of glutelins to the storage vacuoles is via the Golgi complex.

The trafficking of the rice storage proteins within the endomembrane system raises several questions. First, how are the rice prolamines, which lack the ER retention signal K(H)DEL motif, retained within the ER lumen? Second, how do glutelins get around the prolamine intracisternal inclusion granules, which act as potential barriers to the transport of these proteins to the Golgi? Answers to both of these questions lay with the targeting and enrichment of the storage protein mRNAs to specific intracellular sites within the cell (Okita and Rogers 1996).

Involvement of mRNA targeting

As early as 1986, evidence from several laboratories suggested that the rice storage protein mRNAs were not randomly distributed on the ER. Yamagata and Tanaka (1 986) demonstrated that prolamine poly(A+)-RNAs were highly enriched in a purified PB-I fraction. Kim et al (1992) showed that microsomal membrane fractions enriched in cisternal-ER (C-ER) contained a significantly larger proportion (2.4 molar excess) of glutelin mRNAs than prolamine RNAs. These biochemical results suggested that the prolamine and glutelin RNAs were targeted to the PB-ER and C-ER, respectively. The localized distribution of these storage protein RNAs to specific subdomains of the ER complex was unequivocally demonstrated by Li et al (1993). Using both biochemical analyses of subcellular fractions and *in situ* hybridization at the electron microscopy level, these workers showed that prolamine mRNAs are localized primarily on the ER (PB-ER) that constitutes the prolamine PB, whereas glutelin mRNAs are enriched in C-ER. These results suggest that the initial targeting process of rice storage proteins into their different PBs is facilitated by the segregation of their transcripts on the C-ER for glutelins and on the PB-ER for prolamines (see below).

Mechanism of mRNA localization

Several mechanisms have been proposed for the targeting of these storage protein RNAs to specific ER subdomains (Okita and Rogers 1996). To determine whether the RNA itself was targeted or whether RNA localization was a consequence of protein synthesis for the production of peptide signals, a series of synthetic prolamine genes was constructed and introduced into rice by transformation (Choi et al 2000). The distribution of these synthetic wild-type prolamine mRNAs during endosperm development was then studied using the *in situ* reverse transcriptase technique and laser-scanning confocal microscopy. The intact synthetic prolamine RNA and prolamine RNAs lacking the signal peptide coding sequences were targeted to the PB-ER, whereas RNAs containing a substituted glutelin 3'UTR were localized in the C-ER. These observations indicate that prolamine RNA targeting is due to the presence of one or more RNA targeting ("zip code") signals located in the 3'UTR. Interestingly, although prolamine peptide sequences are not essential for RNA targeting, translation initiation was required as elimination of the single AUG codon resulted in C-ER localization of the transcript. More recent results indicate that restricted prolamine mRNA localization requires two RNA zip code signals, one located in the 3'UTR and a second located in the coding sequence (unpublished data). When only one zip code is present, the RNA is localized in both the PB-ER and C-ER.

mRNA localization facilitates storage protein targeting

The targeting of prolamine and glutelin RNAs to two different ER subdomains and the packaging of the polypeptides to separate endomembrane compartments suggest that mRNA localization facilitates protein targeting and deposition. Recent evidence supporting this hypothesis was obtained from our studies on the sites of protein synthesis and deposition of the maize d-zein in rice endosperm cells. A series of transgenic rice plants expressing different d-zein RNA sequences was produced containing the coding sequences fused to a 3'-terminator sequence from *nos* (pTO164), glutelin (pTO166), or prolamine (pTO173) genes. A fourth DNA construct, pTO224, contained a green fluorescent protein (GFP) coding sequence fused upstream of the d-zein RNA lacking the 5'UTR and signal peptide (SP) coding sequence. Expression of these gene constructs was under the control of the endosperm-specific glutelin promoter (GluB1).

Analysis of d-zein RNA localization using *in situ* RT-PCR followed by confocal microscopy showed that d-zein RNA coding sequences containing the *nos* 3'UTR or 3' prolamine sequences were localized to the surface of prolamine PBs (PB-ER). As the *nos* 3'UTR sequences do not contain any apparent zip codes, this result indicates that one or more *cis*-element(s) responsible for mRNA localization are present in the d-zein coding sequence. Moreover, these results suggest that the zip code signals residing in the rice prolamine 3'UTR and in the d-zein RNA coding sequence are compatible and can direct RNA localization to the PB-ER. A possible clue to the nature of the d-zein zip code was suggested by the localization of GFP-zein hybrid RNA in pTO224 plants. These hybrid RNAs, which lack the d-zein SP

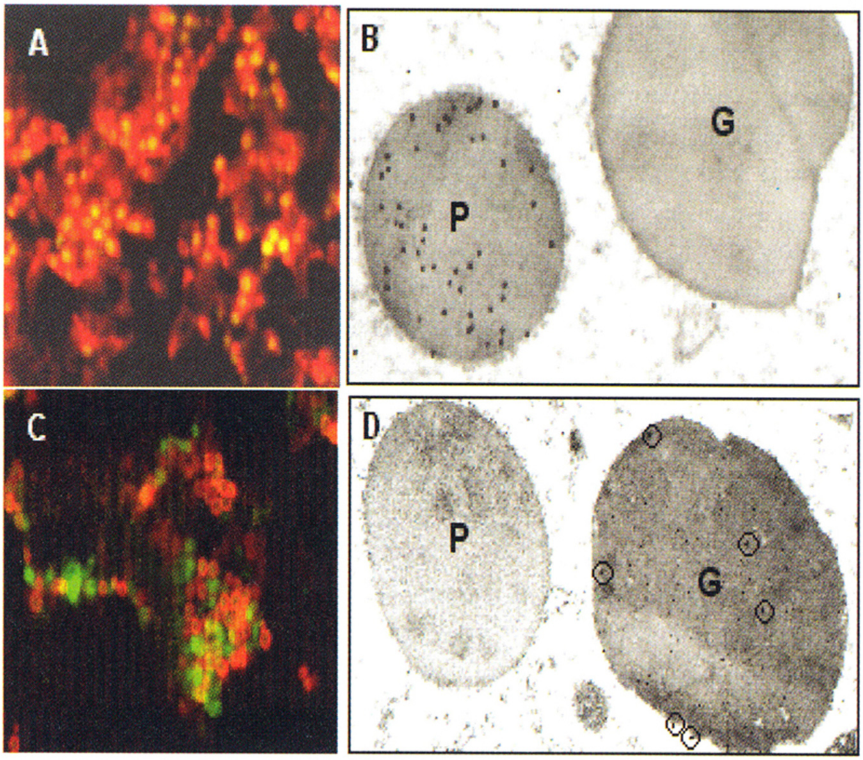


Fig. 4. Localization of d- zein RNA (panels A and C) and protein (panels B and D) in developing rice seeds. d- zein-3' nos RNA is directed to the prolamine protein bodies (PBs) (panel A) where its protein is located (P, panel B). Note the yellow circles indicating overlap between RNA (green) and prolamine PBs (red). d- zein-3' glutelin RNA is localized to the CER (note little overlap between RNA in green and prolamine PBs in red in panel C) and its proteln is observed In the glutelin protein body (G). Gold particles in panel B represent d- zein antigen. Large gold particles (circled) in panel D represent d- zein antigen while small gold particles represent glutelin antigen.

sequence, were targeted to the C-ER, suggesting that the SP sequence is required for d-zein RNA location onto prolamine PBs. Whether the SP sequence alone is sufficient for d- zein localization or whether other zip code elements in the coding sequence may also be required for efficient targeting of d- zein RNA to the PB-ER is being studied.

Recent evidence has also shown that the replacement of the prolamine 3'UTR by the glutelin 3'UTR led to the total mislocalization of rice prolamine RNA to the C-ER. As the prolamine RNA contained a single zip code in the coding sequence, this result indicates that the glutelin 3'UTR contains a zip code that directs the RNA to the C-ER with the glutelin zip code dominate over the prolamine zip code signal (unpublished data). Consistent with this view, d-zein RNA containing the glutelin 3'UTR was redirected from the PB-ER to the C-ER (Fig. 4).

d-zein polypeptide localization depends on RNA localization

Studies on the site of d - zein protein accumulation in rice endosperm cells were conducted using immunocytochemical analysis with the electron microscope. pTO164 plants expressing the d - zein coding sequence::nos 3′UTR RNA (as well as pTO173 expressing the d - zein coding sequence::prolamine 3′UTR hybrid RNA) showed that d - zein polypeptides are located exclusively within PB-I (Fig. 4). These results corresponded to the site of their RNAs, which are localized on the PB-ER. In pTO166 plants expressing the d - zein coding sequence::glutelin 3′UTR hybrid RNA, which was localized on the C-ER, the d - zein polypeptide was found to be accumulated in vacuole-derived PB-II (Fig. 4). This observation suggests that the synthesis of this hybrid RNA on the C-ER may result in the entry and transport of the newly synthesized d - zein polypeptide through the secretory pathway via Golgi bodies and ultimately accumulation in PB-II. Overall, these results support the hypothesis that mRNA localization facilitates protein targeting and localization in the secretory pathway.

Does RNA targeting link carbon and nitrogen metabolism?

As discussed in our introduction, starch (carbon) and storage protein (nitrogen) synthesis are linked by a process that remains to be identified. One possibility that may coordinate the synthesis of these two macromolecules is the cotransport of sucrose and amino acids to developing endosperm cells. The loading of these metabolites into the phloem stream, long-distance transport to the developing seeds, and their transport into the endosperm cells may be coupled. Hence, the reduction in assimilating one of these metabolites from a defect in the expression of one or more starch biosynthetic enzyme genes or storage protein genes would result in a general depression in intracellular levels of these metabolites in endosperm cells. The reduction in the synthesis of one of these macromolecules would result in the reduction of the other because of lower levels of the transported precursors.

A second possibility is that the coordination of the synthesis of these macromolecules is at the RNA level. Indeed, in several systems, localized RNAs are transported as large transport particles or granules up to 0.5-1.0 μm in diameter. The RNA transport particle is a supramacromolecular complex containing multiple RNA species as well as components of the translational apparatus (Jansen 2001). Interestingly, the storage protein RNAs are transported as large particles from the nucleus to the cortical region of the cell, which is rich in cytoskeleton. RNAs that code for nonsecretory proteins are also localized to the cortex, suggesting that this region of the cell is responsible for protein synthesis and that all RNAs have to be transported. Hence, RNAs that code for the starch biosynthetic enzymes and storage proteins may be cotransported in large transport particles whose efficient formation may depend on the interaction of these RNA types.

Conclusions

In this article, we discussed many factors that limit rice yield. We also presented our efforts to overcome the limitation of seed capacity to convert photoassimilate into starch. The expression of allosteric mutant AGPase in rice seeds resulted in an increase in sink strength, starch synthesis, and seed weight. The ability to manipulate starch synthesis was dependent on the location of the expressed AGPase. Based on our results, the cytoplasmic AGPase is the predominant form responsible for ADP-glucose formation for starch synthesis. Our recent studies on storage protein synthesis reinforce the view that mRNA localization facilitates storage protein targeting and deposition. The mechanism responsible for storage protein mRNA localization is dependent on RNA signals located on prolamine and glutelin RNA sequences. As the cortical region is the major site of protein synthesis in developing rice endosperm, RNAs must be transported from the nucleus to this destination. Hence, RNA transport may link starch and storage protein metabolism and may provide the basis for the apparent pleiotropic relationship between these two macromolecules.

References

Chen CL, Li CC, Sung JM. 1994. Carbohydrate metabolism enzymes in CO_2-enriched developing rice grains varying in grain size. Physiol. Plant. 90:79-85.

Choi SB, Wang C, Muench DG, Ozawa K, Franceschi VR, Okita TW. 2000. Messenger RNA targeting of rice seed storage proteins to specific ER subdomains. Nature 407:765-767.

Denyer K, Dunlap F, Thorbjornsen T, Keeling P, Smith AM. 1996. The major form of ADP-glucose pyrophosphorylase in maize endosperm is extra-plastidial. Plant Physiol. 112:779-785.

Giroux MJ, Shaw J, Barry G, Cobb BG, Greene T, Okita TW, Hannah LC. 1996. A single gene mutation that increases maize seed weight. Proc. Natl. Acad. Sci. USA 93:5824-5829.

Ho LC. 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. Annu. Rev. Plant Physiol. Mol. Biol. 39:355-378.

Kim WT, Li X, Okita TW. 1992. Expression of storage protein multigene families in developing rice endosperm. Plant Cell Physiol. 34:595-603.

Krishnan HB, Franceschi VR, Okita TW. 1986. Immunochemical studies on the role of the Golgi complex in protein-body formation in rice seeds. Planta 169:471-480.

Jansen JP. 2001. mRNA localization: message on the move. Nature Rev. Mol. Cell. Biol. 2:247-256.

Li X, Franceschi VR, Okita TW. 1993. Segregation of storage protein mRNAs on the rough endoplasmic reticulum membranes of rice endosperm cells. Cell 72:869-879.

Muller-Rober B, Sonnewald U, Willmitzer L. 1992. Inhibition of the ADP-glucose pyrophosphorylase in transgenic potatoes leads to sugar-storing tubers and influences tuber formation and expression of tuber storage protein genes. EMBO J. 11:1229-1238.

Nakata PA, Okita TW. 1994. Studies to enhance starch biosynthesis by manipulation of ADP-glucose pyrophosphorylase genes. In: Belnap WR, Vayda ME, Park WD, Belnap WR, Vayda ME, Park WD, editors. The molecular and cellular biology of the potato. Wallingford (UK): CAB International. p 31-44.

Nelson OE. 1982. Genetic control of polysaccharide and storage protein synthesis in endosperms of barley, maize and sorghum. In: Pomeranz Y, editor. Advances in cereal science and technology. St. Paul, Minn. (USA): American Association of Cereal Chemists. p 41-71.

Neuhaus NE, Emes MJ. 2000. Nonphotosynthetic metabolism in plastids. Annu. Rev. plant Physiol. Plant Mol. Biol. 51:111-140.

Ogawa M, Kumamaru T, Satoh H, Iwata N, Omura T, Kasai Z, Tanaka K. 1987. Purification of protein body-I of rice seed and its polypeptide composition. Plant Cell Physiol. 28: 1517-1527.

Okita TW, Nakata P, Smith-White B, Preiss J. 1993. Enhancement of plant productivity by manipulation of ADP-glucose pyrophosphorylase. In: Gustafson JP, Appels R, Raven P, editors. Gene conservation and exploitation. 20th Stadler Genetics Symposium. New York, N.Y. (USA): Plenum Press. p 161-191.

Okita TW, Rogers JC. 1996. Compartmentation of proteins in the endomembrane system of plant cells. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47:327-350.

Rowland-Bamford AJ, Baker JT, Allen LH, Bowes G. 1991. Acclimation of rice to changing atmospheric carbon dioxide concentrations. Plant Cell Environ. 14:577-583.

Rowland-Bamford AJ, Allen Jr LH, Baker JT, Boote KJ. 1990. Carbon dioxide effects on carbohydrate status and partitioning in rice. Plant Cell Environ. 14:1601-1608.

Sakulsingharoj C, Choi S-B, Okita TW. 2002. Manipulation of ADP-glucose pyrophosphorylase in starch biosynthesis during rice seed development. In: Advances in rice genetics. Proceedings of the Fourth International Rice Genetics Symposium. Los Baños (Philippines): International Rice Research Institute. (In press.)

Schaffer AA, Zamski E. 1996. Photoassimilate distribution in plants and crops: source-sink relationships. New York, N.Y. (USA): Marcel Dekker, Inc. 905 p.

Shannon JC, Pien F-M, Cao H, Liu K-C. 1998. Brittle-1, an adenylate translocator, facilitates transfer of extraplastidial synthesized ADP-glucose into amyloplasts of maize endosperms. Plant Physiol. 117:1235-1252.

Sharkey TD, Stitt M, Heineke D, Gerhardt R, Raschke K, Heldt HW. 1986. Limitation of photosynthesis by carbon metabolism. Plant Physiol. 81 : 1123-1 129.

Sikka VK, Choi S-B, Kavakli IH, Sakulsingharoj C, Gupta S, Ito H, Okita TW. 2001. Subcellular compartmentation and allosteric regulation of the rice endosperm ADP-glucose pyrophosphorylase. Plant Sci. 161:461-468.

Smidansky ED, Clancy M, Meyer FD, Laming SP, Blake NK, Talbert LE, Giroux MJ. 2002. Enhanced ADP-glucose pyrophosphorylase activity in wheat endosperm increases seed yield. Proc. Natl. Acad. Sci. USA 99:1724-1729.

Stark DM, Timmerman KP, Barry GF, Preiss J, Kishore GM. 1992. Regulation of the amount of starch in plant tissues by ADP-glucose pyrophosphorylase. Science 258:287-292.

Stitt M, Huber S, Kerr P. 1987. Control of photosynthetic sucrose formation. In: Hatch MD, Boardman NK, editors. Photosynthesis. San Diego, Calif. (USA): Academic Press. p 327-409.

Sullivan TD, Kaneko Y. 1995. The maize *brittle-1* encodes amyloplast membrane polypeptides. Planta 196:477-484.

Sullivan TD, Strelow LI, Illingworth CA, Phillips RL, Nelson OE. 1991. Analysis of maize Brittle-1 alleles and a defective *suppressor-mutator-induced* mutable allele. Plant Cell 3:1337-1348.

Sun J, Okita TW, Edwards GE. 1999. Feedback inhibition of photosynthesis in rice measured by O_2 dependent transients. Photosynth. Res. 59:187-200.

Sweetlove LJ, Burrell MM, Rees T. 1996. Starch metabolism in tubers of transgenic potato *(Solanum ruberosum)* with increased ADP-glucose pyrophosphorylase. Biochem. J. 320:493-498.

Tanaka K, Sugimoto T, Ogawa M, Kasai Z. 1980. Isolation and characterization of two types of protein bodies in the rice endosperm. Agric. Biol. Chem. 44:1633-1639.

Thorbjornsen T, Villand P, Denyer K, Olsen O-A, Smith AM. 1996. Distinct isoforms of ADP-glucose pyrophosphorylase occur inside and outside the amyloplasts in barley endosperm. Plant J. 10:243-250.

Thorne GN, Evans AF. 1964. Influence of tops and roots on net assimilation rate of sugar beet and spinach beet grafts between them. Ann. Bot. 28:499-508.

Turgeon R. 1989. The source-sink transition in leaves. Annu. Rev. Plant Physiol. 40:119-138.

Winder TL, Sun J, Okita TW, Edwards GE. 1998. Evidence for the occurrence of feedback inhibition of photosynthesis in rice. Plant Cell Physiol. 39:813-820.

Woodrow IE, Berry JA. 1988. Enzymatic regulation of photosynthetic CO_2 fixation. Annu. Rev. Plant Physiol. Mol. Biol. 39:533-594.

Yamagata H, Tanaka K. 1986. The site of synthesis and accumulation of rice storage proteins. Plant Cell Physiol. 27:135-145.

Notes

Authors' addresses: C. Sakulsingharoj, Sang-Bong Choi, S. Singh, G.E. Edwards, T.W. Okita, Institute of Biological Chemistry; C. Sakulsingharoj, current address, School of Molecular Biosciences; G.E. Edwards, School of Biological Science; Washington State University, Pullman, WA 99164-6340, USA; M. Ogawa, Department of Life Science, Yamaguchi Prefectural University, Japan; J. Preiss, J. Bork, C.R. Meyer, Department of Biochemistry, Michigan State University, East Lansing, MI 48824, USA. E-mail: okita@wsu.edu. C. Sakulsingharoj, Department of Biology, Faculty of Science, Maejo University, Sunsai, Chiang Mai, 50290, Thailand; Sang-Bong Choi, current address, Plant Genomics Research Center, Korea Research Institute of Bioscience and Biotechnology, Taejon 305-333, Korea; S. Singh, current address, Department of Agricultural Biotechnology, Assam University, Jorhat 785 013, Assam, India; C.R. Meyer, current address, Department of Chemistry and Biochemistry, California State University at Fullerton, Fullerton, CA 92631, USA.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Biofortification: the nutrition problem and ways of intervention

M.L. Wahlqvist

Human health is at the crossroads regarding demography and the food supply. Populations are at once growing in number (although not uniformly, with some in decline) and aging and food resources are being developed in often nonsustainable ways. The capacity to live longer and healthier lives, however, is never more clearly in evidence. For this to be achieved requires not only adequacy of energy intake for a population whose size may stabilize at 10 billion or so by about 2050 but also nutritional quality (nutrient- and food component-dense foods and diets) to allow good health and well-being. Global "dysnutrition" can be overcome, in part, through biofortification, whether by cultivar selection and plant breeding or by genetic modification. At the same time, the ultimate goal of food variety for all and sustainability through biodiversity is a stimulus for eco-nutritional science.

Ongoing deficits in energy intake for much of the world's population mandate an approach to poverty and hunger by way of staple foods, which are principally grains (grasses) and root vegetables (Serageldin 2002). It is generally not sustainable to contemplate animal-derived foods, meats, and fish as the principal energy source for large populations. Because of the location of human habitats and the nature of food trade, a few select grains and tubers have accounted for most population expansion (Diamond 1999, Wahlqvist 1992).

Scientific efforts have increasingly complemented these trends in the food-population relationship, most recently through molecular biology (Cantrell and Reeves 2002). The landmark publication (Kennedy 2002) of both rice genomic sequences (Goff et al 2002, Yu et al 2002) and the human genome (Venter 2001, Lander et al 2001) underscores the significance of plant foods, and rice in particular, in human development. So does the genome sequence of *Arabidopsis thaliana,* a weed linked to the cabbage and mustard family (Cantrell and Reeves 2002).

What these developments leave to examine are the nutritional quality of the plant foods on which so many depend. Indeed, there is concern that a loss of many nutritious cultivars of grains, especially rice and maize, and of tubers has been taking place. This is highly relevant to micronutrient deficiencies and to chronic diseases. Hence, a renewed interest has arisen in measuring and promoting the nutritional quality of individual foods and diets.

Biofortification through cultivar selection and breeding is an important approach to both adequacy and quality of the human diet (Welch 2002, Bouis 2002).

Food-related world health needs

Most of the world's population, the economically disadvantaged (EcDis), still suffers from nutritional deprivation, and associated infectious disease, whereas those with an adequate (or excessive) energy intake, the economically advantaged (EcAdv), may or may not have the food quality to ensure optimal health. If not, they may experience a range of so-called chronic diseases. Others, in transitional economies (EcTrans), may experience the succession of nutritional deprivation followed by relative energy excess in the one lifetime, manifesting a double burden of nutritionally related disease themselves, within their family, or within their community (Fig. 1) (Popkin et al 2001, Wahlqvist and Kouris-Blazos 2002).

While nutritional deprivation is generally and understandably thought of as a child health problem, it can have life-long effects, even when corrected in the early years, and can continue to operate to varying degrees (loss of well-being, chronic ill health, and clinically evident disease) at any age (Wahlqvist et al 1999a,b, Barker 1993a,b). More than health, it represents social deprivation (Wahlqvist 1988) and economic handicap as well (Sachs 2001).

Foods and food components: critical factors in nutrition

The concept of "nutritional quality" for food is evolving from one focused on energy or macronutrients, along with micronutrients (vitamins and minerals), to one that embraces other nutritionally beneficial components of food, especially of plant food, by way of phytochemicals not classified as essential nutrients (e.g., carotenoids, polyphenolic compounds, sulfur-containing isothiocyanates, and sulfuraphanes) (Wahlqvist and Briggs 1998).

Nutritional quality is best expressed as the amount of an essential nutrient, or other biologically advantageous food component, per unit energy of that food, that is, nutrient or food component density (ND or FCD):

$$\text{ND (or FCD)} = \frac{\text{Mass of nutrient (or food component) (e.g., mg)}}{\text{Unit energy (e.g., 100 kJ)}}$$

Phytonutrient density, PD, could be expressed in the same way.

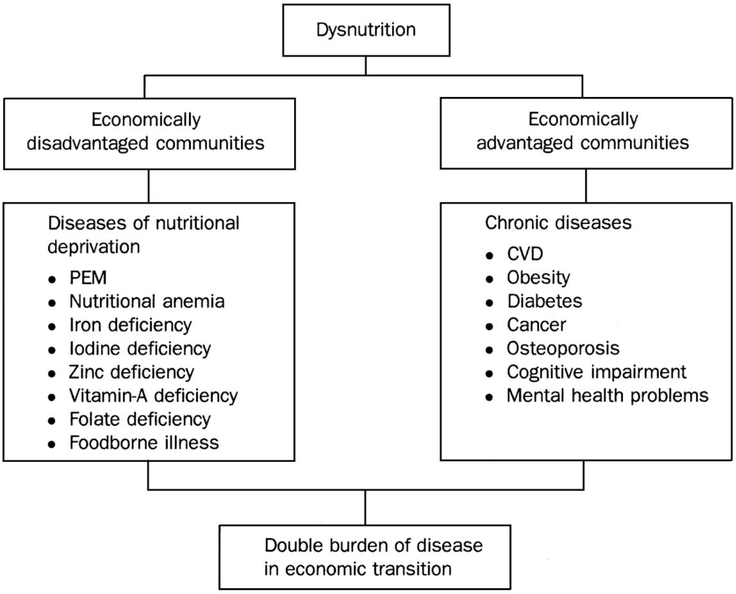


Fig. 1. Global nutritional disorders (dysnutrition).

By contrast, the energy density (ED) of a food is

$$\mathrm{ED} = \frac{\text{Energy (cal or kJ)}}{\text{Mass of food (g, kg)}}$$

The ND (or FCD) of a food can be related to the recommended intake (e.g., RDI) as the RND (recommended nutrient density) of a diet (Wahlqvist and Flint 1989, Mertz 1990, Wahlqvist et al 1998).

Phytochemicals (or phytonutrients) are increasingly recognized to play a role in disease prevention and they probably ameliorate the effects of some micronutrient deficiencies. For example, grains, fruits, vegetables, and nuts can protect against the development of CVD (cardiovascular diseases), diabetes, osteoporosis, and certain cancers and some of their sequelae (Wahlqvist 2002). They might also have a sparing effect on the requirements for certain micronutrients, such as (1) anti-inflammatory factors in certain culinary herbs, for n-3 fatty acids, and (2) antioxidant phytochemicals for vitamin C and E and for selenium.

Again, the interaction and synergy between established micronutrients can be used to advantage in food-based strategies to deal with nutritional problems, such as

(1) adjusting intakes of competitive divalent cations (Fe^{++}, Ca^{++}, Mg^{++}, Zn^{++}, Cu^{++}, etc., Nielsen 1996) and (2) ensuring adequate vitamin-A intake to ameliorate iron deficiency (Schultink and Gross 1996).

Enhancing food and its nutritional quality

There are several ways in which the nutritional utility of a food could be enhanced.

1. *Selection* in favor of a more nutrient (a food component)-equivalent food within the same commodity group, for example, for grains, wheat instead of rice since it has, overall, a superior ND, at least with currently grown cultivars; and, for root crops, colored sweet potato rather than potato because it has more carotenoid (pro-vitamin A).

   The problems with this approach are (1) agricultural feasibility, (2) cultural acceptability, (3) individual tolerance, for example, gluten sensitivity with wheat, but not rice, and (4) processing capability (e.g., to make flour or bread).
2. *Explore the range of cultivars* for nutritionally enhanced varieties. This may mean retrieving discarded cultivars from another food culture, or from a germplasm library. It requires the availability or compilation of food compositional data for many cultivars.

   This is the basis of current biofortification strategies for iron-, zinc-, and vitamin-A (carotenoid)-dense rice (Bouis 2002).

   The advantages of the strategy are many and they have been documented by Bouis et al (2002). They include bioequivalence, associated intake of complementary food components, a food-based approach, acceptability, and sustainability.
3. *Genetic modification* of an existing cultivar (GMF, genetically modified foods). The advantages of biofortification, through elite cultivar selection, have to be established for each GMF, such as Golden Rice with carotenoid enrichment (Beyer et al 2002).
4. *Fortification postharvest.* For each of the major micronutrient deficiencies (iron, iodine, zinc, vitamin A, folic acid), postharvest fortification has utility and attractive economics (Mason et al 1999, Bouis and Hunt 1999). However, some management and quality problems could allow this approach to falter.
5. *How the food is eaten.* Various changes to the food grown may influence its relevance to nutrition problem solving:
   a. Processing, for example, fermentation, as with rice (like tapai in Malaysia).
   b. Cooking, for example, lycopene bioavailability increases with cooking.
   c. With what is eaten:
      - Vitamin C (increases iron bioavailability)
      - Soy sauce may be fortified with iron (an added micronutrient source) (China) (Chen 2000)
      - Spices and condiments (may supply intrinsic and fortified components to enhance a food's nutritional value) (Nguyen 2000)

6. *Dietary diversity.* The most nutritionally sound way to ensure the adequate intake of essential and desirable food components is to achieve dietary diversity (Wahlqvist and Specht 1998, Hodgson et al 1991, 1994, Wahlqvist et al 1989, Hsu-Hage and Wahlqvist 1996, Savige et al 1997). This is because, apart from certain especially nutritious foods (liver, eggs, wheat germ, sprouts, yeast, and human breast milk in the first 6 months of life), we need a range of foods to cover the spectrum of required food components. The evidence points to at least 20, and up to 30, biologically distinct foods over the course of a week being required (Savige et al 1997). The problem is that, unless the consumer hunts and gathers, or acquires, through economic advantage and trade, or is assiduous in an urban environment to obtain a range of foods, such dietary diversity is not usually achieved. In such circumstances, recourse to nutrient-dense animal-derived foods (as above) is required, or plant foods may require fortification (biofortification or postharvest fortification).

Overcoming health problems with characterized and formulated foods

The global current and emerging health problems that may be tackled by well-characterized traditional and/or novel foods are set out in Table 1 (Wahlqvist 2000). Several of these problems could be tackled through biofortification using nutritionally enhanced cultivars and improved plant-breeding techniques.

Clinical nutrition trials (CNTs) and clinical outcomes

Randomized clinical trials are generally regarded as level 1 (highest) evidence for clinical decision-making and, to some extent, this applies to nutrition decision-making. The limitations of CNTs are

1. Only a few (usually not more than 3 or 4) variables can be tested.
2. The time frame of the CNT is limited—usually weeks or months and at the most 3-4 years.
3. It is difficult to do a double-blind study with food.
4. Food cultural considerations that may influence the outcome or extrapolation are rarely taken into account.
5. They are usually not undertaken in representative populations.

Thus, although CNTs are still important and attractive in comparing one cultivar with another, population-based data and cohort studies are also usually required for public health nutrition policy (Wahlqvist et al 1999a).

Public health outcomes

Although the essential nutrient or food component deficiencies of individuals are obviously important, the broader public health significance of endemic (and often multiple) deficiencies requires attention.

Table 1. Examining food-health relationships with food.

Health category	Food characteristics
1. Disease related to environmental degradation and methods of food production	Eco-sensitive foods (e.g., produced in sustainable ways; biodegradable or edible packaging; identifiable biosecurity for animalderived foods; nature of genetic material)
2. Food shortage and PEM (protein energy malnutrition)	Technologies that minimize postharvest loss, increase shelf life, and maintain palatability
3. Disease related to protein quality, fat quality, and micronutrient status	Nutrient-dense foods; fish or its plant or microbial food surrogates
4 Physical inactivity and health (especially overweight, also loss of lean mass, particularly muscle)	Food of low energy density and high nutrient density
5. Phytochemical-deficiency disorders including menopause, macular degeneration, osteopenia	Greater emphasis on plantderived foods and their variety
6. *Diseases of changing demography*	
Aging	Antiaging foods, especially ones to delay body compositional change (bone, muscle, and fat); loss of sensory function; decline in immune function; proneness to neoplastic disease; decline in cardio-respiratory function; decline in cognitive function; and anti-inflammatory foods
Rapid loss of traditional food culture and acquisition of new food cultures	Maintenance of traditional foods in convenient, affordable, and recognizable form
7. New psycho-social stressors and mood change	Food that favorably affects mood
8. Foodborne illness and microbiological safety of foods	Pre- and pro-biotic foods; immune-system enhancing foods
9. Illness related to chemical safety of foods (e.g., pesticide residues)	Regional origin and certification of foods

Another consideration is that there may be unintended consequences of a public health intervention, whose unfolding may take time, even years. The introduction of new crops into particular locations is illustrative of this, such as the potato, with population increase, and maize, with pellagra (Wahlqvist 1992).

Increasingly, a knowledge of the genetic predisposition of a population (and its prevalence) and its changing demography to nutritionally related disease will influence the required evidence and its management. Thus, biofortification strategies, at best, take account of population genetic polymorphisms (Stover and Garza 2002).

Risk analysis, management, and communication in biofortification

Risk science now allows increasingly good analysis of risk-benefit and cost-benefit. It can be applied when a problem is defined, in the amount of study to try to solve it, and in implementation strategies.

Most important, the community increasingly requires the opportunity to consider risk and benefit. Not to communicate this may reduce the value of the findings to the community, if, for example, unwarranted concern arises or overly confident action is taken.

Biofortification and sustainability

There will be a need to consider the short- and long-term consequences of the agricultural production of biofortified crops. Well-managed, these crops ought to contribute to optimal biodiversity and sustainability of the food supply (Wahlqvist and Specht 1998).

References

Barker DJ. 1993a. The intrauterine origins of cardiovascular disease. Acta Paediatr. Suppl. 82(suppl)391:93-99.

Barker DJ. 1993b. Maternal nutrition and cardiovascular disease. Nutr. Health 9(2):99-106.

Beyer P, Al-Babili S, Ye X, Lucca P, Schaub P, Welsch R, Potrykus I. 2002. Golden Rice: introducing the ß-carotene biosynthesis pathway into rice endosperm by genetic engineering to defeat vitamin A deficiency. J. Nutr. 132:506S-510S.

Bouis H, Hunt J. 1999. Linking food and nutrition security: past lessons and future opportunities. In: Asian development review. Studies of Asian and Pacific Economic Issues. Asian Dev. Bank 17(1&2):168-213.

Bouis HE. 2002. Plant breeding: a new tool for fighting micronutrient malnutrition. J. Nutr. 132:4918-4943.

Cantrell RP, Reeves TG. 2002. The cereal of the world's poor takes centre stage. Science 296:53.

Chen C. 2000. Plans for soy sauce fortification in the People's Republic of China. In: Manila Forum 2000: Strategies to fortify essential foods in Asia and the Pacific. Manila (Philippines): Asian Development Bank, Washington, D.C. (USA): International Life Sciences Institute, and Ottawa (Canada): Micronutrient Initiative.

Diamond J. 1999. Guns, germs, and steel: the fates of human societies. New York City (USA): W.W. Norton & Company. 480 p.

Goff SA, Ricke D, Lan T-H, et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92-100.

Hodgson JM, Hage B, Wahlqvist ML, Kouris-Blazos A, Lo CS. 1991. Development of two food variety scores as measures for the prediction of health outcomes. Proc. Nutr. Soc. Aust. 16:62-65.

Hodgson JM, Hsu-Hage BH-H, Wahlqvist ML. 1994. Food variety as a quantitative descriptor of food intake. Ecol. Food Nutr. 32:137-148.

Hsu-Hage B, Wahlqvist ML. 1996. Food variety of adult Melbourne Chinese: a case study of a population in transition. World Rev. Nutr. Diet. 79:53-69.

Kennedy D. 2002. The importance of rice. Science 296:13.

Lander ES, Linton LM, Birren B, et al. 2001. International Human Genome Sequencing Consortium: initial sequencing and analysis of the human genome. Nature 409(6822):860-921.

Mason J, Mannar V, Mock N. 1999. Controlling micronutirent deficiencies in Asia. In: Asian Development Review. Studies of Asian and Pacific Economic Issues. Asian Dev. Bank 17(1&2):66-93.

Mertz W. 1990. The role of trace elements in the aging process. In: Prinsley DM, Sandstead HH, editors. Nutrition and aging. New York (USA): Alan R. Liss Inc. p 203-228.

Nguyen TL. 2000. Condiment fortification in Viet Nam: the challenge ahead. In: Manila Forum 2000: Strategies to fortify essential foods in Asia and the Pacific. Manila (Philippines): Asian Development Bank, Washington, D.C. (USA): International Life Sciences Institute, and Ottawa (Canada): Micronutrient Initiative.

Nielsen FH. 1996. Other trace elements. In: Ziegler EE, Filer Jr. LJ, editors. Present knowledge in nutrition. Seventh edition. Washington, D.C. (USA): ILSI Press. p 353-377.

Popkin B, Horton S, Kim S. 2001. The nutrition transition and prevention of diet-related chronic diseases in Asia and the Pacific. Manila (Philippines): Asian Development Bank.

Sachs J. 200 I. Macroeconomics and health: investing in health for economic development. Geneva (Switzerland): World Health Organization.

Savige GS, Hsu-Hage B, Wahlqvist ML. 1997. Food variety as nutritional therapy. Curr. Therapeutics March:57-67.

Schultink W, Gross W. 1996. The influence of vitamin A on iron status and possible consequences for micronutrient deficiency alleviation programs. In: Micronutrient interactions: impact on child health and nutrition. Washington, D.C. (USA): ILSI Press.

Serageldin I. 2002. World poverty and hunger: the challenge for science. Science 296:54-58.

Stover PJ, Garza C. 2002. Considerations for long-term nutrition interventions. Asia Pacific J. Clin. Nutr. (In press.)

Venter JC, Adams MD, Myers EW, et al. 2001. The sequence of the human genome. Science 291(5507):1304-1351.

Wahlqvist ML, Briggs DR. 1998. Other biologically active substances in food. In: Mann J, Truswell AS, editors. Essentials of human nutrition. Oxford (UK): Oxford University Press. p 245-256.

Wahlqvist ML, Flint DM. 1989. Nutrition requirements and recommended dietary intakes for the elderly: vitamins. In: Horwitz A, Macfadyen DM, Munro H, Scrimshaw NS, Steen B editors. Nutrition in the elderly. World Health Organisation. New York City (USA): Oxford University Press. p 123-136.

Wahlqvist ML, Hsu-Hage BH-H, Lukito W. 1999a. Clinical trials in nutrition. Asia Pacific J. Clin. Nutr. 8(3):231-241.

Wahlqvist ML, Kouris-Blazos A, Savige GS. 1999b. Food security and the aged. In: Ogunrinade A, Oniang'o R, May J, editors. Not by bread alone: food security and governance in Africa. Toda Institute for Global Peace and Policy Research. South Africa: Witwatersrand University Press. p 206-221.

Wahlqvist ML. Kouris-Blazos A. 2002. Food and nutrition policies in the Asia-Pacific region: nutrition in transition. In: Wahlqvist ML, editor. Food and nutrition in Australasia, Asia and the Pacific. New South Wales (Australia): Allen & Unwin. p 575-598.

Wahlqvist ML, Lo CS, Myers KA. 1989. Food variety is associated with less macrovascular disease in those with type II diabetes and their healthy controls. J. Am. Coll. Nutr. 8(6):515-523.

Wahlqvist ML, Specht RL. 1998. Food variety and biodiversity: econutrition. Asia Pacific J. Clin. Nutr. 7(3/4):314-319.

Wahlqvist ML, Wattanapenpaiboon, Kouris-Blazos A, Mohandoss P, Savige GS. 1998. Dietary reference values for phytochemicals. Proc. Nutr. Soc. Aust. 22:34-40.

Wahlqvist ML. 1992. Critical nutrition events in human history. Asia Pacific J. Clin. Nutr. 1(2):101-105.

Wahlqvist ML. 1988. Social activity and food. In: Santich B, Symons M, editors. Proceedings of the Third Symposium of Australian Gastronomy, Melbourne, 8-10 March 1987. p 130-135.

Wahlqvist ML. 2000. Principles for safety and efficacy in the development of novel and functional foods. Scand. J. Nutr. 44:128-129.

Wahlqvist ML. 2002. Food and nutrition in Australasia, Asia and the Pacific. New South Wales (Australia): Allen & Unwin.

Welch RM. 2002. Breeding strategies for biofortified staple plant foods to reduce micronutrient malnutrition globally. J. Nutr. 132:495S-499S.

Yu J, Hu S, Wang J, et al. 2002. A draft sequence of the rice genome *(Oryza sativa* L. ssp. *indica*). Science 296:79-92.

Notes

Author's address: President, International Union of Nutritional Sciences, and professor, Asia Pacific Health & Nutrition Centre, Monash Asia Institute, PO Box 11A, Monash University, Melbourne, Victoria 3800, Australia, fax: 61-3-9905 8146, email: mark.wahlqvist @adm.monash.edu.au.

Citation: Mew Tw, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Micronutrient-dense rice: developing breeding tools at IRRI

G.B. Gregorio and Tin Htut

The nutritional quality of rice can be improved by a breeding approach. Initial evaluations have shown that some rice varieties have high Fe, Zn, and other micronutrient in their edible portion. The genetic mechanisms of grain mineral density (GMD) to determine the best selection technique were studied. A complete diallel population was developed using nine rice varieties with varying GMD. The diallel population was planted in a randomized complete block design in the IRRI field and the grain Ca, Cu, Fe, K, Mg, Mn, P, S, and Zn contents were analyzed. Combining ability analysis showed a highly significant general combining ability (GCA), specific combining ability (SCA), and reciprocal mean square for all GMD. Rice varieties with a positive GCA effect for most of the GMD were the micronutrient-dense parents. All commercial varieties showed a negative combining ability for GMD. The size of the GCA effect of a parent varies, depending on the mineral element. A differential SCA effect of crosses across mineral elements and highly significant positive correlation coefficients among SCA effects of the crosses on grain Fe, Zn, Mg, P, K, and S were observed. However, there were significant negative correlation coefficients between the SCA effect on grain Ca and other minerals such as Mg, Mn, P, S, and Zn. Similarly, the SCA effect on grain Mn showed a negative correlation effect on grain Cu, Fe, K, Mg, Mn, P, S, and Zn. This suggests that selection of parents to breed for enhancing the overall GMD based on GCA and SCA should be applied with caution. This genetic study showed the complexity of the mode of inheritance of GMD, demonstrating the role of additive and dominant gene action and environmental effects. Breeding strategies were developed based on these genetic findings.

Three important quantitative trait loci (QTLs) were detected for the high-Fe trait and these are located on chromosomes 7, 8, and 9, explaining 30.3%, 21.3%, and 19.0%, respectively, of phenotypic variation. The use of biotechnological tools such as the molecular marker-assisted selection approach will significantly increase the prospects of breeding to improve the Fe concentration of rice.

The prevalence of micronutrient malnutrition is alarming, especially among people in developing countries. The World Health Organization (WHO) estimated that 3.7 billion people worldwide suffer from micronutrient malnutrition (WHO 1999). An accelerated rate of widespread micronutrient malnutrition is observed among children and women of child-bearing age whose staple food is rice (ACC/SCN 1992). Among micronutrients, Fe, Zn, Ca, iodine, and vitamin A are seriously deficient among many people. Deterioration of the quality of life of humans because of the deficiency of these micronutrients is well documented throughout medical literature. If these micronutrients could be incorporated through breeding in a staple food crop such as rice, expenditures for a micronutrient intervention program could decrease markedly. Although rice is not considered to be a major mineral supplier, any increase in its mineral concentration could help significantly reduce the iron- and zinc-deficiency problem.

Breeding can improve the nutritional quality of crops. The philosophy of breeding for nutritional improvement has been developed and is well perceived. However, an important requirement is that improved varieties with nutritional characteristics must meet farmers' agronomic criteria. When increasing micronutrients such as iron and zinc in the grain, improvement of both nutritional characters and agronomic criteria should be concurrent. A high micronutrient concentration in the seed will certainly permit rapid crop establishment, especially in nutrient-deficient soil. The seed is the main mineral nutrient source for seedlings and the seed iron concentration is high in plants adapted to soils that are low in available iron.

The success of any breeding program depends greatly on the genetics of plant traits—understandingthe nature of combining ability among donor parents and recipient parent germplasm and consequently developing appropriate breeding strategies. So far, only limited information is available for such study in rice. Therefore, it is essential to investigate the combining ability of modern rice varieties and donor rice germplasm to establish breeding strategies to enhance grain mineral density for human nutrition.

Genetic analysis of micronutrient-dense traits

Knowing the genetic action of a trait will help identify the best breeding strategy to effectively incorporate the trait of interest into the recipient plant. A nine-parent diallel population was developed by crossing nine parental rice varieties in all possible combinations. The parental rice varieties involved were Azucena, Basmati 370, BG-300, IR64, IR68144, IR72, IR74, Madukhar, and Xua Bue Nuo. Azucena, Basmati, Madukhar, and Xua Bue Nuo were selected as donor rice varieties for their higher grain Fe and Zn density according to preliminary germplasm screening conducted at the International Rice Research Institute. The 72 F_1s and 9 parental genotypes were evaluated at the IRRI experimental farm with three replications. Dehulled brown rice was analyzed for micronutrient density using inductively coupled plasma-atomic emission spectrometry (ICP-AES). Combining ability analysis was performed according to Griffing's (1956) model-1, method-3.

Results showed highly significant variations among 72 crosses for grain Fe, Zn, Ca, Mg, Cu, Mn, P, S, and K density (Table 1). When variation among the crosses was partitioned into general combining ability (GCA), specific combining ability (SCA), and reciprocal sums of squares, highly significant GCA, SCA, and reciprocal mean squares for all grain mineral densities (GMDs) were observed.

The GCA effects of the parental rice varieties were both positive and negative for all GMDs. Parental rice varieties Azucena, Basmati 370, IR68144, Madukhar, and Xua Bue Nuo had a positive GCA effect for most GMDs. This suggested that donor parental rice varieties could transfer the high GMD to the next generation. All commercial high-yielding rice varieties showed negative combining ability for GMD, suggesting that these parental rice varieties did not contribute higher mineral density traits to the next generation. However, because of the highly significant SCA mean square, some crosses between donor parents and commercial rice varieties are expected to be promising breeding materials. Among donor parents, Xua Bue Nuo showed the largest GCA effect on grain Fe density, followed by Madukhar and Azucena. New highly mineral-dense line IR68144 showed a larger GCA than Basmati 370. Generally, the size of the GCA effect of a parent varied according to the mineral element. For instance, Xua Bue Nuo showed the lowest GCA effect for grain Zn density, whereas Madukhar showed the largest GCA effect and Azucena the second-largest GCA effect. However, for grain Ca density, Xua Bue Nuo showed the third-largest GCA, whereas Azucena showed the largest negative GCA effect. Similar phenomena were also true for other parents and mineral elements. Therefore, the association of GCA effects of the parents on nine mineral nutrients needed to be examined.

Generally, high correlation coefficients among GCA effects on some mineral densities were observed. However, the GCA effects of the parents on certain mineral densities showed a low correlation and were statistically nonsignificant, for instance, the GCA effects of the parents on grain Fe and Zn, with Ca density showing low correlation coefficients. Similarly, the GCA effects of the parental rice varieties on grain Mn and other grain minerals showed low correlation coefficients. This suggested that parental selection to breed for enhancing GMD based on the GCA could not be applied for enhancing overall mineral concentration of the rice grain, perhaps because the parental rice varieties were originally selected for high Fe and Zn only. Therefore, caution should be taken in selecting parental rice varieties based on only a few mineral nutrients to not upset the biological ratio of nutritionally important grain minerals in future rice varieties. Therefore, further breeding for enhancing grain mineral elements should aim at optimizing the mineral elements important for human nutrition or using selection strategies for multiple traits needed for enhancing GMD. That would call for more collaboration between nutritionists and plant breeders.

A differential SCA effect of crosses across mineral element was observed. For grain Fe, Zn, Mg, P, S, and K, IR68144 × Madukhar, Azucena × Basmati 370, Basmati 370 × Xua Bue Nuo, and Azucena x Madukhar showed large SCA effects. However, these crosses did not show a large SCA effect on grain Ca. Therefore, it was necessary to examine the correlations among SCA effects on grain minerals. Highly significant

Table 1. Analysis of variance for rice grain mineral density of a 9 × 9 diallel population according to model-1, method3 of Griffing (1956).

Source[a]	df[b]	Mean square				
		Fe	Zn	Ca	Mg	Cu
Rep	2	1.53 ns	8.2 ns	352.0**	15,468.5*	0.08 ns
Crosses	71	18.13**	188.3**	324.1**	90,821.0**	1.60**
GCA	8	97.53**	941.7**	2,101.1**	429,487.6**	7.80**
SCA	27	16.55**	190.3**	130.0**	99,656.2**	0.87**
Reciprocal	36	1.68*	19.3**	74.9**	8,935.3**	0.77*
Error	142	1.03	3.6	25.8	4,393.0	0.46

Source[a]	df[b]	Mean square			
		Mn	P	S	K
Rep	2	10.2 ns	9,595 ns	3,273 ns	328,692 ns
Crosses	71	94.8**	1,030,021**	70,143**	281,390**
GCA	8	627.4**	5,461,346**	294,795**	1,511.549**
SCA	27	38.7**	963,051**	85,219**	238,042**
Reciprocal	36	18.5**	95,509**	8,913**	40,532*
Error	142	5.4	7,024	4,334	23,128

[a] GCA = general combining ability, SCA = specific combining ability. [b] df = degrees of freedom. * = significant at the 5% probability level, ** = significant at the 1% probability level.

and large positive correlation coefficients among SCA effects of the crosses on grain Fe, Zn, Mg, P, K, and S were observed. However, significant negative correlation coefficients were observed between the SCA effect on grain Ca and other minerals such as Mg, Mn, P, S, and Zn. Similarly, the SCA effect on grain Mn showed a negative correlation effect on grain Cu, Fe, K, Mg, Mn, P, S, and Zn. Therefore, selection of particular crosses for some GMDs would have a negative effect on other grain minerals. Therefore, selection based on SCA should be done on the most nutritionally limited grain minerals on the condition that negative consequences on other nutrients would not alter either the human or plant nutritional requirement. Alternatively, selection should be based on all traits involving GMD. In fact, correlation among GCA effects of the parents and SCA effects of the crosses on nine mineral densities could be considered as genotypic Correlation; thus, this relationship can still be modified by the environment or a cancellation between GCA and SCA effects. It was clear that the phenotypic correlation among the mean density of each mineral nutrient based on F_1s and reciprocal F_1s showed no negative relationship, suggesting some cancellation effect of GCA and SCA or environment. According to SCA values, there were interesting crosses between/among commercial rice varieties and traditional donor rice varieties whose SCA effects were relatively large. These crosses were IR64 × Xua Bue Nuo, IR72 × Madukhar, IR68144 × IR72, IR64 × IR74, and IR64 × IR72. However, selections based on SCA alone cannot guarantee higher GMD because the SCA was composed of dominance and some type of epistasis components. Therefore, primary selection should be done based on GCA and then on SCA for better parental combination coupled with their mean performance. Although there were significant reciprocal effects on GMD traits, this was considered unimportant because the size of the reciprocal mean square was relatively smaller than the GCA and SCA effects.

Based on the inheritance study, selection during breeding should be undertaken in a later generation (such as F_5), when the dominance effect (unfixable genes) is not present. A bulk breeding method is suggested in early generations, during which selection for other agronomic characteristics should be undertaken—without selection yet for the high-Fe trait. An alternative method that might work well is single-seed descent using the F_5 generation. Because of the influence of environment and cultural practices in determining Fe concentration, selection should be done in an optimum environment such as application of N and P to maximize genetic variability (Gregorio et al 2000).

A genetic study revealed that the high-iron trait is heritable and has a maternal effect (Table 2). These results suggest that high-iron donors such as Basmati 370 and Xua Bue Nuo should be used as females in the crossing program to obtain progenies with higher Fe rather than using them as males.

Grain Fe analysis of selected F_1 crosses showed very high iron (Table 3), suggesting the high potential of these crosses to produce higher iron and zinc than their donor parents. High-Fe donors Milagrosa (17 mg kg^{-1} Fe) and Banjaiman (21.3 mg kg^{-1} Fe) were able to transfer their desirable traits to their progenies and some

Table 2. Reciprocal effect on grain Fe density of four selected rice varieties.

Female	Male	Fe density (ppm)
Basmati 370	Basmati 370	18.31
	IR64	17.02
	IR72	19.30
Xua Bue Nuo	Xua Bue Nuo	14.32
	IR64	14.78
	iR72	14.52
IR64	IR64	12.37
	Basmati 370	16.47
	Xua Bue Nuo	15.43
iR72	IR72	12.00
	Basmati 370	14.40
	Xua Bue Nuo	16.20

Table 3. Promising breeding populations for iron-dense rice.

F_2	Parentage	Fe (mg k^{-1})
IR71927	Pulot G/Milagrosa	18.5
IR71928	Fuji/Milagrosa	19.3
IR71929	Hayayuki/Milagrosa	23.2
IR71930	IR62446/Milagrosa	17.4
IR71931	Jimbyeo/Milagrosa	19.0
IR71932	Koshikihari/Milagrosa	19.1
IR72482	Banjaiman/iR62446	19.5
IR72483	Banjaiman/iR61356	17.0
IR72486	Banjaiman/Koshikihari	17.3
IR72508	Tong Lang Momi/IR8866	19.6
IR72509	Tong Lang Momi/IR61640	16.9
	Banjaiman	21.3
	Milagrosa	17.0

crosses had an even higher Fe than the highest parent. These breeding populations are now in the F_6-F_7 generation and will be analyzed for micronutrient.

More than 100 crosses were produced and advanced in the IRRI breeding nurseries. Early generation selection was done for yield, good plant type, and resistance to diseases, but no selection was done for high micronutrient till the later generation, F_6 or F_7. The aim in this breeding program is to develop high-yielding adaptable varieties with enhanced Fe and Zn in the grain.

Table 4. Mapping populations available for high-micronutrient traits in rice grain.

Trait/cross	Mapping status[a]	No. of markers
High Fe in grain		
IR64/Azucena	Mapped RRP/RAPD	175
IR74/Jalmagna	ARP map available	201
IR1552/Azucena	ARP/RRP map available	207
High zinc in grain		
IR26/Madhukar	Mapping in progress	

[a] RFLP = restriction fragment length polymorphism, RAPD = random amplified polymorphic DNA, AFLP = amplified fragment length polymorphism.

Mapping and genetics of the high-Fe trait in the grain

Rapid and cheaper means of selecting efficient micronutrient loading in the grain are urgently needed. Breeding programs for complex traits were usually delayed primarily because of the slow detection of segregants in breeding populations. The advent of the molecular marker technique provided greater prospects for doing precise breeding for such complex traits. A previously genotyped rice population was used to tag the genes (QTLs) for the high-Fe trait in the grain. A total of 180 polymorphic markers (including 146 restriction fragment length polymorphism, RFLP, 8 isozymes, 14 random amplified polymorphic DNA, RAPD, and 12 cloned genes) on a linkage map of doubled-haploid-derived lines from the cross IR64 and Azucena (Huang et al 1997) were analyzed to map the genes/QTLs for high-Fe traits and aroma in the grain. The population was phenotyped for Fe concentration in the grain and analyzed together with the molecular markers available. Three important QTLs were detected for the high-Fe trait. These were located on chromosomes 7, 8, and 9, with 30.3%, 21.3%, and 19.0% phenotypic variation, respectively. Three QTLs were identified for aroma. These were located on chromosomes 5, 7, and 8, with 16.4% to 38.3% variation. Two QTLs for the high-Fe trait and aroma were common on two chromosomes (7 and 8), but on different loci, with 24.8 and 36.4 cM between the QTLs, respectively. This indicates a linkage between aroma and the high-Fe trait.

Permanent mapping populations of F_8 recombinant inbred lines (RIL) were developed to map for high-Fe and -Zn traits (Table 4). These populations were also used to map for tolerance of other abiotic stresses such as Al toxicity, Zn deficiency, and excess water. Mapping the genes is an important component in developing polymerase chain reaction (PCR)-based marker-assisted selection (MAS) for any trait of interest.

This MAS technique is rapid, highly reliable, and less expensive. Analyses of samples can be done with a small portion of the leaf as early as the 2-week seedling stage for a cost of only US$2 per sample. This is highly reliable because the environment does not affect molecular markers. For ICP-AES, plants must be in the mature stage of 130 days to produce seeds. Seeds are processed, dehulled, and ground before they are analyzed. Analysis costs approximately $11 per sample, excluding processing. For less cost, MAS can also be used to select two to three traits at a time. This new technique will significantly increase the prospects of breeding to improve the nutritional value of rice.

References

ACC/SCN. 1992. Second report on the world nutrition situation. Vol. 1. Global and regional results. Geneva (Switzerland).

Gregorio GB, Senadhira D, Htut T, Graham RD. 2000. Breeding for trace mineral density in rice. Food Nutr. Bull. 21:382-386.

Griffing B. 1956. Concepts of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9:463-493.

Huang N, Parco A, Mew TW, Magpantay G, McCouch SR, Guiderdoni E, Xu J, Subudhi P, Angeles ER, Khush GS. 1997. RFLP mapping of isozymes, RAPD and QTLs for grain shape and brown planthopper resistance in a doubled haploid rice population. Mol. Breed. 3:1-8.

WHO (World Health Organization). 1999. www.who.int/nut/malnutition/worldwide.htm.

Notes

Authors' address: Plant Breeding, Genetics, and Biochemistry Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Golden Rice: concept, development, and its availability to developing countries

I. Potrykus

The "Golden Rice" project was, from the beginning, conceived as a humanitarian project with the idea of exploring genetic engineering technology for its potential to contribute to a reduction in vitamin-A malnutrition in developing countries by complementing traditional interventions. To achieve this goal, a series of challenges had to be met, extending far beyond normal scientific concepts. To be able to transfer the technology, in case of success, free of charge and limitations, care was taken to carry out the project within the public domain and with public funding only. The scientific challenge—to engineer the biochemical pathway into rice endosperm—was considered unfeasible for numerous good reasons and Golden Rice became finally possible only thanks to the coincidence of uncommon circumstances: (1) a most fruitful collaboration between two research teams with complementing expertise–that of Professor Peter Beyer, Freiburg, Germany, and that of the author. P. Beyer contributed the necessary scientific expertise and the author the engineering skills and determination to carry the project through against better knowledge; (2) long-term stable funding, from the Swiss Federal Institute of Technology and from The Rockefeller Foundation; and (3) good fortune with the underlying biology of the rice endosperm and the final choice of the transgenes. Golden Rice—accumulating provitamin A in the endosperm to concentrations that may be sufficient to prevent vitamin-A deficiency on the basis of a daily diet of 200 g of rice—is now available with "freedom-to-operate" for "humanitarian projects," defined as income below $10,000, in collaboration with bona fide public research institutions in developing countries, thanks to the generous donation of free licenses from the ag-biotech industry. It will be made available to resource-poor farmers free of charge for the trait as soon as appropriate local varieties have been developed and have received "deregulation" from the national bioregulatory authorities. The humanitarian "Golden Rice" project is guided across all the numerous genetically modified organism-specific hurdles by a Humanitarian Board and is further advanced to local varieties within an international Golden Rice Network involving public rice research institutions in the major rice-consuming countries. Financial support for the project comes from national governments and is attracted on

a case-by-case basis, and, where necessary, from international altruistic organizations.

Malnutrition disorders are the cause of 24,000 deaths per day. “Golden Rice” represents a genetic engineering concept for the development of nutrient-dense staple crops as a contribution to the reduction of malnutrition in developing countries. Major micronutrient-deficiency disorders concern protein/energy, iron/zinc, vitamin A, and iodine. These deficiencies are especially severe where rice is the major staple. Traditional interventions such as distribution, fortification, dietary diversification, and measures against infectious diseases are very helpful in reducing deficiency disorders, but they have not solved, and probably cannot solve, the problem. Statistics clearly demonstrate that, despite enormous efforts in support of these traditional interventions, the world still has about 2.4 billion iron-deficient women and children and 400 million vitamin-A-deficient children per year. Approaches toward nutrient-dense staple crops, such as biofortification, offer an alternative and sustainable opportunity to complement traditional interventions. Genetic engineering has the potential to substantially enhance breeding for nutrient-dense staple crop varieties and, most importantly, to enable the introduction of traits that are not accessible to traditional breeding.

The scientific challenge

Protein deficiency relates to both the amount and the quality—the content in essential amino acids—of dietary protein. Rice is rich in carbohydrates (energy), but low in protein (and vitamins and minerals) and provides, with a typical daily diet of 300 g, only about 10% of the required essential amino acids. Genetic engineering of an ideal balanced mixture of the missing nine essential amino acids isoleucine, leucine, lysine, methyonine, cysteine, phenylalanine, tyrosine, threonine, tryptophane, and valine is beyond our technical possibilities to date. However, the synthetic gene *Asp-1,* developed by Jesse Jaynes in Raleigh, North Carolina, and coding for an “ideal” high-quality storage protein (providing a balanced mixture of all nine essential amino acids), offered a unique opportunity to approach this otherwise unfeasible task. It was, however, completely unpredictable whether the rice endosperm would provide the necessary biochemical background for the synthesis and assembly of such a protein with the information provided and acted upon. To test this question, the *Asp-1* gene was placed under endosperm-specific control and linked to an appropriate target sequence for import into the endosperm protein storage vesicles and transformed into rice (japonica TP309). Surprisingly and fortunately, the *Asp-1* transgenic rice plants recovered accumulated Asp-1 protein in their endosperm to a range of concentrations, thus (hopefully) providing the balanced mixture of the essential amino acids required. Detailed biochemical analysis has to verify these preliminary data, based so far on Southern and western analysis only. The analysis also has to determine whether the concentrations achieved are nutritionally relevant.

Iron deficiency caused by a rice diet is the consequence of (1) far too low amounts in rice of iron, (2) the presence of an extremely potent inhibitor of iron resorption (phytate), and (3) the lack of any iron resorption-enhancing factors in a vegetative diet. Our genetic engineering task for the endosperm was therefore (1) to increase iron content, (2) to reduce the inhibitor, and (3) to add resorption-enhancing factors. Transgenic ferritin (from *Phaseolus vulgaris*) so far increased the iron content by twofold, a transgenic metallothionin (from *Oryza sativa*) led to a sevenfold increase in an iron resorption-enhancing cysteine-rich polypeptide, and a transgene coding for a heat-stable phytase (from *Aspergillus fumigatus*) produced high inhibitor-degrading phytase activity, which, to date, however, did not maintain its heat-stability character (Lucca et al 2001). A heat-stable phytase in the apoplast would have been the ideal solution because it would not have touched the phytate-stored phosphate, which is important for germination. As this approach did not work because the enzyme could not refold when present in the cellulose mesh of the plant cell, we have developed alternative strategies and further experiments on the phytate problem are in progress.

Vitamin-A deficiency in rice-depending populations is due to the fact that milled rice is totally devoid of any provitamin A, and that these people are too poor to afford a diversified diet. The situation is especially severe where children are raised on rice gruel. To add provitamin A to rice endosperm required the engineering of a complete biochemical pathway, a task considered unfeasible throughout the course of our experiments. The final success was possible because of (1) the complementary expertise of two laboratories (Dr. P. Beyer, University of Freiburg, provided the scientific knowledge and the necessary genes, and my group was specialized in the genetic engineering of rice), (2) long-term public funding (from Swiss agencies and The Rockefeller Foundation), (3) a firm "engineering spirit" to solve the problem, and (4) "good fortune" with the biology of the rice endosperm. The introduction of transgenes for phytoene synthase (*Narcissus*), a phytoene/x-carotene double-desaturase (*Erwinia*), and lycopene cyclase (*Narcissus*), to everybody's surprise, completed the biochemical pathway leading from the latest available precursor geranyl-geranyl-pyrrhophosphate to ß-carotene—the desired provitamin A. Biochemical analysis of the polished rice kernels confirmed that the "golden" endosperm color was due to varying amounts of provitamin A and further terpenoids of dietary interest (such as lutein and zeaxanthin) (Ye et al 2000). The concentration of 1.6 $\mu g\ g^{-1}$ endosperm may, according to the calculation of an experienced vitamin-A nutritionist (Prof. Robert Russell, Boston), be sufficient to prevent vitamin-A deficiency disorders from a daily diet of 200 g of Golden Rice. Nutritional studies with human volunteers testing this hypothesis are in preparation. Conclusive data, however, will not be available before 2004. This was a surprising scientific breakthrough, however, in view of the task set, and only the beginning of a series of rather demanding and, for scientists, rather unusual hurdles.

The challenge of free donation to developing countries

The Golden Rice project had been designed from the beginning as a humanitarian project for poor people in developing countries. To reach this goal and to provide relief from malnutrition in poor populations in developing countries, this scientific success has to be passed on to subsistence farmers and the urban poor free of charge and limitations. To be in a position to give away the technology, we took care throughout the project to use public funding only. However, independent from our invention (which we could give away), the basic genetic engineering technology used to develop provitamin-A rice had to use many patented technologies. "Freedom-to-operate for humanitarian use," the necessary basis for variety development by partner institutions in developing countries, therefore became a major undertaking. The inventors solved the problem thanks to an alliance with the ag-biotech industry, based on an agreement in which the rights for commercial exploitation are transferred to the ag-biotech industry, which in turn provides free licenses for involved intellectual property rights and sublicenses the inventors for and supports the humanitarian project. The difficult problem of a definition of "humanitarian use" was solved by defining humanitarian use as "income from Golden Rice per farmer or trader in developing countries below $10,000 per annum." This definition safely includes the target population. Thanks to this agreement, the technology is now available with "freedom-to-operate'' via sub-sublicense agreements between the inventors and public research institutions for breeding, variety development, and de novo transformation. Such sub-sublicense agreements have been signed, so far, with (1) IRRI and (2) PhilRice (Philippines); (3) Cuu Long Delta Rice Research Institute (Vietnam); (4) Department of Biotechnology, Delhi, (5) DRR, Hyderabad, (6) IARI, New Delhi, (7) UDSC, New Delhi, (8) TNAU, Tamil Nadu (India); (9) Institute of Genetics, Academia Sinica, Beijing, and (10) National Key Laboratory of Crop Genetic Improvement, Wuhan (China); (11) Agency for Agricultural Research and Development, Jakarta (Indonesia); and (12) DSIR, Brumeria, Pretoria (South Africa); and are in preparation with (13) BRRI in Bangladesh. These institutions constitute the still-growing International Humanitarian Golden Rice Network.

The challenge of safe technology transfer and variety development

To ensure proper handling of the GMO material, a "Humanitarian Board" has been established to supervise the choice of partners; to support further improvement; to look over needs, availability, biosafety, and socioeconomic assessments; to coordinate the activities in the different countries; to support fund raising from public resources; to support deregulation; to facilitate the exchange of information; and to mediate information of the public and general support for the humanitarian project. Members of the board are the inventors Prof. Peter Beyer and Prof. Ingo Potrykus (chairman), Gary Toenniessen (Rockefeller Foundation), Robert Bertram (USAID), Adrian Dubock (Syngenta), William Padolina, (IRRI), Prof. Robert M. Russell (Tufts University/USDA), Howarth E. Bouis (IFPRI), Gurdev Khush (IRRI), and Katharina

Jenny (Indo-Swiss Collaboration in Biotechnology). Prof. Anatole Krattiger (Cornell University) supports the board as an executive-to-the-board. Variety development in the partner institutions is via backcrossing into, or direct transformation of, popular local varieties. Backcrossing is being done from one carefully selected single and regulatory "clean" event in the popular indica variety IR64, which also has a high combining ability. Working toward the introgression of the trait into other varieties from one carefully selected transgenic event is mandatory for the time- and money-consuming process of "deregulation," which otherwise would have to be worked through for every single transgenic event. So far, one "regulatory clean" event is available from IR64, but with a provitamin-A concentration of only 0.8 $\mu g\ g^{-1}$. This will serve as starting material for breeding within the network. As we want a concentration of 1.6 $\mu g\ g^{-1}$, however, and as data show that the site of integration can play an important role in the level of expression, further *Agrobacterium* -mediated transformation experiments will be done by network members, with a "deregulation-optimized" construct, to produce a large number of transformation events from which to choose the best event by the end of 2003.

The challenge of a radical GMO opposition and consumer accep tance

Golden Rice has, unfortunately, become a key topic in the fight between proponents and opponents of plant biotechnology in food production. A radical GMO opposition is one of the last major stumbling blocks, with the potential to prevent the poor in developing countries from benefiting from the project. Greenpeace and numerous other NGOs are determined to prevent the development and use of Golden Rice for the benefit of the poor. Their major reason for opposition, obviously, is the fact that they see Golden Rice as a kind of Trojan horse, opening the road for the application of GMO technology in developing countries. As the opposition has lost, however, with the Golden Rice case, all its standard arguments used so far (because, in reality, Golden Rice benefits the poor, not industry; it has been developed in the public domain, not by industry; it will be available for the poor free of charge and limitations; subsistence farmers can use part of their harvest for the subsequent sowings; Golden Rice cultivation does not require any additional inputs; environmentalists cannot conceive of any realistic risks to the environment; Golden Rice does not create any new dependencies, etc.) and, as the public and the media understand the moral dimension of the project, the opposition is in a difficult situation, and is therefore trying to bypass this moral dilemma by claiming that Golden Rice is useless anyhow because children have to eat 3.75 kg per day. This is, according to the following calculation by Prof. Robert M. Russell (head of the USDA Human Nutrition Research Center and professor of medicine and nutrition at Tufts University, Boston, and an expert in vitamin-A malnutrition), definitely wrong, but data to prove Dr. Russell's hypothesis, that probably 200 $g\ d^{-1}$ of Golden Rice will be sufficient, unfortunately, will be available only early in 2004 because the necessary bioavailability and nutrition studies with human volunteers will take until then.

The RDA (Recommended Daily Allowance) in the United States is 0.3 mg d^{-1} *for 1-3-year-old children, based on 4-month body stores, not on the prevention of the deficiency state. The average amount needed to prevent the deficiency state is one-half of that needed for adequate storage (0.15 mg* d^{-1} *). The conversion factor to RAE (Retinol Activity Equivalents) is for fruits and vegetables 12:1 and for ß-carotene in oil 2:1. The amount of available vitamin A depends upon bioavailability (absorption and bioconversion). Golden Rice contains 0.16 mg per 100 g of endosperm, stored in membranes (possibly most comparable to oil). Golden Rice has a simple and digestible food matrix, Assuming, therefore, a 2:1 conversion, 100 g of Golden Rice may provide 50% of the amount needed to prevent vitamin-A deficiency diseases.*

The challenge of deregulation

It is widely accepted that food derived from transgenic plants must successfully pass all the requirements set up by regulatory authorities and the Golden Rice Humanitarian Board has stated that all work in this context has to follow the highest regulatory standards. Increasingly, however, we get the impression that sticking to the existing regulatory framework may be sufficient to severely delay, or even prevent, the use of Golden Rice for a reduction in malnutrition-caused diseases in poor populations of developing countries. The regulatory framework has become so extensive, and the requirements so sophisticated, that the financial input alone required becomes rather unrealistic for a "humanitarian" project. A further severe limitation is the time factor: Golden Rice has been a reality since February 1999. Since spring 2002, the trait has been available in IR64, a popular indica rice variety grown in many developing countries. New experimental adjustments are required, however, to make Golden Rice more amenable to the regulatory procedure. All this has the consequence that exploitation of the technology is delayed for many more years. Because we are not discussing the sensitivities of well-fed European consumers, but large populations whose life and health depend on contributions to a sustainable reduction in malnutrition (causing 24,000 deaths per day), the question is justified: What level of sophistication in regulation is scientifically and morally justified, and how much of it is just the consequence of weak politicians giving in to the pressure of activists, operating extremely successfully on an emotional level? The Golden Rice Humanitarian Board is determined to perform the humanitarian project at the highest regulatory levels, but the question remains: Who is taking responsibility for delaying the use of the technology for many years because of some unidentified and hypothetical risks if the consequence is that many thousands are dying or have severe health problems (e.g., irreversible blindness), who otherwise could live a healthy and productive life? What is more important to our society—a regulatory framework for minor and mostly hypothetical risks, or the life and health of numerous underprivileged human beings? I believe that deregulation should compare risks to benefits! Probably, it is time to reevaluate the regulatory framework (at least in the context of humanitarian projects) to identify those features that are essential and meaningful, and those that are there just in response to political pressure.

The expected benefit and the risk of not using the technology

In an *ex ante* study, "Projecting the benefits of Golden Rice in the Philippines," Zimmermann and Qaim (2002) from the Center for Development Research in Bonn, Germany, tried to estimate the potential impact of the introduction of Golden Rice to the Philippines. The following is their abstract taken from their paper presented at the 6th ICABR Conference on Agricultural Biotechnology, Ravallo (Italy), July 2002:

"This paper analyzes the potential impacts of Golden Rice in the Philippines. Since the technology is still at the stage of R&D, benefits are simulated within a scenario approach. The health effects are quantified through the methodology of disability-adjusted life years (DALYs). Golden Rice will not completely eliminate the problems of vitamin-A deficiency (VAD), so it should be seen as a complement rather than a substitute for alternative interventions. Yet, the technology will reduce VAD-related health costs significantly. In monetary terms, annual gains will lie between $32 million and $152 million, depending on the underlying assumptions. Micronutrient-enriched crops are an efficient way to reduce deficiency problems among the poor, and related research projects should receive higherpolitical priority."

The costs for the scientific development of Golden Rice were in total $2.4 million. The costs for variety development for Southeast Asia (not just the Philippines) will be approximately $30 million. This investment is only necessary once! The annual gains from Golden Rice could be extrapolated to $1500-750 million for Southeast Asia—annually! And the annual costs for the "alternative intervention" of distribution of vitamin-A capsules amounts to $125 million—annually! These figures clearly support the statement in the above abstract, "that ... related projects (breeding micronutrient-enriched crops) should receive higher priority."

References

Lucca P, Hurrell R, Potrykus I. 2001. Genetic engineering approaches to improve the bioavailability and the level of iron in rice grains. Theor. Appl. Genet. 102:392-397.

Ye X, Al-Babili S, Kloti A, Zhang J, Lucca P, Beyer P, Potrykus I. 2000. Engineering the provitamin A (ß-carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. Science 287:303-305.

Zimmermann R, Qaim M. 2002. Projecting the benefits of Golden Rice in the Philippines. ZEF-Discussion Papers on Development Policy No. 51. Center for Development Research, Bonn, Germany, September 2002. 33 p.

Notes

Author's address: Professor emeritus, formerly Institute of Plant Sciences, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Improving nutritious rice: the transgenic approach at IRRI

K. Datta, N. Baisakh, M. de Vasconcelos, L. Torrizo, E. Abrigo, N. Oliva, J. Tan,
I. Meienberger, A. Senner, M. Rai, M. Khalekunaman, S. Rehana, and S.K. Datta

Malnutrition, especially vitamin-A deficiency (VAD) and iron deficiency, is a major problem in South Asia, where rice is the primary food, providing 40–60% of the total calorie intake. Hence, bioengineering rice to produce provitamin A and store high iron in the endosperm tissues is an attractive alternate strategy for alleviating these two severe problems. We at the International Rice Research Institute (IRRI) in the Philippines have developed transgenics in the background of several tropical rice cultivars suited to Bangladesh, India, Vietnam, Myanmar, the Philippines, and Indonesia that synthesize beta-carotene and have a high iron content in the seed endosperm through the biolistic approach and using either the antibiotic or nonantibiotic selection system. Molecular, biochemical, and histochemical analyses confirmed the stable integration and inheritance of all three genes— *psy, crt1,* and *lcy* — for the Parotene biosynthesis, *ferritin* iron enhancement, and *FR02* for iron uptake. The transgenics showed accumulation of beta carotene and iron in their seeds.

Until recently, much research has concentrated on attaining food security and sustainability in terms of stabilizing the yield or elevating the yield ceiling of cereal crops, especially rice, which is the principal staple food crop and the largest source of calories for more than two-thirds of the world population. However, malnutrition is a severe problem in developing countries that depend on rice for their mineral and micronutrient requirement. Among these problems, vitamin-A deficiency (VAD) and iron-deficiency anemia (IDA) are recognized as important. These affect millions of people, particularly women and children. Statistics show that around 124 million children worldwide suffer from VAD. VAD manifestations range from early night blindness symptom to corneal xerosis, keratomalacia, and total blindness in severe cases. Especially in children, VAD causes increased morbidity and mortality (Gerster 1997). In Southeast Asia, an estimated quarter of a million people go blind each year because of VAD. Diet is the only source of vitamin A since mammals cannot

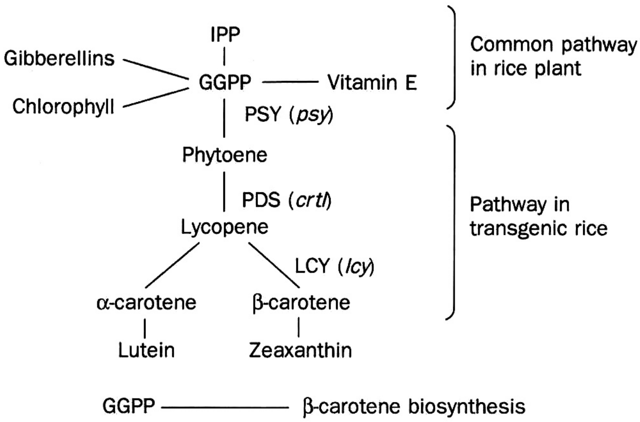


Fig. 1. Biosynthetic pathway of ß-carotene. IPP = isopentenyl diphosphate, GGPP = geranyl geranyl diphosphate, PSY = phytoene synthase, PDS = phytoene desaturase, LCY = lycopene cyclase.

manufacture it on their own. Most of the dietary vitamin A is of plant food origin in the form of provitamin A, which is converted into vitamin A in the body (Sivakumar 1998). But, rice germplasm screened so far does not possess beta-carotene in the polished seeds that are usually consumed (Tan et al, manuscript in preparation), although a trace amount is present in the brown rice. Conventional interventions such as diet diversification and fortification have been used with limited success.

Similarly, iron deficiency affects an estimated 30% of the world population. Although brown rice contains a considerable amount of iron, the removal of the outer layers by commercial milling dramatically reduces the iron level as most of the minerals are accumulated in the aleurone layers (de Vasconcelos et al 2002, Drakakai et al 2000, Doesthale et al 1979).

The unavailability of rice germplasm with ß-carotene, dearth of genotypes with high iron in the polished seeds, and less effectiveness of conventional interventions suggested the improvement of mineral and micronutrient nutrition through plant biotechnology (e.g., transgenic rice) as a more sustainable strategy to combat nutrition deficiencies in human populations (Zimmerman and Hurrel 2002).

Through transgenesis, the first "golden rice" was developed in japonica rice cultivar T-309, with a characteristic yellow color in the endosperm producing p-carotene (Ye et al 2000). This was a landmark in the proof-of-concept of installing a complete functional metabolic pathway for beta-carotene biosynthesis that involves mainly three key enzymes (phytoene synthase, PSY phytoene desaturase, PDS; and lycopene cyclase, LCY) (Fig. 1). Likewise, high-iron transgenic rice cv. T-309 was developed with ferritin, an iron-storage protein (Goto et al 1999) that takes up iron, stores it in a nontoxic and bioavailable form, and releases it when needed for metabolic functions. The transgenic technology would be more beneficial if it were extended to the indica rice cultivars consumed by 90% of the Asian population because these

Table 1. Transgenic rice obtained from eco-geographically diverse indica genotypes with ß-carotene biosynthesis genes.[a]

Cultivars/ genotypes	Genes of interest	Selectable marker gene	Number of plants regenerated[a]	Transgenics (PCR/Southern)
IR64	*psy, crtl, lcy*	Pmi	60	54
	psy, crtl	Hpt	36	1
	crtl	Hpt	106	34
IR68144	*psy, crtl, lcy*	Pmi	300	61
BR29	*Psy, crtl, lcy*	Pmi	155	48
	psy, crtl, lcy	Hpt	759	396
	psy, crtl	Hpt		12
	lcy	Hpt		20
Nang Hong Cho Dao	*psy, crtl, lcy*	Hpt	15	3
Mot Bui	*psy, crtl, lcy*	Hpt	13	2
Immyeobaw	*psy, crtl, lcy*	Hpt	30	1
IR68899B	*Psy, crtl, lcy*	Hpt	15	7

[a] All transformation was done using the biolistic system. *Agrobacterium* - mediated transformation is in progress.

are adapted to different agroecological zones of several tropical Asian countries (Khush 2001). Moreover, this technology would directly serve the need of the farmers in a specific ecosystem by saving time and labor and avoiding the sterility problems often associated with conventional breeding involving indica × japonica crosses. Furthermore, the functional expression of the genes in question in the recipient line may not be the same as in the donor line.

Here, we report the progress in transgenic research at the International Rice Research Institute (IRRI), Philippines, for the development of "golden indica rice" and "high-iron indica rice" with an objective of alleviating VAD and IDA.

Development of golden indica rice

Several indica cultivars (Table 1) were used to develop golden indica rice through the biolistic method of transformation.

The plasmid vectors used were pBaal3 carrying the daffodil phytoene synthase *(psy)* gene under the control of an endosperm-specific Gt1 promoter and a bacterial phytoene desaturase *(crtI)* gene fused to a transit peptide sequence of the pea-Rubisco small subunit to direct the expression of this bacterial gene into the plastids driven by the constitutive 35S promoter (Ye et al 2000). The plasmid pTCL6 carried lycopene ß-cyclase *(lcy)* cDNA of daffodil under the control of the 35S promoter and nopaline synthase terminator. For the selectable marker gene, either plasmid pNOV2820 that carried the phosphomannose isomerase gene driven by a constitutive cestrum promoter of yellow leaf curling virus (Syngenta International Patent Application #WO 01/

73087 A1) or plasmid pGL2 with the *hph* gene for hygromycin phosphotransferase under the CaMV 35S promoter was used (Datta K et al 2002b, Datta SK et al 1990).

Transformation, regeneration of putative transformants, transfer to containment facilities, molecular analyses (PCR, Southern, RT-PCR), and biochemical analyses were done following methods described earlier (Datta SK et al 1997, Datta K et al 2002a, Baisakh et al 2001).

Carotenoid extracted from 1 g of polished seeds with acetone was quantified with the spectrophotometer at A_{max} 470 nm. Twenty µL of extract of carotenoid were applied to the high-performance liquid chromatograph (HPLC) under the run conditions modified after Ye et al 2000 (Tan et al, manuscript in preparation). The total carotenoid (µg g^{-1}) was calculated based on the spectrophotometer reading, taking the dilution factor and extinction coefficient (134.5) into account. The amount of ß-carotene was estimated based on the percentage coverage of its peak area with respect to the total area of carotenoids.

More than 600 primary transgenic rice plants were produced from independent calli resistant to mannose and the hygromycin selection agent (Datta et al 2002b; Table 1). The primary transformants were initially screened by polymerase chain reaction (PCR) analysis and were then confirmed by Southern blot analysis (data not shown). The transgenics contained one to more than 10 copies of the individual transgenes analyzed with the use of restriction enzymes that cut once in the coding region. Apart from the expected size bands corresponding to the transgenes, many transgenics carried rearranged copies of the three genes.

In the subsequent selfing generation (T_1) for most of the progenies of independent transgenics, the transgenes were inherited in a 3:1 segregation ratio, indicating their single Mendelian locus integration. But in some cases the segregation ratio was variable, thereby confirming the fact that the transgenes were inserted into more than one locus. This was further evidenced from the variable banding pattern of the transgenes among the progenies of a single parental line. However, in most cases, the transgenes (at least one copy from the three) were clustered at a single site, as was seen from their cosegregation. Such variable segregation and integration pattern are not uncommon in the biolistic method (Baisakh et al 1999). The transgenics were advanced to a further generation for the development of homozygous lines.

Reverse transcription–polymerase chain reaction (RT-PCR) and Coomassie brilliant blue staining analyses showed the expression of the transgenes at both the mRNA and protein level. Furthermore, as expected, the yellow color of polished mature seeds from individual transgenic lines confirmed the accumulation of ß-carotene in the transgenic lines (Fig. 2), which was absent in the endosperm of the control seed. The variation in the yellow color intensity of the endosperm seemed to indicate the variation in the level of carotenoid formation and accumulation among individual lines of different cultivars. Similarly, the localization of the beta-carotene in the endosperm of transgenic grains was observed by a characteristic blue color of the thin microtome sections when treated with Carr-Price reagent under acidic conditions, whereas the color was not found in the sections of nontransgenic grains (Krishnan et al 2002).

Fig. 2. Polished seeds of homozygous transgenic golden indica rice cv. IR64 showing yellow color of the endosperm (right) compared with the white endosperm of the nontransgenic control rice (left).

Spectrophotometry and HPLC analyses of the carotenoid extract from polished seeds or the endosperm from individual lines showed the quantitative and qualitative assessment of ß-carotene and other xanthophylls. Estimation of carotenoids from yellow seeds showed the total carotenoid level ranging from 0.297 to 1.05 µg g^{-1}. Some of the lines even having all three genes integrated in the genome did not accumulate a detectable amount of carotenoid. But some transgenics carrying only the *psy* and *crt1* genes accumulated beta-carotene as had been found earlier by Ye et al (2000). This could be due to either feedback regulation originating from carotene intermediates and activation of endogenous carotenoid biosynthesis genes or to the constitutive expression of downstream carotenoid biosynthetic enzymes in rice endosperm such as lycopene cyclase. Moreover, in our studies, we found out that the transgenics having more copies of the transgenes accumulated higher ß-carotene in the endosperm than the ones having single or low-copy numbers. This could be the case in the metabolic biosynthetic pathway. This is substantiated by an earlier report that the dosage effect because of higher copy numbers leads to high expression (Hobbs et al 1993). However, more detailed comprehensive studies would give a better understanding in this regard.

After we found the effect of cooking on carotenoid level, we cooked polished homozygous seeds of transgenic IR64 for 10 to 15 min and, as seen from the chromatograms (Fig. 3), the total carotenoid content decreased by about 10% in the cooked grains compared with the noncooked rice. The ß-carotene (provitamin A; BC) level was not affected much by the cooking process, but a major fraction of lutein (L)/zeaxanthin (Z) not possessing provitamin-A activity as well as some cryptoxanthin (C) was lost. Studies are under way to determine the effect of other factors such as time and conditions of storage, time of milling, etc., on the carotenoid profile.

Most transgenics (more than 90% of the plants) were normal in their morpho-agronomic characters, with normal seed setting like that of the wild-type plants.

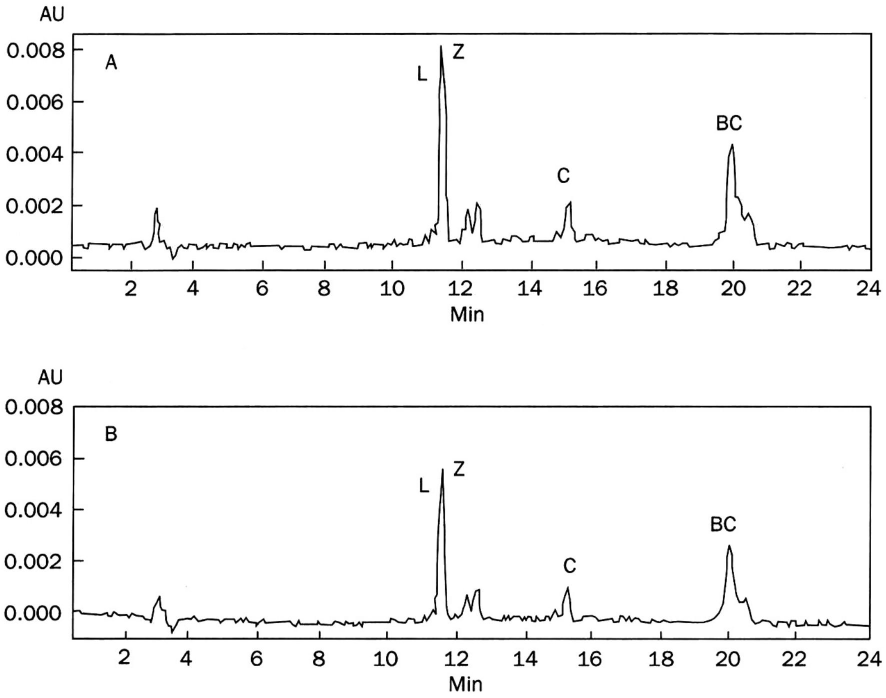


Fig. 3. Chromatograms showing the comparative carotenoid profile of uncooked (A) and cooked (B) rice of transgenic golden indica rice cv. IR64. L = lutein, Z = zeaxanthin, C = cryptoxanthin, BC = ß-carotene. AU = absorbance units.

This indicated that the alterations in the metabolic pathway of the rice plant did not involve any phenotypic cost in general. Nonetheless, less than 10% of the transgenic plants were of short stature, dark and of a stay-green nature, late-flowering, and highly sterile. For the competition for the common precursor (GGPP) shared between carotenoid and the gibberellin biosynthesis pathway, overexpression of phytoene synthase might cause the lack or deficiency of gibberellin, which resulted in dwarfism (Fray et al 1995). The pleiotropic effect could also be attributed to somaclonal variation and not necessarily to alien gene integration or expression. Such variation cannot be ruled out in any breeding program aiming at genetic improvement of crops. Hence, the selection of the correct transgenic line is important based on agronomic performance without any phenotypic cost, which requires the production of a large number of independent transgenics.

Selection with the *hph* gene (Datta et al 1990) is routinely used in rice transformation. But, considering public concern on the use of the antibiotic resistance gene, we successfully used the Positech™ selection system involving the *pmi* gene under a novel promoter to produce efficiently many normal and healthy transgenic indica rice plants with genes for ß-carotene biosynthesis that could help to obtain acceptance of transgenic nutritional rice (Datta 2000). Furthermore, to avoid the problem of frequent integration of the vector backbone beyond the gene(s) of interest that might carry the bacterial antibiotic gene, we also used the minimal vector approach (expression cassette without backbone), which did not affect the transformation events or expression level (data not shown).

The current level of carotenoid in our transgenic seeds might already be sufficient to prevent vitamin-A malnutrition on the basis of a daily diet of 300 g (R. Russel, personal communication). However, an increase in the amount of carotenoids, especially ß-carotene (provitamin A) and cryptoxanthin that are precursors for vitamin A, would be desirable. Efforts are under way with modified constructs with different endosperm-specific promoters (globulin, glutelin, and prolamin) to enhance the expression of the transgenes in collaboration with Dr. F. Takaiwa, NIAS, Japan. Care would be taken to identify lines with clean transgene integration with the Positech selection system without the vector backbone; however, with high expression but no phenotypic and agronomic trade-off that would go to farmers' fields and ultimately to end-users.

Development of high-iron indica rice

An IRRI-bred genotype, IR68144, with inherently high-iron content and BR29, a popular cultivar in Bangladesh, were used for high-iron loading in the endosperm. A cointegrate plasmid vector carrying the *ferritin* gene under the control of an endosperm-specific promoter, GluB^{-1}, and *bar* as the selectable marker gene driven by the constitutive CaMV 35S promoter (Goto et al 1999) was used for the biolistic experiment.

From the transformation experiments, a total of 16 independent primary transgenics were produced from IR68144 (de Vasconcelos et al 2002) and eight from BR29. Molecular (PCR and Southern) analyses confirmed the stable integration of the transgenes into the rice genome. All the transgenic plants were normal in phenotype and in seed setting. Several homozygous lines from IR68144 have already been developed at the T_2 level, whereas the first selfed progenies of BR29 are currently growing in the transgenic greenhouse. The monogenic (3:1) inheritance data indicated the single-locus integration of the *ferritin* gene in the rice genome in all the lines except one, which had a variable segregation ratio.

Immunoblot analysis showed the expression of the ferritin protein in the endosperm (polished seeds) by the presence of a 28-kDa protein in the transgenics, which was absent in the nontransgenic control. The distribution of the ferritin protein was also found from the immunological tissue-imprinting technique, in which the endosperm tissue print of transformed seeds showed dark brown coloration compared with very faint or no color in the control material. The loading of iron in the grain was also evident from the histochemical technique using Prussian blue staining reaction. The endosperm, including all other tissues of the transgenic grains, showed dense blue color, whereas the nontransformed grains did not have detectable blue

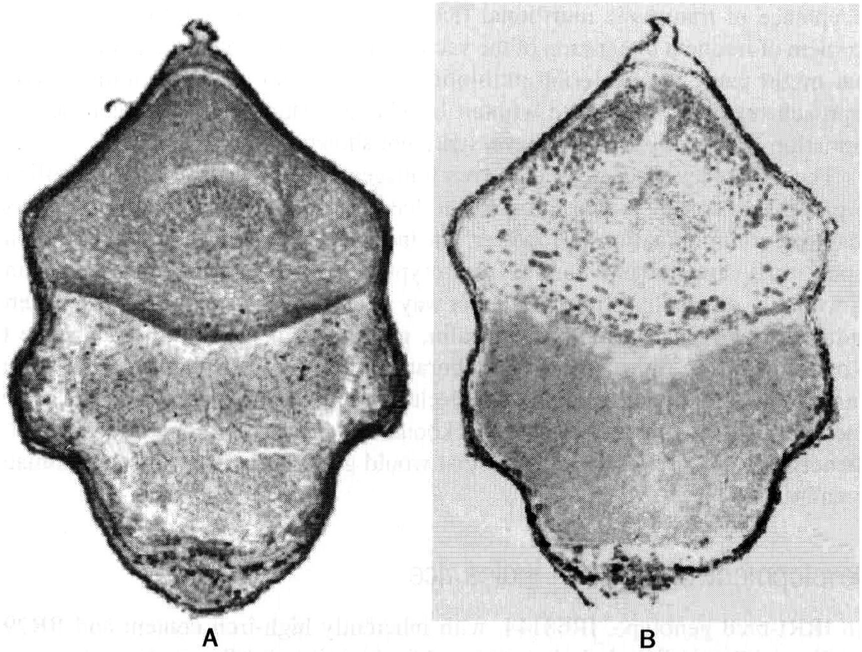


Fig. 4. Histochemical localization of iron in the transgenic (A) and nontransgenic (B) rice grain.

color (Fig. 4) in the endosperm, but iron was localized in the embryo and aleurone layers (Krishnan et al 2002).

The iron content of both polished and brown rice was estimated by using either atomic absorbance mass spectrometry (AA-MS) or inductively coupled plasma–optical emission spectrophotometry (ICP–OES). Pooled mean values indicated that the transgenics had a significantly higher iron in the polished seeds than the control ($P < 0.05$). The iron level varied from 9.0 to 37.0 $\mu g\ g^{-1}$ dry weight in transgenic seeds, whereas the value was 10 $\mu g\ g^{-1}$ in the control seeds (de Vasconcelos et al 2002). The zinc levels in the transgenic grains were markedly higher than that in the nontransgenic seeds. This could be possible because of a common mechanism of iron and zinc transport in the vegetative tissues and loading in the sink.

We have also introduced a ferric chelate reductase gene (*FR02*) into rice that enhances the uptake of the iron by the roots under iron-deficiency (Robinson et al 1999) into an IRRI-bred maintainer line (IR68899B). The transgenics showed stable integration and inheritance of *FRO2* in subsequent progenies. Dihaploid homozygous lines have been developed and were studied for some agronomic traits under iron-deficient alkali soil. The transgenics showed higher chlorophyll and more vigor than the control plants. Some of the transgenics showed increased iron content in the root, leaf, and grains.

In summary, we have successfully developed transgenic golden indica rice and high-iron rice with the stable accumulation of beta-carotene, dense loading of iron in the endosperm tissues of rice grain, and iron uptake by the roots. Experiments are in the pipeline for studying the use of the nonantibiotic marker system *(pmi* or *bar)* and minimal transformation vector, which would allow us to examine concerns regarding public acceptance. Our efforts to combine beta-carotene with ferritin as well as lysine (a limiting aminoacid in rice grain) would lead to the development of "nutritious rice" that would help increase their absorption and bioavailability. These second-generation transgenic products with improved micronutrients, protein, and vitamins would be perceived to be worthwhile by consumers (Philips 2000). Moreover, plant systems also minimize safety risks from contamination with human pathogens, in contrast to expression systems relying on cultured human or animal cells for the production of pharmaceuticals (Daniell 1999).

References

Baisakh N, Datta K, Rai M, Rehana S, Beyer P, Potrykus I, Datta SK. 2001. Development of dihaploid transgenic golden rice homozygous for genes involved in the metabolic pathway for ß-carotene biosynthesis. Rice Genet. Newsl. 18:91-94.

Baisakh N, Datta K, Oliva NP, Datta SK. 1999. Comparative molecular and phenotypic characterization of transgenic rice with *chitinase* gene developed through biolistic and *Agrobacterium* - mediated transformation. Rice Genet. Newsl. 16:149-152.

Daniell H. 1999. GM crops: public perception and scientific solutions. Trends Plant Sci. 4:467-469.

Datta K, Baisakh N, Thet KM, Tu J, Datta SK. 2002a. Pyramiding transgenes for multiple protection in rice against bacterial blight, stem borer and sheath blight. Theor. Appl. Genet. 106:1-8.

Datta K, Baisakh N, Oliva N, Torrizo L, Abrigo E, Tan J, Rai M, Rehana S, Al-Babili S, Beyer P, Potrykus I, Datta SK. 2002b. Bioengineered *'golden'* indica rice cultivars with b-carotene metabolism in the endosperm with hygromycin and mannose selection systems. Plant Biotechnol. J. (In press,)

Datta SK. 2000. Potential benefit of genetic engineering in plant breeding: rice, a case study. Agric. Chem. Biotechnol. 43:197-206.

Datta SK, Torrizo LB, Tu J, Oliva NP, Datta K. 1997. Production and molecular evaluation of transgenic rice plants. IRRI Discussion Paper Series No. 21.

Datta SK, Peterhans A, Datta K, Potrykus I. 1990. Genetically engineered fertile indica-rice plants recovered from protoplasts. Bio/Technology 8:736-740.

De Vasconcelos M, Datta K, Oliva N, Khalekuzzaman M, Torrizo L, Krishnan S, Olivejra M, Goto F, Datta SK. 2002. Enhanced iron and zinc accumulation in transgenic rice with the *ferritin* gene. Plant Sci. (In press.)

Doesthale Y, Devara S, Rao S, Belavady B. 1979. Effect of milling on mineral and trace element composition of raw and parboiled rice. J. Sci. Food Agric. 30:40-46.

Drakakai G, Christou P, Stoger E. 2000. Constitutive expression of soybean cDNA in transgenic wheat and rice results in increased iron levels in vegetative tissues but not in seeds. Transgenic Res. 9:445-452.

Fray RG, Wallace A, Fraser PD, Valero D, Hedden P, Bramley PM, Grierson D. 1995. Constitutive expression of a fruit phytoene synthase gene in transgenic tomatoes causes dwarfism by redirecting metabolites from the gibberellin pathway. Plant J. 8:693-701.

Gerster H. 1997. Vitamin A functions, dietary requirements and safety in humans. Int. Vit. Nutr. Res. 67:71-90.

Goto F, Yoshihara T, Shigemoto S, Toki F, Takaiwa E 1999. Iron fortification of the rice seed by the soybean ferritin gene. Nature Biotechnol. 17:282-286.

Hobbs SLA, Warkentin TD, DeLong CMO. 1993. Transgene copy number can be positively or negatively associated with transgene tobacco transformants. Plant Mol. Biol. 15:851-864.

Khush GS. 2001. Green revolution: the way forward. Nature Rev. Genet. 2:815-821.

Krishnan S, Datta K, Baisakh N, de-Vasconcelos M, Datta SK. 2002. Tissue-specific localization of ß-carotene and iron in transgenic indica rice (*Oryza sativa* L.). Current Sci. (In press.)

Philips RL. 2000. Biotechnology and agriculture in today's world. Food Nutr. Bull. 21:457-459.

Robinson NJ, Procter CM, Connolly EL, Guerinot ML. 1999. A ferric-chelate reductase for iron uptake from soils. Nature 397:694-697.

Sivakumar B. 1998. Current controversies in carotene nutrition. Ind. J. Med. Res. 108:157-166.

Ye X, Al-Babili S. Klöti A, Zhang J, Lucca P, Beyer P, Potrykus I. 2000. Engineering the provitamin A (ß-carotene) biosynthetic pathway into (carotenoid free) rice endosperm. Science 287:303-305.

Zimmerman M, Hurrel R. 2002. Improving iron, zinc and vitamin A nutrition through plant biotechnology. Curr. Opin. Biotechnol. 13:142-145.

Notes

Authors' address: International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines. Email: s.datta@cgiar.org.

Acknowledgments: We thank Drs. I. Potrykus and P. Beyer for providing the plasmids pBaal3 and pCyBlue, Dr. E Goto for the plasmid pGTV-fer 35S-bar with *ferritin,* and Dr. N. Robinson for the *FRO2* clone. This work was supported in part by the United States Agency for International Development.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Breeding for iron-dense rice in Bangladesh

K.A. Kabir, M. Haque, M.A. Hossain, S.S. Dipti, and I. Tetens

Fifty rice varieties were collected under different categories from different sources and were grown in the Bangladesh Rice Research Institute (BRRI) field during the 2001 transplanted aman season (July-November). Precautions were taken during harvest and further processing to avoid any mineral contamination. All samples were handpounded before being analyzed for their content of iron and zinc.

The iron and zinc content varied considerably within the different categories of rice measured. Overall, the local varieties had a higher content of iron and zinc than the highyielding varieties. Furthermore, our study confirms that aromatic rice varieties in general have a higher-content of iron and zinc than nonaromatic rice varieties. A positive correlation between the iron and zinc content of milled rice was found in the varieties measured.

Based on the preliminary iron and zinc data, about 34 varieties were selected as parent materials to be used in the breeding program. A crossing program has been undertaken by the Breeding Division of BRRI to incorporate/accumulate irondensity regulatory genes in popular modern varieties of rice.

Rice is the staple food for Bangladeshi people and will continue to remain so in the future. In Bangladesh, rice alone constitutes about 92% of the total food grains produced annually. It provides about 75% of the calorie intake, 55% of the protein intake, and a considerable proportion of several micronutrients in the average daily diet of the people. Furthermore, rice is the only major source of several micronutrients (especially iron and zinc) among the part of the population that has limited access to animal foods.

The main source of iron in rice is the nonheme iron, which has a low bioavailability. As a result, iron deficiency is common among the poor population. Iron deficiency hinders growth and development in early childhood, pregnancy, and lactation. In rural Bangladesh, about 50% of pregnant women and 45% of nonpregnant women and 53% of children below 5 years of age suffer from iron deficiency.

Most of the iron in rice is bound to phytates, which reduce its bioavailability. Iron bioavailability from rice is as low as 1-2%. Based on these facts, a strategy to increase the concentration of iron in rice has been undertaken to develop high-yielding, iron-dense rice varieties adapted to growing environments in different parts of Bangladesh.

Materials and methods

Fifty rice varieties were collected from different sources under the following categories: high-yielding varieties (HYV)—14; HYV aromatic varieties—3; local popular varieties—6; local aromatic varieties—16; imported varieties—11.

The rice varieties were all grown in the BRRI field during the 2001 transplanted aman season (July-November). The crop was harvested at the end of November to early December 2001. Precautions were taken to avoid any iron contamination during harvest. Rice samples for the mineral analyses were milled by a wooden mortar and pestle at BRRI and care was taken to ensure that all rice was milled to the same degree. The samples were sent to Waite Analytical Service, Department of Plant Science, University of Adelaide, Australia, for analyses of iron and zinc. The results on iron and zinc content are presented by different categories.

Results and discussion

The iron and zinc content of milled rice of HYVs are presented in Table 1. Among the 14 HYVs, the iron content varied from 5.5 to 10.0 mg kg^{-1}. BR11 had the lowest and BRRI Dhan 40 had the highest iron content. Of the 14 HYVs, the zinc content

Table 1. Iron and zinc content of high-yielding rice varieties.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
BR4	7.88	21.40
BR10	8.77	21.32
BR11	5.50	15.39
BR22	7.77	21.68
BR23	6.71	15.33
BR25	6.59	17.52
BRRI Dhan 30	8.77	24.43
BRRI Dhan 31	7.81	19.57
BRRI Dhan 32	6.90	17.33
BRRI Dhan 33	6.64	22.21
BRRI Dhan 37	8.68	18.41
BRRI Dhan 39	9.51	22.20
BRRI Dhan 40	10.00	17.43
BRRI Dhan 41	8.80	15.86
Mean	7.88	19.29
SD[a]	1.29	2.93

[a] SD = standard deviation.

Table 2. Iron and zinc content of high-yielding aromatic rice varieties.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
BR5	10.26	20.31
BRRI Dhan 34	11.22	21.72
BRRI Dhan 38	10.34	19.70
Mean	10.61	20.58
SD[a]	0.53	1.03

[a]SD = standard deviation.

Table 3. Iron and zinc content of local rice varieties.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
Pajam	9.18	21.71
Nizersail	10.24	20.51
Rajasail	7.25	18.33
Latasail	11.19	19.88
Binni	11.31	27.30
Rangabinni	10.32	25.67
Mean	9.91	22.23
SD[a]	1.52	3.51

BSD = standard deviation.

varied from 15.33 to 24.43 mg kg^{-1}. BR23 showed the lowest and BRRI Dhan 30 showed the highest zinc content. The mean (± SD) values of iron and zinc content in these HYVs were 7.88 (± 1.29) and 19.29 (± 2.93) mg kg^{-1}, respectively. Iron content among the three HYV aromatic rice varieties varied from 10.26 to 11.22 mg kg^{-1} (Table 2). The highest value was found in BRRI Dhan 34 (11.22 mg kg^{-1}) and the lowest in BR5 (10.26 mg kg^{-1}). The zinc content varied from 19.70 to 21.72 mg kg^{-1}. The highest zinc content was measured in BRRI Dhan 34 (21.72 mg kg^{-1}) and the lowest in BRRI Dhan 38 (19.70 mg kg^{-1}). The zinc content was almost double the iron content in these aromatic rice varieties.

The iron and zinc content of the six local rice varieties are presented in Table 3. The iron content varied from 7.25 to 11.31 mg kg^{-1}. The highest iron content was in Binni and the lowest in Rajasail. The zinc content varied from 18.33 to 27.30 mg kg^{-1}. Binni had 27.30 mg kg^{-1} and Rajasail had 18.33 mg kg^{-1}. Among the six local rice varieties, Binni had the highest content of iron and zinc, whereas Rajasail had the lowest value of these micronutrients. The mean (± SD) value of iron and zinc content in these local rice varieties was 9.91 (± 1.52) and 22.23 (± 3.5 1) mg kg^{-1}, respectively.

Among the 16 local aromatic rice varieties, the iron content varied from 9.34 to 16.94 mg kg^{-1} (Table 4). Barisal Kataribhog had the lowest (9.34 mg kg^{-1}) and Kalosail had the highest (16.94 mg kg^{-1}) iron content. The zinc content varied from 20.09 to 36.56 mg kg^{-1}. Barisal Kalijira had the lowest (20.09 mg kg^{-1}) and Jira Katair had the highest (36.56 mg kg^{-1}) zinc content.

Table 4. Iron and zinc content of local aromatlc rice varieties.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
Kalijira	10.56	24.69
Chinigura	10.31	24.30
Barisal Kataribhog	9.34	20.94
Kalosail	16.94	26.90
Begarhat local	11.52	35.67
Bogra Kalosail	9.89	25.43
Sakkurkhora	10.11	26.51
Jira Katair	13.56	36.56
Kataribhog (232)	10.92	20.71
Kataribhog (4363)	11.09	20.58
Sada sailla	13.01	25.61
Surjomukhi	11.82	21.46
Chiniatap	10.51	24.02
Barisal Kalijira	10.21	20.09
Lalsailla	10.20	25.43
Jeera	9.60	22.32
Mean	11.22	25.08
SD[a]	1.91	4.86

[a] SD = standard deviation.

Table 5. Iron and zinc content of imported aromatic varieties.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
Basmati 370	11.24	26.34
Basmati 385	8.43	23.52
Basmati 386	9.35	25.50
Colonel Basmati	12.06	26.30
Basrnati super	14.05	27.74
Shadi	12.36	27.30
Mean	11.25	26.07
SD[a]	2.31	1.67

[a] SD = standard deviation.

The iron and zinc content of the six imported aromatic rice varieties are presented in Table 5. Iron content of the varieties varied from 8.43 to 14.05 mg kg^{-1}. The highest iron content was found in Basmati super and the lowest in Basmati 385. Zinc content of the varieties varied from 23.52 to 27.74 mg kg^{-1}. The highest zinc content was found in Basmati super and the lowest in Basmati 385.

Among the five IRRI varieties, the iron content varied from 8.04 to 11.75 mg kg^{-1} (Table 6). The highest was in Milagrosa and the lowest in IR72. The zinc content varied from 20.46 to 31.33 mg kg^{-1}. IR64 had the lowest and IR68144 had the highest zinc value. The mean values of iron and zinc content in these varieties were 10.25 and 25.81 mg kg^{-1}, respectively.

Table 6. Iron and zinc content of some varieties obtained from IRRI.

Variety	Fe (mg kg^{-1})	Zn (mg kg^{-1})
Milagrosa	11.75	25.26
IR68144	11.47	31.33
Azucena	11.13	28.40
IR64	8.87	20.46
IR72	8.04	23.38
Mean	10.25	25.81
SD[a]	1.68	4.22

[a] SD = standard deviation.

Table 7. Iron and zinc content of different categories of rice variety:

Rice category	N	Fe ± SD (mg kg^{-1})	Zn ± SD (mg kg^{-1})
BRRI HW rice	14	7.88 ± 1.29	19.29 ± 2.93
BRRI HW aromatic rice	3	10.61 ± 0.53	20.56 ± 1.03
Local rice	16	9.91 ± 1.52	22.23 ± 3.51
Local aromatic rice	16	11.22 ± 1.91	25.08 ± 4.86
Imported aromatic rice	6	11.25 ± 2.31	26.07 ± 1.67
IRRI rice	5	10.25 ± 1.68	25.81 ± 4.22

[a] Values are mean ± SD.

The summary of the analysis is presented in Table 7. Mean iron and zinc content varied from 7.88 to 11.25 and 19.29 to 26.07 mg kg^{-1}, respectively. Imported aromatic varieties had the highest iron and zinc content, followed by local aromatic varieties.

A positive correlation was found between iron and zinc content of all the milled rice (Fig. 1).

Based on the preliminary data on iron and zinc content, about 34 varieties were selected as parent materials to be used in the breeding program. A crossing program has been undertaken by the Breeding Division of BRRI to incorporate/accumulate iron-density regulatory genes in popular modern varieties of rice. All the local varieties and some high-yielding varieties are photoperiod-sensitive and flower only during October to November in Bangladesh. To produce an F_2 population within 2002, two crops must be grown and thus a special technique must be applied to induce flowering. The F_2 population will be produced from these crosses and selected plants will be bulked for future advanced generations. Advanced lines obtained through hybridization will be screened for high iron and zinc and other acceptable agronomic characters right from the F_2 generation. Our study showed a positive correlation between the content of iron and zinc, which indicates that no separate breeding program is required for developing high-zinc rice varieties.

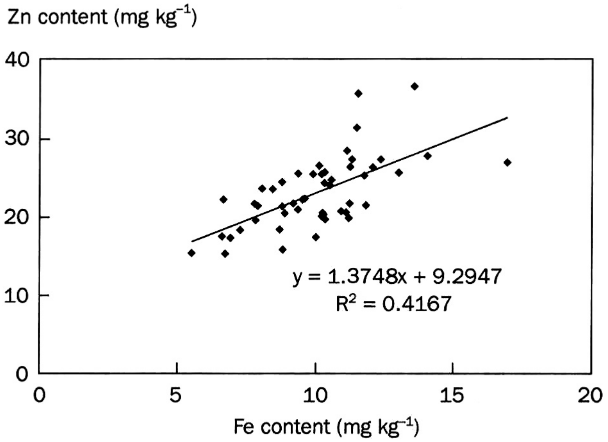


Fig. 1. Correlation between iron and zinc content in 50 milled rice samples.

Conclusions

Iron-deficiency anemia has a high prevalence in Bangladesh. The dietary intake is one of the main determinants of this situation. The development of iron-dense rice varieties may be a suitable strategy to help eradicate iron-deficiency anemia, especially among children, pregnant women, and lactating mothers.

Our study shows that there is a wide range in the content of iron and zinc in different categories of Bangladeshi-grown rice. The results indicate that the content of iron and zinc is higher in the local rice varieties than in the high-yielding rice varieties and that aromatic rice varieties tend to have a higher content of iron and zinc. The content of iron and zinc in milled rice is closely correlated.

Notes

Authors' addresses: K.A. Kabir, M. Haque, M.A. Hossain, and S.S. Dipti, Bangladesh Rice Research Institute, Gazipur, Bangladesh; I. Tetens, The Royal Veterinary and Agricultural University, Frederiksberg, Denmark.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Improving the bioavailability of iron and zinc low-phytate rice mutants

S.K. Rasmussen, L. Josefsen, H. Leung, and M. B. Sørrensen

Cereal grains contain antinutritional factors that reduce the bioavailability of iron and zinc. Phytate has for a long time been known to lower the uptake of these and other minerals. In the cell, phytate is stored together with iron, zinc, and calcium as densely packed particles similar to protein storage bodies. It can be regarded as a phosphorus storage compound as, in fact, up to 80% of the grain phosphorus is bound in phytate, while the remaining is in nucleic acids and phospholipids and present as phosphate. Mutational breeding for low-phytate barley has shown that it is possible to substantially reduce the content of phytate in the grain while still maintaining high germination and grain yield. The grain content of minerals, for example, Fe, does not change in the mutant lines. Furthermore, feeding trials with small animals confirmed that bioavailability of iron and zinc is improved in low-phytate barley. From the knowledge gained with barley grain mutants, we have shown that the pathway to phytate is seed-specific and that biosynthesis of phytate in vegetative tissues and pollen is not affected by these mutations. Low-phytate mutants in rice have been isolated and the material currently in use consists of M_4 seeds from diepoxybutane-treated IR64. Single grains from 144 rice accessions were extracted and tested for free phosphate by molybdate blue staining and two putative mutants were collected.

Phytate acts as an antinutritional factor in diets primarily based on cereal grains such as rice and wheat by lowering the uptake of iron in the typical nonheme form of plants. Poor families in developing countries primarily get their daily intake of iron and other micronutrients from cereals (Bouis 1996) because they have limited access to foods such as meat, fish, and poultry rich in heme iron. A recent survey on vitamin-A and iron deficiencies (Ruel 2001) provides optimism concerning the possibility of developing strategies to reduce or eliminate phytate as a potent inhibitor of nonheme iron absorption and hence contribute to solving some of the malnutrition from insufficient bioavailability of trace elements. Here, we report on the screening for low-phytate rice with the aim of providing breeding material in which more nonheme iron is available for uptake. This trait may be combined with varieties with elevated levels of minerals (Graham et al 2001) and thus contribute to food biofortification based on minerals. As a background for modulating the grain phytate content, our current knowledge of its biosynthesis, deposition, and hydrolysis is provided.

Biosynthesis of phytate

Seed-specific accumulation of large amounts of phytate (*myo*-inositol 1,2,3,4,5,6-hexa*kis*phosphate, $InsP_6$) is a unique feature of inositol phosphate metabolism in the plant kingdom. Being the storage compound for phosphorus, phytate can account for 50-80% of total seed phosphorus in many species (Raboy 1990, Loewus et al 1990, Raboy and Gerbasi 1996). Although phytate is the major compound, inositol-pentaphosphates, InsPs, are also found in rice, wheat, and maize as shown by the MDD-HPLC elution profile in Figure 1. $InsP_5$ accounts for approximately 10% of the inositolphosphates, with only minor differences between species. Another function of plant phytate is mineral storage that is conveyed by the high density of negatively charged phosphate groups located around the *myo*-inositol ring. Thus, phytate forms salts with mineral cations (mostly K^+, Mg^{2+}, Zn, and Ca^{2+}, but also Fe), which on electron micrographs appear as globular inclusions in protein bodies (Lott 1984). Depending on the plant species, phytate globoids are predominantly localized in the aleurone layer (rice, wheat, and barley) or in the embryo (maize) (O'Dell et al 1972). During germination, phytate is continuously degraded by phytases followed by acid phosphatases, providing phosphate to the growing seedlings as well as mineral cations and *myo*-inositol.

In spite of the numerous physiological investigations of phytate accumulation and storage, many questions remain unanswered regarding the biochemical set-up of phytate metabolism in plants. It is not fully understood how plants synthesize phytate and how phytate metabolism is coordinated with signaling mechanisms involving other inositol phosphates. Figure 2 outlines the only completely described plant phytate synthesis pathway known at present, delineated in the duckweed *Spirodelu polyrhiza* (Brearley and Hanke 1996b), and some of the known intermediates identified in, for example, barley mutants. Using an in vivo labeling approach, a sequence of phosphorylation steps was established that proceeds via Ins(3)P, $Ins(3,4)P_2$, $Ins(3,4,6)P_3$, $Ins(3,4,5,6)P_4$, and $Ins(1,3,4,5,6)P_5$ to phytate. However, investigations of inositol phosphate kinases from *Arabidopsis thaliana* (Wilson and Majerus 1997) and soybean (Phillippy 1998) indicated that phytate synthetic pathways operating in land plants may be quite different from that in the aquatic species *Spirodela.* In both soybean and *Arabidopsis,* an $Ins(1,3,4)P_3$ 5/6-kinase activity was identified that yielded $Ins(1,3,4,5,)P_4$ as the major phosphorylation product. An additional kinase activity from soybean seeds used $Ins(1,3,4,5)P_4$ to produce $Ins(1,3,4,5,6)P_5$, which, together with a previously described $Ins(1,3,4,5,6)P_5$ 2-kinase (Phillippy et al 1994), established a biosynthetic route to phytate. This hypothetical pathway bears some resemblance to the phytate pathway in *Schizosaccharomyces pombe* (Ongusaha

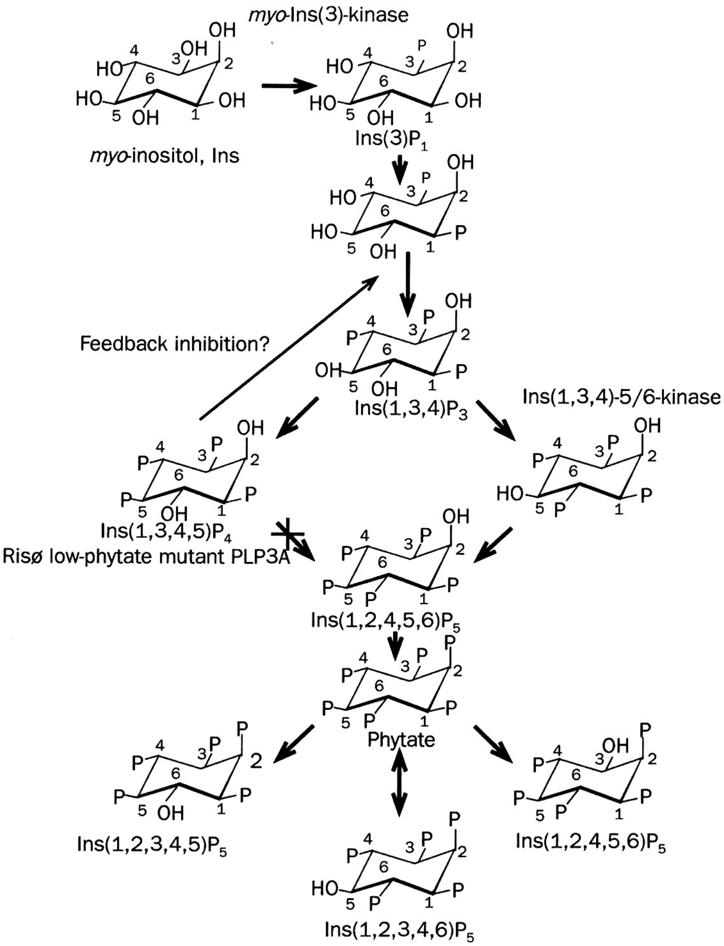


Fig. 1. Biosynthetic pathway of phytate.

et al 1998) and the nucleus-associated pathway in *Dictyostelium discoidium* (Van der Kaay et al 1995). In both pathways, phytate synthesis proceeds via Ins(1,4,5)P_3, which is phosphorylated to Ins(1,3,4,5)P_4 (*D. discoidium* and *S. pombe*) and Ins(1,4,5,6)P_4 (*S. pombe* only). As found in *Spirodela* and soybean, Ins(1,3,4,5,6)P_5 is the final intermediate in both slime mold and baker's yeast.

Although a comprehensive analysis of phytate synthesis in a land plant species is still lacking, detailed studies on phytate degradation have been carried out in wheat bran (Johnson and Tate 1969, Lim and Tate 1971), barley aleurone layer (Brearley and Hanke 1996a), germinating mung bean (Stephens et al 1991) and soybean seeds (Phillippy and Bland 1988), maize roots (Hubel and Beck 1996), as well as in lily

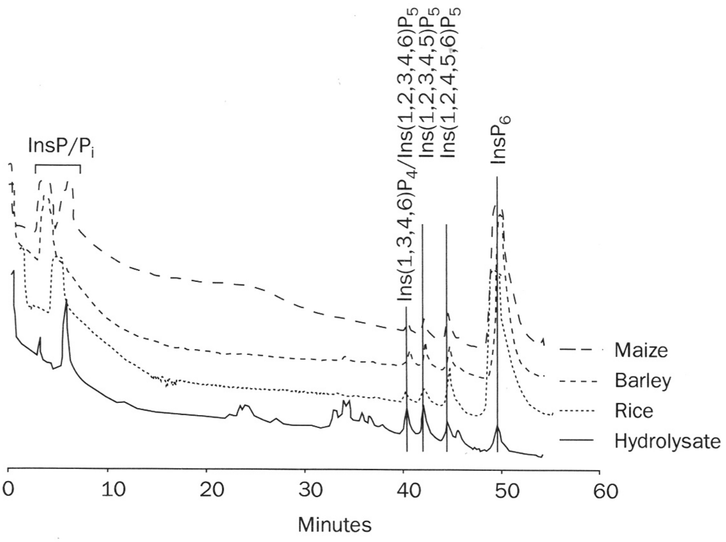


Fig. 2. Profile of phytate and inositolphosphates in three cereals.

pollen (Barrientos et al 1994). Although stereochemical similarities of phytate breakdown products can be recognized in closely related species such as wheat and barley (Brearley and Hanke 1996a), a general consensus of intermediates indicating conserved substrate processing by plant phytases does not appear to exist.

The identification of low-phytic acid mutants in maize (Raboy 1990, Pilu et al 2002) and in the barley varieties Harrington (Larson et al 1998) and Pallas-P01 (Rasmussen and Hatzack 1998) has opened up new opportunities to investigate the biochemistry and genetics of plant phytic acid metabolism. Mutants found in maize and Harrington barley were categorized into two phenotypes (1pa1 and 1pa2) and linkage mapping identified chromosomal locations of 1pa1 and 1pa2 mutations (Larson et al 1998). Subsequent mapping studies indicated *myo* -inositol 1-phosphate synthase (MIPS, EC 5.5.1.4) as a likely candidate gene for the lpal mutation (Larson et al 1998, Hatzack et al 2001). Maize is known to have five MIPS genes and *Arabidopsis* three. For inositol phosphate composition, lpa2 mutants were reported to contain elevated amounts of lower inositol phosphates, namely, penta*kis*phosphates, but a detailed biochemical analysis has not yet been published. Based on TLC analysis, Pallas-P01 low-phytate (PLP) barley mutants were initially divided into two distinct phenotype classes (Rasmussen and Hatzack 1998, Larson et al 1998). Grain extract from A-type mutants contained extremely high levels of phosphate, low levels of phytate, and traces of unidentified inositol phosphates, which were not observed in the parent line. Grains from B-types showed increased phosphate levels and moderately reduced phytate levels, while accumulations of other inositol phosphates were not detected. Genetic testing revealed that A- and B-phenotypes are caused by recessive mutations in separate loci. The structure of the accumulating Ins(1,3,4,5)P_4 in barley mutant PLP3A is described extensively in Hatzack et al (2000, 2001).

A mutant line in soybean seeds has reduced phytate content and more inorganic phosphate but also reduced raffinosaccharide (Hitz et al 2002). The mutation was located to a single amino acid change in the coding region of the *myo*-inositol 1-phosphate synthase gene, which reduced the activity of the MIPS to 10%. Soybean may have an additional one or two MIPS genes, which, however, did not compensate for the mutated gene.

Screening for low-phytate rice seed mutants

Screening for low-phytate rice grain mutants has been started on the M_4 generation of a 1,2,3,4-diepoxybutane (DEB) induced mutant population. Seeds of IR64 were treated with 0.004-0.006% DEB, a chemical known to create deletion mutations in human cells. The microtiter-plate screening procedure is based on protocols developed for barley and relies on testing for high free phosphate content as indicative of reduced phytate content (Rasmussen and Hatzack 1998). Four single grains from each M_4 accession were extracted and tested for free phosphate by molybdate blue staining (Fig. 3). In an initial experiment, 144 accessions gave two putative positives, M4D6-2070-5 and M4D6-2072-4, which are now being propagated for subsequent confirmation of the mutation. An unusually high number of mutants can be expected, following the experience obtained by screening for barley low-mutants (Rasmussen and Hatzack 1998). Evidence of heterozygotes at the M_4 stage was found, for example, when two or three out of four seeds scored positive (Fig. 3). This has been noted when screening the population for other traits as well.

Phytate particles

Phytate accumulates during grain filling and maturation in the aleurone cells as compact particles making salts with Fe, Zn, Ca, and other minerals. Yamagata et al (1979) have purified aleurone particles from rice bran, which contains phytate, but also acid phosphatase isozymes. Aleurone particles were isolated by differential centrifugation in nonaqueous solutions and four phosphatases were purified (Yamagata et al 1980). Similarly, Ory and Henningsen (1969) isolated protein bodies from aleurone cells of mature barley seeds by centrifugation through a sucrose cushion showing that acid phosphatase activities were associated with these. By the use of toluidine blue staining, globoids were detected in the scutellum and aleurone layer from 4 days after flowering of rice seeds (Yoshida et al 1999). No globoids could be detected in the starchy endosperm.

In rice, barley, and wheat, phytate is found predominantly in the aleurone, less in the embryo, and only trace amounts in the starchy endosperm. Phytate particles have been purified from rice and barley and acid phosphatases, which potentially can degrade the packed phytate, were found to copurify. This would require a distinct localization of the phytate to keep it separated from hydrolytic enzymes during seed

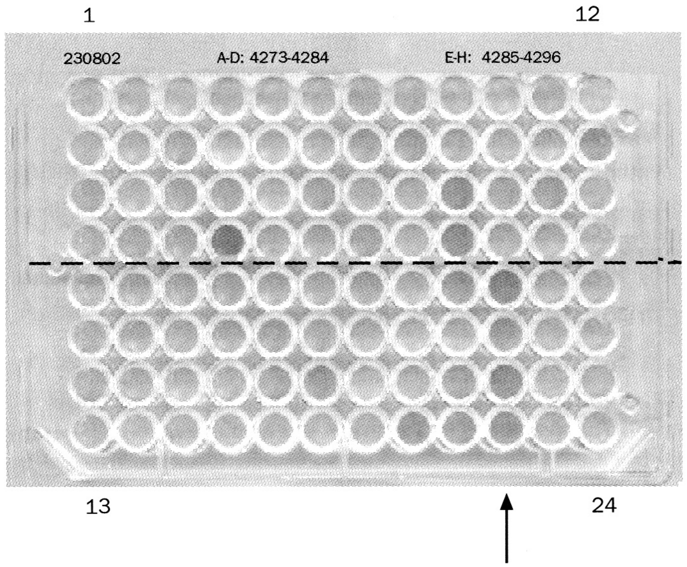


Fig. 3. Screening for low-phytate rice mutants. Four seeds from each of 24 M_4 accessions were tested for free phosphate by molybdate staining. The arrow points to a putative low-phytate rice mutant.

maturation and storage. This can be achieved either by densely packed structures that only upon hydration will become accessible to phytase or by phytate storage in separate organelles. In fact, in a recent study on mature tomato seeds, Jiang et al (2001) hypothesize that protein storage vacuoles contain crystals of phytate in organelles resembling lytic vacuoles. By having vacuoles within storage body vacuoles, metabolites can be separated from hydrolytic enzymes that are presumed to act in remobilization of, for example, storage proteins and phytate. However, reports on the structure of phytate bodies in cereals are somewhat contradictory and need clarification by additional subcellular localization taking advantage of low-phytate mutant lines.

Human health

Humans are lacking enzymes that can degrade phytate efficiently and they are thus prevented from an efficient use of magnesium, calcium, iron, and zinc because their cations are balanced by negatively charged phytate. Several reports on anticancer effects of $InsP_6$ have been published during the last few years. Feeding experiments with rats have demonstrated that labeled $InsP_6$ given in the drinking water is rapidly taken up and distributed in the body (Nishino et al 1999). Here, it leads to a 33.5% reduction in mammary tumor incidences as compared to a control group. The *myo*-inositol moiety of phytate itself has a similar effect on lung and liver carcinogenesis in mice and it is therefore postulated that phosphorylation or dephosphorylation of phytate or its inositol-phosphate intermediate compounds must occur in the cells. The evidence of phytate as an anticancer agent has been demonstrated with several experimental tumors as reviewed by Shamsuddin (1999).

Removal of phytate

Mutation breeding is an efficient and promising way to remove phytate from plant-based diets as mentioned above. The production of transgenic crops such as barley, wheat, maize, or rice that express a fungal phytase gene in the grain with an inherent capacity of storing hydrolytic enzyme activities constitutes an alternative approach to remove phytate. This possibility was first demonstrated in rapeseed oil seeds (Pen et al 1993) and recently in wheat grains (Brinch-Pedersen et al 2000). The transgenic plant strategy may be further improved by modifying the plant's own phytase to meet the industry's demands for functionality. The phytase purified from wheat bran is highly active and provides an optimal choice for protein engineering and subsequent reintroduction into plants (Rasmussen et al 2000). Which of these solutions will enter the market depends not only on technical and economic considerations but also on consumers' preferences. Organic farmers in most countries accept mutational breeding, whereas a transgenic approach and supplementation with technical enzymes is still not in harmony with the ecological concept. Some consumers may find transgenic wheat that overproduces an endogenous phytase acceptable but not a phytase from an entirely unrelated species such as *Aspergillus.* Transgenics for human consumption also face resistance, whereas their use in the feed industry might find more acceptance by end-consumers.

Cloned plant phytase

We have purified a phytase enzyme from wheat bran and amino acid sequence information was obtained, thus enabling the identification of related proteins from soybean and other plant species, which have been characterized as purple acid phosphatases but not as phytases (Johansen et al 2001). The first report of a cloned plant phytase is from maize (Maugenest et al 1997). Based on sequence similarity in a 100-base-pair segment of the full-length DNA sequence, the maize phytase was suggested by the authors as belonging to the family of histidine acid phosphatases sharing this feature with most microbial phytases. Our data indicate that, even though maize and wheat are both monocots, differences in their storage of phytate, and, in the absence (maize) or presence (wheat) of phytase activity in the resting grain, may be reflected at the protein level. Three phytases have been purified and cloned from maize (Maugenest et al 1997), wheat (Rasmussen et al 2000), and soybean (Hegeman et al 2001). Many papers describe partially purified phytases from many plant sources; however, amino acid data to compare with are absent.

References

Barrientos L, Scott JJ, Murthy PPN. 1994. Specificity of hydrolysis of phytic acid by alkaline phytase from lily pollen. Plant Physiol. 106:1489-1495.

Bouis H. 1996. Enrichment of food staples through plant breeding: a new strategy for fighting micronutrient malnutrition. Nutr. Rev. 54: 131-137.

Brearley CA, Hanke DE. 1996a. Inositol phosphates in barley *(Hordeum vulgare* L.) aleurone tissue are stereochemically similar to the products of breakdown of InsP6 in vitro by wheat-bran phytase. Biochem. J. 318:279-286

Brearley CA, Hanke DE. 1996b. Metabolic evidence for the order of addition of individual phosphate esters in the *myo*-inositol moiety of inositol hexa*kis*phosphate in the duckweed *Spirodela polyrhiza* L. Biochem. J. 314:227-233.

Brinch-Pedersen H, Olesen A, Rasmussen SK, Holm PB. 2000. Generation of transgenic wheat *(Triticum aestivum* L.) for constitutive accumulation of an *Aspergillus* phytase. Mol. Breed. 6: 195-206.

Graham RD, Welch RM, Bouis HE. 2001. Addressing micronutrient malnutrition through enhancing the nutritional quality of staple foods: principles, perspectives and knowledge gaps. Adv. Agron. 70:77-142.

Hatzack F, Hubel F, Zhang W, Hansen PE, Rasmussen SK. 2001. Inositol phosphates from barley low-phytate grain mutants analysed by metal-dye detection HPLC and NMR. Biochem. J. 354:473-480.

Hatzack F, Johansen KS, Rasmussen SK. 2000. Nutritionally relevant parameters in low-phytate barley *(Hordeum vulgare* L.) grain mutants. J. Agric. Food Chem. 48:6074-6080.

Hegeman CE, Good LL, Grabau EA. 2001. Expression of D-*myo*-inositol-3-phosphate synthase in soybean: implications for phytic acid biosynthesis. Plant Physiol. 125:1941-1948.

Hitz WD, Carlson TJ, Kerr PS, Sebastian SA. 2002. Biochemical and molecular characterization of a mutation that confers a decreased raffinosaccharide and phytic acid phenotype on soybean seeds. Plant Physiol. 128:650-660.

Hiibel F, Beck E. 1996. Maize root phytase: purification, characterization and localization of enzyme activity and its putative substrate. Plant Physiol. 112:1429-1436.

Jiang LW, Phillips TE, Hamm CA, Drozdowicz YM, Rea PA, Maeshima M, Rogers SW, Rogers JC. 2001. The protein storage vacuole: a unique compound organelle. J. Cell Biol. 155:991-1002.

Johansen KS, Hatzack F, Mønster H, Engvild KC, Rasmussen SK. 2001. Improved bioavailability of phosphorus in barley. In: Logue, S, editor. 8th International Barley Genetics Symposium, Adelaide, Australia. p 291-293.

Johnson LF, Tate ME. 1969. The structure of *myo*-inositol pentaphosphates. Ann. New York Acad. Sci. 165:526-532.

Larson SR, Young KA, Cook A, Blake TK, Raboy V. 1998. Linkage mapping of two mutations that reduce phytic acid content of barley grain. Theor. Appl. Genet. 97:141-146.

Lim PE, Tate ME. 1971. The phytases. I. Lysolecithin-activated phytase from wheat bran. Biochim. Biophys. Acta 250:155-164.

Loewus FA, Everard JD, Young KA. 1990. Inositol metabolism: precursor role and breakdown. In: Morre J, Boss WF, Loewus FA, editors. Inositol metabolism in plants. Wiley-Liss. p 21-46.

Lott JNA. 1984. Accumulation of seed reserves of phosphorus and other minerals. In: Murray DR, editor. Seed physiology. New York, N.Y. (USA): Academic Press. p 139-163.

Maugenest S, Martinez I, Lescure AM. 1997. Cloning and characterization of a cDNA encoding a maize seedling phytase. Biochem. J. 322:511-517.

Nishino H, Murakoshi M, Masuda M, Tokuda H, Satomi Y, Onozuka M, Yamaguchi S, Bu P, Tsuruta A, Nosaka K, Baba M, Takasuka N. 1999. Suppression of lung and liver carcinogenesis in mice by oral administration of *myo* -inositol. Anticancer Res. 19:3663-3664.

O'Dell BL, de Boland AR, Koirtyohann SR. 1972. Distribution of phytate and nutritionally important elements among the morphological components of cereal grains. J. Agric. Food Chem. 20:718-721.

Ongusaha PP, Hughes PJ, Davey J, Michell RH. 1998. Inositol hexakisphosphate in *Schizosaccharomyces pombe:* synthesis from Ins(1,4,5)P-3 and osmotic regulation. Biochem. J. 335:671-679.

Ory RL, Henningsen KW. 1969. Enzymes associated with protein bodies isolated from ungerminated barley seeds. Plant Physiol. 44:1488-1498.

Pen J, Verwoerd TC, Vanparidon PA, Beudeker RF, Vandenelzen PJM, Geerse K, Vanderklis JD, Versteegh HAJ, Vanooyen AJJ, Hoekema A. 1993. Phytase-containing transgenic seeds as a novel feed additive for improved phosphorus utilization. Bio-Technology 11:811-814.

Phillippy BQ. 1998. Identification of inositol 1,3,4-trisphophate 5-kinase and inositol 1,3,4,5-tetrakisphosphate 6-kinase in immature soybean seeds. Plant Physiol. 116:291-297.

Phillippy BQ, Bland JM. 1988. Gradient ion chromatography of inositol phosphates. Analyt. Biochem. 175:162-166.

Phillippy BQ, Ullah AHJ, Ehrlich KC. 1994. Purification and some properties of inositol 1,3,4,5,6-penta*kis*phosphate 2-kinase from immature soybean seeds. J. Biol. Chem. 269:28393-28399,

Pilu R, Gavazzi G, Nielsen E. 2002. Isolation and preliminary characterization of a maize low phytic acid mutant. Maize Genet. Coop. Newsl. 76.

Raboy V. 1990. Biochemistry and genetics of phytic acid synthesis. In: Morre J, Boss WF, Loewus FA, editors. Inositol metabolism in plants. New York, N.Y. (USA): John Wiley-Liss & Sons, Inc. p 55-76.

Raboy V, Gerbasi P. 1996. Genetics of *myo*-inositol phosphate synthesis and accumulation. In: Biswas BB, Biswas S, editors. Subcellular biochemistry: *myo*-inositol phosphates, phosphoinositides, and signal transduction. New York, N.Y. (USA): Plenum Press. p 257-285.

Rasmussen SK, Hatzack E 1998. Identification of two low-phytate barley *(Hordeum vulgare* L.) grain mutants by TLC and genetic analysis. Hereditas 129:107-112.

Rasmussen SK, Johansen KS, Sorensen MB. 2000. Phytase polypeptides. [WO 01/83763]. Patent application.

Ruel MT. 2001. Can food-based strategies help reduce vitamin A and iron deficiencies? Washington, D.C. (USA): International Food Policy Research Institute. p 1-54.

Shamsuddin AM. 1999. Metabolism and cellular functions of IP6: a review. Anticancer Res. 19:3733-3736.

Stephens LR, Hawkins PT, Stanley AF, Moore T, Poyner DR, Morris PJ, Hanley MR, Kay RR, Irvine RF. 1991. Myoinositol pentakisphosphates: structure, biological occurrence and phosphorylation to *myo*inositol hexa*kis*phosphate. Biochem. J. 275:485-499.

Van der Kaay J, Wesseling J, Van Haastert PJ. 1995. Nucleus-associated phosphorylation of Ins(1,4,5)P3 to InsP6 in *Dictyosfelium.* Biochem. J.312:911-917.

Wilson MP, Majerus PW. 1997. Characterization of a cDNA encoding *Arabidopsis thaliana* inositol 1,3,4-trisphosphate 5/6-kinase. Biochem. Biophys. Res. Commun. 232:678-681.

Yamagata H, Tanaka K, Kasai Z. 1979. Isoenzymes of acid-phosphatase in aleurone particles of rice grains and their interconversion. Agric. Biol. Chem. 43:2059-2066.

Yamagata H, Tanaka K, Kasai Z. 1980. Purification and characterization of acid-phosphatase in aleurone particles of rice grains. Plant Cell Physiol. 21:1449-1460.

Yoshida KT, Wada T, Koyarna H, Mizobuchi-Fukuoka R, Naito S. 1999. Temporal and spatial patterns of accumulation of the transcript of Myo-inositol-1-phosphate synthase and phytin-containing particles during seed development in rice. Plant Physiol. 119:65-72.

Notes

Authors' addresses: S.K. Rasmussen, L. Josefsen, and M.B. Sorensen, Plant Research Department, Plant Products, PRD-301, Riso National Laboratory, DK-4000 Roskilde, Denmark; H. Leung, International Rice Research Institute (IRRI), Entomology and Plant Pathology Division, Los Baños, Philippines. E-mail: soren.rasmussen@risoe.dk.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The economics of micronutrient interventions and the niche for biofortification

H.E. Bouis

The biofortification strategy seeks to take advantage of the consistent daily consumption of large amounts of food staples by all family members, including women and children who are most at risk for micronutrient malnutrition. As a consequence of the predominance of food staples in the diets of the poor, this strategy implicitly targets low-income households.

After the one-time investment is made to develop seeds that fortify themselves, recurrent costs are low and germplasm may be shared internationally. It is this multiplier aspect of plant breeding across time and distance that makes it so cost-effective.

Once in place, the biofortified crop system is highly sustainable. Nutritionally improved varieties will continue to be grown and consumed year after year, even if government attention and international funding for micronutrient issues fade.

Biofortification provides a truly feasible means of reaching malnourished populations in relatively remote rural areas, delivering naturally fortified foods to people with limited access to commercially marketed fortified foods, which are more readily available in urban areas. Biofortification and commercial fortification are therefore highly complementary.

Breeding for higher trace mineral density in seeds will not incur a yield penalty. In fact, biofortification may have important spinoff effects for increasing farm productivity in developing countries in an environmentally beneficial way. Mineral-packed seeds sell themselves to farmers because, as recent research has shown, these trace minerals are essential in helping plants resist disease and other environmental stresses. More seedlings survive and initial growth is more rapid. Ultimately, yields are higher, particularly in trace mineral–“deficient” soils in arid regions.

The permanent solution to micronutrient malnutrition in developing countries is a substantial improvement in dietary quality—higher consumption of pulses, fruits, vegetables, fish, and animal products, which the poor already desire but cannot currently afford. Meanwhile, breeding staple foods that are dense in minerals and vitamins provides a low-cost, sustainable strategy for reducing levels of micronutrient malnutrition. No single type of intervention can by itself solve the micronutrient malnutrition problem. A comprehensive strategy involving multiple types of interventions adapted to conditions in specific countries and regions is required. Biofortification complements existing strategies and has its own unique “niche,” as conditioned by the comparative advantages outlined and technical characteristics, most importantly, the level of the “dose” that biofortification can be expected to deliver. On any given day, biofortified staple foods cannot deliver as high a level of minerals and vitamins as supplements or industrially fortified foods.

To provide some background, it is useful first to summarize briefly the dimensions and consequences of micronutrient malnutrition in developing countries. It is estimated that more than 3 billion people in developing countries are iron-deficient (ACC/SCN 2000). The problem for women and children is more severe because of their greater physiological need for iron. In poor countries, more than half of the pregnant women and more than 40% of nonpregnant women and preschool children are anemic. Iron deficiencies during childhood and adolescence impair physical growth, mental development, and learning capacity. In adults, iron deficiency reduces the capacity to do physical labor. Iron deficiency is a leading cause of death among women during childbirth.

Globally, about 3 million preschool-age children have visible eye damage because of a vitamin-A deficiency. Annually, an estimated 250,000 to 500,000 preschool children go blind from this deficiency and about two-thirds of these children die within months of going blind. Estimates of the subclinical prevalence of vitamin-A deficiency range from 100 to 250 million. Several clinical trials in developing countries have shown than vitamin-A capsule distribution can reduce mortality rates among preschool children on the order of 30%.

The World Bank (1994) estimates that, at the levels of micronutrient malnutrition existing in South Asia, 5% of the gross national product is lost each year because of deficiencies in the intakes of just three nutrients: iron, vitamin A, and iodine. For each 50 million in population, that translates into an economic loss of $1 billion per year. Deficiencies in several other micronutrients, zinc in particular, may be similarly widespread, with equally serious consequences for health. However, because there are no specific indicators to screen for deficiencies in these nutrients (other than a positive health response to supplementation), they have not received as much attention.

The remainder of this paper examines particular aspects of biofortification, not examined in the other papers presented in this symposium. Particular emphasis is placed on the apparent cost-effectiveness of biofortification.

Will breeding for micronutrient-dense seeds change the processing or consumer characteristics of staple foods?

Mineral micronutrients make up a tiny fraction of the physical mass of a seed, 5-10 parts per million in milled rice. Dense bean seeds may contain as many as 100 parts per million. It is not expected that such small amounts will alter the appearance, taste, texture, or cooking quality of foods. The dissemination strategy for trace minerals, then, would be to convince agricultural research institutes to include the mineral-density trait in as many varietal releases as possible to benefit a high proportion of the population—without the necessity of consumers changing their behavior as a condition for success, much as fluoride is added to drinking water in developed countries.

In contrast, higher levels of beta-carotene will turn varieties from white or light colors of yellow to dark yellow and orange. Often, white varieties are much preferred by consumers (e.g., milled rice, wheat flour, maize, cassava). Major nutrition education programs will have to be mounted to encourage consumers to switch to more nutritious varieties. If these nutrition education programs are successful, however, the yellow-orange color will mark the more nutritious varieties from the less nutritious ones and a disadvantage will have been turned into an advantage (Hagenimana and Low 2000).

Will micronutrient intakes be increased to a significant degree?

For poor populations, food staple consumption so dominates diets (their low incomes preclude the consumption of desired levels of nonstaple foods) that primary food staples provide, for example, in the range of 40-55% of total iron intake for lower-income households. If a single food staple provides 50% of total iron intake for a poor population (e.g., for rice in Bangladesh), then a doubling of the iron density in that food staple will result in a 50% increase in total iron intake (Bouis et al 1998).

Iron intake for low-income women in developing countries ranges perhaps from 50% to 75% of recommended daily allowances. Despite well-known difficulties with determining useful benchmarks for recommended daily allowances of iron, it would seem evident that a 50% increase in the intake of bioavailable iron would be of considerable benefit to anemic women with such a low iron intake. Some empirical evidence is available from a recently published study of a population of Bangladeshi rural women (Bhargava et al 2001). This study measured the relationship between foods in the diet and blood hemoglobin. The estimated relationships suggest that a 50% increase in iron intake from biofortified rice would reduce rates of anemia among these women by a minimum of 3% (e.g., from 53% to 50%) and perhaps by as much as 6%. This is an estimate of the percentage of women who would cross above the threshold of 12 g dL^{-1} hemoglobin as a result of consuming biofortified rice. Women who remain below this threshold presumably also derive some benefit from a 50% increase in iron intake.

For this same rural Bangladeshi population, it is also possible to estimate the percentage increase in total provitamin-A intake provided by “Golden Rice” (1.6 µg ß-carotene per gram of dry rice endosperm; Ye et al 2000). For this poor population, animal and fish intakes provide only 3% of total energy (Bouis et al 1998) so that retinol intake is negligible and vegetables provide more than 90% of total provitamin-A intake. If the provitamin A in both vegetables and Golden Rice are converted to retinol equivalents at a rate of 26 to 1, total provitamin-A intake is increased by 23-26% for adult women and preschool children. If provitamin A in vegetables is converted to retinol equivalents at a rate of 26 to 1 and provitamin A in Golden Rice at a rate of 6 to 1, total provitamin-A intake is increased by 79-90% for adult women and preschool children. There is some speculation that the beta-carotene in rice endosperm will be more easily converted to retinol than beta-carotene in vegetables because of the physical characteristics of the rice endosperm matrix.

What are the costs and benefits of a biofortification strategy? How do these compare with supplementation and fortification?

Although their benefit-cost ratios are quite high, supplementation and fortification programs must be sustained at more or less the same level of funding year after year in any given country. If investments are not sustained, benefits of course disappear. Some back-of-the-envelope calculations can be made for the costs of supplementation and fortification in South Asia, which has a total population of roughly 1.25 billion people.

Although the costs of vitamin-A pills themselves are low, an often-quoted cost of vitamin-A supplementation that includes the delivery cost is US$0.50 per person per year ($0.25 per capsule; World Bank 1994). If one in 12.5 persons in South Asia were to receive supplements (100 million people in total), this would cost $50 million per year, or $500 million over ten years. An often-quoted cost of iron fortification is $0.12 per person per year (World Bank 1994). If a particular food vehicle to be fortified with iron were to reach 33% of the total (but untargeted) population in South Asia (412 million people), the total cost would again be $50 million annually, or $500 million over ten years. In absolute terms, these may seem to be large amounts of money, but they are very worthwhile investments and are actually quite small percentages of the total economic activity of the South Asian economies.

Nevertheless, in contrast, investments in plant breeding research and dissemination are far lower. The development of iron- and zinc-dense varieties of rice or wheat might cost as much as $10 million each over ten years, including the costs of nutrition-efficacy tests, the costs of dissemination in selected regions, and the costs of a nutrition and economic impact evaluation. Moreover, such an investment of $20 million in two crops, rice and wheat, would have multiplicative effects-benefits may accrue to countries all over the world, which then need only invest in adaptive breeding and dissemination. Moreover, benefits are sustainable at low maintenance costs-benefits from breeding advances typically do not disappear after initial investments and research are successful, as long as an effective domestic agricultural research infrastructure is maintained.

As an example of the enormous economic benefits of the biofortification strategy, a simulation model was developed for Bangladesh and India, based on the development of iron- and zinc-dense varieties of rice and wheat and assumed to be adopted on only 10% of approximately 83 million hectares planted to the two crops. The somewhat conservative assumptions suggest that the returns that come on-stream during the second decade of research and development would be about $4.9 billion on a total investment of $42 million, $1.2 billion in benefits from better nutrition and $3.7 billion in benefits from higher agricultural productivity (Hunt 2002).

A more formal economic evaluation, in which the ratio of the present value of benefits to the present value of costs (discounted at 3%, the rate commonly used for the evaluation of social benefits) was 19 for returns to better iron nutrition in humans alone, showed a ratio similar to that found by Horton and Ross (2001) for fortification in South Asia. This benefit-cost ratio rises to 79 if the benefits to higher agricultural productivity are included. A different way of expressing the concept of discounting over time is the internal rate of return, in which the interest rate at which benefits equal costs plus interest if the funds were borrowed to make the investment is calculated. In this case, the internal rate of return is 29% if only benefits to human nutrition are considered and is 44% if both benefits to human nutrition and higher agricultural productivity are considered.

In the longer term (years 11–25 of the simulation), it is estimated that a total of 44 million annual cases of anemia will be prevented if nutritionally improved varieties are adopted on 10% of the rice and wheat area in Bangladesh and India. This is based on a conservative assumption of only a 3% reduction in anemia among those consuming the high-iron rice (see above). This is a cost of about $1 per annual case of anemia prevented and a cost of $0.03 per person per year for those whose iron intake increases by 50% by consuming the high-iron rice and wheat,

Niche for biofortification

No single type of intervention can by itself solve the micronutrient malnutrition problem. A comprehensive strategy involving multiple types of interventions adapted to conditions in specific countries and regions is required. Biofortification complements existing strategies and has its own unique “niche,” as conditioned by the comparative advantages outlined above and technical characteristics, most importantly the level of the “dose” that biofortification can be expected to deliver. Biofortified crops do not need to provide the entire recommended daily allowance (RDA) to be effective in substantially reducing micronutrient deficiencies.

On any given day, biofortified staple foods cannot deliver as high a level of minerals and vitamins as supplements or industrially fortified foods, but they can help to bring millions over the threshold from malnourishment to micronutrient sufficiency. This potential is shown schematically in Figure 1, in which a high percentage of the iron-deficient population is shown to be relatively mildly deficient. For those who are severely deficient, supplements (the highest-cost intervention) are required.

Commercial fortification and biofortification (lower-cost, lower-“dose” strategies) then are highly complementary, in at least two ways, in treating the bulk of the iron-deficient population. First is a time dimension. Commercial fortification is a proven intervention and is already being implemented. If biofortification proceeds successfully, those being reached by biofortified crops will gradually reduce the

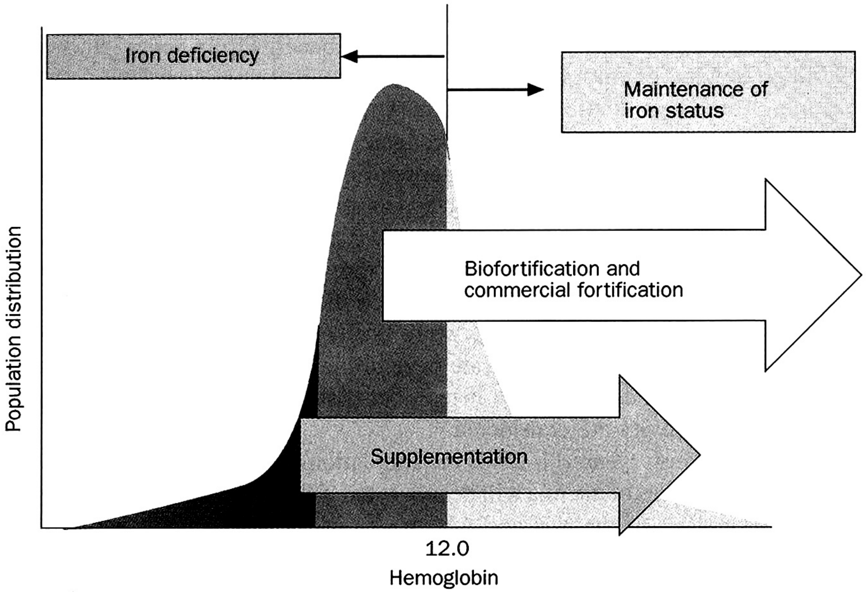


Fig. 1. Biofortification improves the status for those who are less deficient and maintains the status for all at a low cost.

need for commercial fortification. Second is a geographic dimension. Biofortification will reach rural populations most effectively and commercial fortification will reach urban populations most effectively.

Conclusions

Human nutritionists were once optimistic that supplementation and commercial fortification programs could do much to reduce micronutrient malnutrition prevalence rates. These programs can be cost-effective and they will continue to be needed for the foreseeable future, but a growing consensus is emerging among nutritionists (I) that the recurrent costs involved in these programs are unsustainable if they are to be comprehensive, (2) that these programs do not and cannot reach all who are in need, and (3) that the primary solution lies in better-quality food, which the poor desire but cannot afford.

Although plant breeding involves comparatively long lead times before it can have an appreciable impact, a significant start has now been made. The pace of progress in the years ahead will depend to a significant extent on the acceptance and support that this nontraditional approach receives from the plant breeding and human nutrition communities. For example, beginning in 2001, the Asian Development Bank has funded the development of a high-iron rice as part of a comprehensive strategy to overcome iron-deficiency anemia in Asia (Hunt 2002).

In conceptualizing solutions for a range of nutritional deficiencies, interdisciplinary communication between plant scientists and human nutritionists holds great potential. Human nutritionists need to be informed, for example, about the extent to which the vitamin and mineral density of specific foods, as well as compounds that promote and inhibit their bioavailability, can be manipulated through plant breeding. Plant breeders need to be sensitized to the major influence that they may have had on nutrient use in the past (e.g., are trace minerals in modern varieties more or less bioavailable than in traditional varieties?) and to the potential of plant breeding for future improvements in nutrition and health. As the world's resources for food production and other purposes become increasingly stressed, such interdependencies between agricultural systems and human nutrition will become increasingly obvious—and impossible to ignore in formulating solutions.

References

ACC/SCN (Administrative Committee on Coordination/Subcommittee on Nutrition of the United Nations and International Food Policy Research Institute (IFPRI). 2000. Fourth report on the world nutrition situation. Geneva (Switzerland): United Nations.

Bhargava A, Bouis H, Schrimshaw N. 2001. Dietary intakes and socioeconomic factors are associated with the hemoglobin concentration of Bangladeshi women. J. Nutr. 131(3):758-764.

Bouis H, de la Brière B, Guitierrez L, Hallman K, Hassan N, Hels O, Quabili W, Quisumbing A, Thilsted S, Zihad Z, Zohir S. 1998. Commercial vegetable and polyculture fish production in Bangladesh: their impacts on income, household resource allocation, and nutrition. Washington, D.C. (USA): International Food Policy Research Institute.

Hagenimana V, Low J. 2000. Potential of orange-fleshed sweet potatoes for raising vitamin A intake in Africa. Food Nutr. Bull.21(4):414-418.

Horton S, Ross J. 2001. The economics of iron deficiency. Toronto (Canada): Economics Department, University of Toronto.

Hunt JM. 2002. Reversing productivity losses from iron deficiency: the economic case. J. Nutr. 132(4S):794S-801S.

World Bank. 1994. Enriching lives: overcoming vitamin and mineral malnutrition in developing countries. Development in Practice Series. Washington, D.C. (USA): World Bank.

Ye X, Al-Babili S, Kloti A, Zhang J, Lucca P, Beyer P, Potrykus I. 2000. Engineering the provitamin A (ß-carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. Science 287:303-305.

Notes

Author's address: International Food Policy Research Institute, Washington, D.C., USA.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Differential rates of energy release from rice and effects on satiety

I. Tetens, K.A. Kabir, S. Parvin, and S.H. Thilsted

Consumers characterize rice varieties based on how “filling” they are, that is, their satiety capacity. As starch provides almost 90% of the energy from rice, the rate of starch digestion and absorption has been suggested as an indicator of satiety of rice.

In vitro studies on rice have shown that the rate of starch digestion is significantly associated with rice variety and processing methods. In vivo studies measuring the glycaemic index of rice have confirmed that the rate of rice starch digestion and absorption is significantly associated with several of the physical and chemical parameters included in most breeding programs (amylose content, gelatinization temperature, and minimum cooking time).

Studies in healthy humans have suggested that an increased rate of starch digestion and absorption is associated with lessened satiety. A recent study conducted among low-income males in rural Bangladesh suggested that the satiety capacity of rice varieties was measurable. In this study, a high-amylose rice had a significantly ($P < 0.05$) higher satiety capacity than a low-amylose rice.

Methods to measure satiety capacity of rice need to be validated further in other population groups and for longer periods. To ensure the successful introduction of future high-quality rice varieties, indicators of consumer preferences of satiety capacity should be incorporated in breeding programs.

Rice grain quality becomes more important in the selection of future rice varieties as rice supply increases and/or consumer income grows (Unnevehr et al 1992). Rice grain quality and quality preferences vary across countries and regions but some quality preferences are widely shared. In an international study on consumer demands for rice grain quality, it was found that low-income consumers often prefer rice that is more filling (Unnevehr et al 1992). With the rapid global increase in the prevalence of overweight and obesity, also in low-income countries (WHO 1998), we can expect that the international demand for foods with a high satiety capacity will increase.

Rice eating and cooking quality has been correlated with the chemical composition and physical properties of rice. Especially the properties of rice starch—apparent amylose content, starch gelatinization temperature, and, among high-amylose rice, gel consistency—have been shown to influence the eating and cooking quality of milled rice (Juliano 1990).

Starch is the major constituent of energy in rice and provides almost 90% of the dry matter in milled rice. The rate of starch digestion and absorption has therefore been suggested as a useful indicator of the rate of energy availability of different rice varieties (Tetens et al 1997).

Measurements of rate of starch digestion and absorption from rice

In vitro studies

Different in vitro methods are available for measuring starch digestion. Some methods are set up to measure the release of glucose from total starch while others attempt to measure the rate of glucose release from starch. In most in vitro digestion methods, different enzymes are added and pH is controlled to simulate the digestion of starch in the gastrointestinal tract. The amount of glucose released is measured at different times, depending on the purpose of the study. A minor part of the starch not broken down by the enzymatic treatment is designated resistant starch (RS).

In selected Bangladeshi indica rice variety samples (n = 13), the total amount of starch and the rate of starch digestion were measured using the in vitro method of Englyst et al (1992) (Tetens et al 1997). Total starch (TS) was determined as the glucose released by controlled enzymatic hydrolysis following gelatinization in boiling water and treatment with 7 M KOH to disperse retrograded amylose. Rapidly digestible starch (RDS) and slowly digestible starch (SDS) were determined on aliquots as the glucose released by enzymatic hydrolysis after 20 min and 120 min, respectively. To express the rate of starch digestion, the starch digestion index (SDI) was calculated as RDS as a percentage of TS. Thus, the higher the SDI values, the more rapid is the digestion of the starch. The results showed that the SDI values of the selected rice varieties varied from (mean ± SD) 70.4 ± 2.5 to 96.5 ± 2.1 in milled unparboiled rice and from 65.9 ± 4.9 to 97.6 ± 4.7 in milled parboiled rice (Fig. 1). Overall, parboiling significantly ($P < 0.0001$) reduced the amount of the RDS in the rice samples and resulted in lower SDI values (Table 1). A significant ($P < 0.001$) negative correlation of r = -0.79 between SDI and the apparent amylose content was found in both the unparboiled and parboiled rice samples. Minimum cooking time was significantly ($P < 0.05$) and inversely related to SDI in the parboiled rice (with a correlation coefficient of r = –0.61). Widths and shapes of the raw grains and elongation after cooking were significantly correlated with the SDI values for the unparboiled rice, but not for the parboiled rice (Table 2) (Tetens et al 1997).

Resistant starch is mainly amylose that escapes digestion in the small intestine. RS acts as soluble dietary fibers in the large intestine, being fermented to volatile short-chain fatty acids (SCFA) by the microflora. The energy contribution from SCFA is only around 70% of the energy from glucose absorption in the small intestine

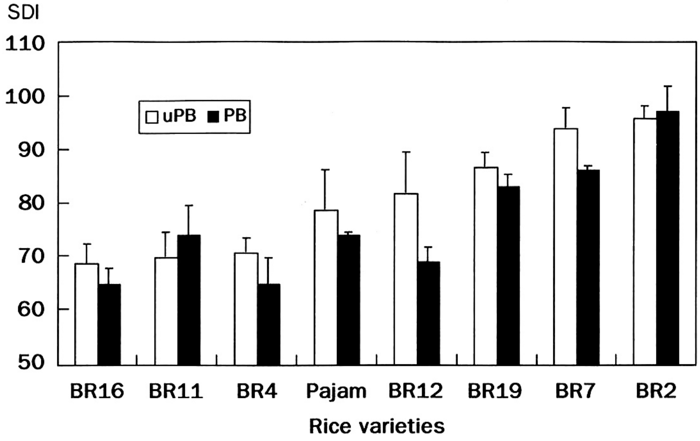


Fig. 1. Starch digestion index (SDI) of selected unparboiled (uPB) and parboiled (PB) modern Bangladeshi rice varieties (mean ± SD).

Table 1. Total starch (TS), types of starch (RDS[a], SDS[b]), and starch digestion index (SDI) of unparboiled (uPB) and parboiled (PB) milled rice samples (g 100 g^{-1} as eaten).

Item	Dry matter	TS	RDS	SDS	SDI
uPB rice (n = 13)	25.6	22.2	17.6	4.5	80.0
PB rice (n = 13)	25.0	21.9	16.0	5.4	73.7
SE[c]	–	0.6	0.9	0.9	3.4
Statistical significance of					
Variety, *P*<	–	0.001	0.001	0.001	0.001
Parboiling, *P*<	–	ns	0.001	ns	0.001
Variety × parboiling, *P*<	–	0.001	ns	ns	0.001

[a] RDS = rapidly digestible starch. [b] SDS = slowly digestible starch. [c] SE = standard error of analysis between processing method within varieties. ns = not significant.
Source: Tetens et al (1997).

Table 2. Correlation coefficients[a] between starch digestion index (SDI) and physico-chemical characteristics of 13 unparbolied (uPB) and parboiled (PB) milled rice samples.

Characteristic	UPB	PB	uPB and PB
Amylose content	–0.77**	–0.91***	–0.79***
Width	–0.73**	4.17	–0.40
Shape, length/width ratio	0.67*	0.21	0.42*
Elongation ratio	4.61*	–0.30	–0.44*
Minimum cooking time	–0.24	–0.61*	–0.40*

[a] Pearson's correlation coefficients. * = P <0.05, ** = P <0.01, *** = P <0.001.
Source: Tetens et al (1997).

(Cummings 1983). The content of RS in milled rice has been reported in few studies. However, different studies using different methods have resulted in slightly different values. Juliano (1992) reported that the content of RS measured by the method of Berry (1986) in milled cooked rice varieties ranged from 1.5% to 2.8% of dry matter (DM) and that the content of RS in milled parboiled rice ranged significantly higher, from 3.8% of DM in rice parboiled at 100 °C to 4.7% of DM in rice parboiled at 120 °C. In our study, we measured RS by the method of Englyst et al (1992) and obtained mean values of 0.1 % of DM in the unparboiled rice and 0.4% of DM in the parboiled rice (Tetens et al 1997). Low values of RS were found in both studies and it was seen that parboiling increased the amount of RS significantly. Other heat-processing methods such as noodle extrusion are reported to result in similar increases in RS (Juliano 1992). Theoretically, an increase in RS leads to a small reduction in total energy availability, which is difficult to measure.

It is well documented that changes in the chemical and physical properties of rice grains occur during aging of rice and thus affect the overall eating quality of the rice grain. Aging or storage for 3-4 months after harvest makes the resulting cooked rice more flaky and is desirable for indica rice but not for japonica rice (Juliano 2001). It is common practice to store the rice for a few months before consumption. Compared with freshly harvested rice, aged rice has a higher imbibition ratio and is less sticky. In a study on the effect of aging on the rate of starch digestion in selected Bangladeshi indica rice varieties, we used the Englyst in vitro method described above. The study examined three modern high-yielding rice varieties with high apparent amylose (27%) content, one modern high-yielding rice variety with intermediate apparent amylose (24%) content, two traditional popular rice varieties with high apparent amylose (25%) content, and one traditional rice variety with low apparent amylose (8%) content. All varieties were grown in the same season under the same conditions at the Bangladesh Rice Research Institute (BRRI), thus minimizing the environmental effect on the grain. After harvest, samples of the rice varieties-unparboiled and parboiled-were stored at ambient temperatures for up to 135 days after harvest. The low-amylose rice variety was stored only as unparboiled rice. On day 0 and day 15 and then with 30-day intervals postharvest, samples were taken and stored at -20 °C until further analysis. The SDI was measured in all samples over consecutive days in a random order. No significant differences were found for any of the rice varieties between the rate of rice starch digestion and time of storage, up to 4.5 months at ambient temperature. It was confirmed that the apparent amylose content of rice was inversely correlated to the rate of starch digestion and that parboiling resulted in significantly lower rates of starch digestion. No differences in rate of starch digestion were found between modern high-yielding and traditional rice varieties (Kabir et al 2001).

In vivo studies

In vivo studies include both animal and human studies in which blood glucose concentrations are measured at different times after intake of a meal and the results are expressed in relation to the blood glucose concentrations of a standard food. The standard food is usually white bread. The results are expressed as glycaemic index (GI) or incremental area under the curve (AUC). In human studies, the GI is often supported by an insulinaemic index (Brand Miller et al 1992).

Rat digestibility studies have traditionally been used to measure availability of total starch and total energy from rice. By adding antibiotics to the feed, the microflora in the large intestine are suppressed, making it possible to estimate the amount of starch resistant to digestion and absorption in the small intestine. By using this method, the abovementioned in vitro studies confirmed that the amount of resistant starch was significantly higher in cooked parboiled rice than in unparboiled rice, with parboiling reducing the total energy availability from 1.8% to 3.2% (Eggum et al 1993). However, the in vivo RS and unavailable energy did not correlate well with the in vitro RS, leading to the conclusion that the differences in starch properties are expressed better in terms of the rate than the extent of digestion of cooked rice starch (Juliano 1992).

In a series of rat studies, we investigated whether the in vitro results for the rate of starch digestion could be confirmed in the rat model. After a 12-hour fast, the rate of glucose digested and absorbed was measured from blood samples collected from the tip of the tail at 15 min before a test meal and at 0, 15, 30, 45, 60, 90, 120, and 180 min after. The test meals used comprised selected rice varieties, differing with respect to the content of apparent amylose, gelatinization temperature, and other physico-chemical parameters. The results showed that the incremental AUC for the blood glucose concentrations was significantly ($P < 0.05$) higher for the low-amylose parboiled rice than for the high-amylose parboiled rice. These results indicate that the rat may be a useful model for measuring the rate of starch digestion and absorption.

The rate of rice starch digestibility and absorption has been reported in numerous human test meal studies, with GI values ranging from 54 to 132 (Wolever et al 1986, Foster-Powell and Brand Miller 1995). This wide range has led to disagreements as to whether rice should be considered a high or a low GI food (Brand Miller et al 1992). Some of the discrepancies among the GI values of rice are related to the physico-chemical characteristics of the rice.

Amylose content has been found to be a strong determinant for the rate of rice starch digestion and absorption in human studies. In several studies, a high amylose content has been associated with a lower glycaemic response compared with intermediate or low-amylose rice (Juliano and Goddard 1986, Brand Miller et al 1992, Larsen et al 1996). The lower rate of starch digestion and absorption of rice with a high amylose content can partly be explained by the lower enzyme attack in the more compact starch structure of the linear amylose compared with the more spherical amylopectin structure. Further, the amylose molecules may form extensive hydrogen bonds that render the molecules less susceptible to enzymatic degradation. In addition, amylose has been reported to form amylose-lipid complexes that may reduce the starch digestion rate. Cereals with a high amylose-amylopectin ratio have been found to give lower glycaemic responses than those with a low amylose-amylopectin ratio (Granfeldt et al 1994).

Wolever et al (1986) were the first researchers to report that parboiling of rice may elicit a lower glycaemic response than unparboiled rice. In a group of non-insulin-dependent diabetic (NIDDM) and insulin-dependent diabetic (IDDM) subjects, they found that the GI (mean ± SE) of long-grain white parboiled rice (67 ± 5) was significantly lower than that of regular long-grain white rice (83 ± 5). A later study on the GI of different rice products available in the Australian market included a comparison of unparboiled and parboiled rice samples (Brand Miller et al 1992). No significant difference was found between the GI (mean ± SE) of the parboiled rice (121 ± 10) and that of the unparboiled rice (130 ± 15) (results converted from a glucose reference to a white bread reference by multiplying with a factor of 1.4).

Parboiling is popular in certain regions and, on the international market, the demand for parboiled rice appears to be increasing (Larsen et al 2000, Juliano 2001). To elucidate the possible effects of parboiling per se, we conducted a study in NIDDM subjects measuring the glycaemic responses to rice parboiled by different methods (Larsen et al 2000). An indica long-grain rice variety (BR16) with apparent amylose content of 27% was chosen for the study. The rice was grown at the BRRI and all rice used for the study was from the same batch. One rice sample was not parboiled, a second rice sample was parboiled at BRRI using a mild traditional method, and a third sample was pressure-parboiled at a German pilot plant using an industrialized method. All three rice samples elicited significantly (P <0.05) lower GI values than white bread. The pressure-parboiled rice resulted in a significantly (P < 0.05) lower GI value (mean ± SE) of 39 ± 6 compared with that of the traditionally parboiled rice (46 ± 8), which was not significantly different from the GI of the unparboiled rice (55 ± 5). Differential scanning calorimetry showed the presence of amylose-lipid complexes in all rice samples and of retrograded amylopectin in the pressure-parboiled rice.

The importance of cooking time for the rate of starch digestion and absorption has been investigated in few human studies. In a study with NIDDM and IDDM subjects, Wolever et al (1986) reported that undercooking of regular rice (cooking time 5 min) resulted in significantly lower GI values (mean ± SE) of 58 ± 3.7 compared with GI values of 83 ± 3.7 for the same rice that had been cooked for 15 min. No effects on GI were measured when parboiled rice was overcooked (Wolever et al 1986). When the glycaemic response in healthy humans was measured after intake of three high-amylose rice varieties that were all cooked for 22 min, the GI values (mean f SE) obtained differed significantly, ranging from 61 ± 9 to 91 ± 12 (Panlasigui et al 1991). However, when the study was repeated with the same three rice varieties using their minimum cooking times, similar starch digestion rates and glycaemic responses were obtained. Use of the minimum cooking time ensures that the starch of the different rice varieties reaches the same degree of gelatinization. On the basis of these results, the authors emphasized that the amylose content alone is not the only predictor for starch digestion rate or glycaemic response. They concluded that other selected physico-chemical properties, such as gelatinization temperature, minimum cooking time, amylograph consistency, and volume expansion upon cooking, may all be valid predictors for the rate of starch digestibility and absorption in humans (Panlasigui et al 1991).

Different types of processing of rice have been shown to affect the rates of starch digestion and thereby the glycaemic response. The GIs of 12 different rice products available in the Australian market were measured in healthy subjects. The products included white and brown rice, rice cakes, and rice bran. With the exception of the low mean GI value of 27 for rice bran, all other rice products had mean GI values from 90 to 130 (using white bread as the reference food) (Brand Miller et al 1992). The authors concluded that the results "emphasize the need for individual countries to carry out their own GI testing, particularly of raw products that are more likely to vary from one geographical location to another than do processed products, such as breakfast cereals" (Brand Miller et al 1992).

The use of low-GI foods and diets has been advocated as a tool in the prevention and dietary management of diabetes and hyperlipidemia. Several researchers have suggested that the GI may be associated with hunger and satiety (Holt et al 1992, 2001, Raben et al 1996, Holt and Brand Miller 1995, Roberts 2000) and that low-GI foods that produce longer blood glucose responses increase satiety compared with high-GI foods (A. Raben, personal communication). Most studies in this area have been conducted in Western countries.

Measurements of satiety with rice

Satiety is defined as the state where there is little or no general drive or motivation for eating. Satiety can be categorized as "acute satiety" or "long-term satiety," covering the time of eating during the meal and the time between two meals, respectively (Blundell 1979). Different methods are available to obtain information about the degree of satiety of an individual. One method often applied in satiety studies is the use of a visual analogue scale (VAS) in which subjective satiety and hunger are assessed at different times before and after a meal by the use of a rating scale. A different way to assess satiety and hunger is to measure directly at a meal the *ad libitum* food intake of the individual with free access to the food that is to be tested. This method assumes that an individual eats to the same degree of fullness at each meal when the food is being tested. In several studies, the two abovementioned methods are combined.

Satiety measurements of rice products were first reported for Australian rice products, comparing pairs of rice foods containing the same amount of starch: high-amylose vs. low-amylose puffed rice cakes and an ordinary vs. a quick-cooking rice (Holt and Brand Miller 1995). After consumption of the products, subjective satiety ratings and plasma glucose and insulin concentrations were measured over a 2-h period. Immediately afterward, the subjects ate freely from a limited range of food items and the amount of food and drinks consumed was recorded. The satiety of the different rice products (using the AUC for subjective satiety) was 1.5 times higher for the high-amylose rice cakes than for the low-amylose rice cakes and 1.5 times higher for the ordinary rice than for the quick-cooking rice. Conversely, glucose

Table 3. Rice and energy intake by rice variety (mean ± SD).

Meal and energy intake	Low-amylose rice	High-amylose rice	Level of significance
Breakfast			
Rice intake, g person^{-1a}	309 ± 29	309 ± 29	ns[b]
Energy from rice, kJ	1,940 ± 180	1,535 ± 145	$P<0.001$
Lunch			
Rice intake, g person^{-1}	633 ± 259	566 ± 180	ns
Energy from rice, kJ	3,965 ± 1,625	2,810 ± 890	$P<0.001$
Breakfast + lunch			
Energy from rice, kJ	5,880 ± 1,655	4,345 ± 895	$P<0.001$

[a] No. of persons in study = 23. [b] ns = nonsignificant.

response was 1.5 times higher for the low-amylose rice than for the high-amylose rice and 1.6 times higher after the quick-cooking rice than after the ordinary rice, 2 h after consumption of the products. These results clearly suggest that a slower rate of rice starch digestion is associated with a lower satiety capacity. However, it is unknown whether similar results would be obtained in different population groups.

We conducted a satiety study in Bangladesh where rice is the staple food, constituting about 80% of total energy intake in the rural population. Based on the previous results from the human glycaemic index studies, two rice varieties were selected: a high-amylose rice and a low-amylose rice with an apparent amylose content of 26.5% and 7.6%, respectively. Twenty-three healthy Bangladeshi men aged (mean ± SD) 40 ± 12 years participated in the study on two separate days. The men were randomly assigned to one of the two rice varieties using a crossover design. On one day, the same rice variety, together with an amount of spicy vegetable sauce equivalent to 10% of the weight of the cooked rice, was served at both breakfast and lunch. At breakfast, an amount of cooked rice calculated to provide the same amount per kg of body weight for each individual was consumed. At lunch, rice was served *ad libitum* until each individual reached full satiation and the consumption of rice and vegetable sauce was carefully weighed. The average rice and energy intakes at both breakfast and lunch and for both meals together are shown in Table 3. The rice intake at lunchtime tended to be higher for the low-amylose rice than for the high-amylose rice. However, the energy intake from the low-amylose rice was significantly ($P<0.001$) higher than that from the high-amylose rice. At breakfast, the mean energy intake was 1.3-fold higher after the low-amylose rice than after the high-amylose rice. At lunchtime, the mean energy intake was 1.4-fold higher after the low-amylose rice than after the high-amylose rice. These results are thus in line with the abovementioned Australian study and indicate that low-amylose rice has a lower satiety capacity than high-amylose rice. High-amylose rice is commonly preferred in certain Southeast Asian countries (Juliano 2001).

Conclusions

Satiety is an important quality parameter for rice consumers. There are different direct and indirect methods to measure the satiety capacity of different rice varieties. More long-term studies are needed to verify that these methods are valid for different population groups of rice consumers (for example, with high and low rice intakes, young and old consumers). The few studies that have been conducted on satiety of rice suggest that high-amylose rice varieties exert a higher satiety capacity than low-amylose rice varieties. To ensure the successful introduction of future high-quality rice varieties, indicators for the satiety capacity of rice should be incorporated in breeding programs.

References

Berry CS. 1986. Resistant starch: formation and measurement of starch that survives exhaustive digestion with amylolytic enzymes during the determination of dietary fibre. J. Cereal Sci. 4301-314.

Blundell J. 1979. Hunger, appetite and satiety: constructs in research of identities. In: Turner M, editor. Nutrition and lifestyles. Proceedings of the British Nutrition Foundation, First Annual Conference. London (UK): Applied Science Pub. Ltd. p 21-42.

Brand Miller J, Pang E, Bramall L. 1992. Rice: a high or low glycemic index food? Am. J. Clin. Nutr. 56:1034-1036.

Cummings JH. 1983. Fermentation in the human large intestine: evidence and implications for health. Lancet 1:1206-1208.

Eggum BO, Juliano BO, Perez CM, Adeco EF. 1993. The resistant starch, undigestible energy and undigestible protein contents of raw and cooked milled rice. J. Cereal Sci. 18:159-170.

Englyst HN, Kingman SM, Cummings JH. 1992. Classification and measurement of nutritionally important starch fractions. Eur. J. Clin. Nutr. 46(suppl):S33-50.

Foster-Powell K, Brand Miller J. 1995. International tables of glycaemic index. Am. J. Clin. Nutr. 62:8718-893S.

Granfeldt Y, Liljeberg H, Drews A, Newman R, Bjorck I. 1994. Glucose and insulin responses to barley products: influence of food structure and amylose-amylopectin ratio. Am. J. Clin. Nutr. 59: 1075-1082.

Holt S, Brand J, Soveny C, Hansky J. 1992. Relationship of satiety to postprandial glycaemic, insulin and cholesystokinin responses. Appetite 18: 129- 141.

Holt SHA, Brand Miller J. 1995. Increased insulin responses to ingested foods are associated with lessened satiety. Appetite 24:43-54.

Holt SHA, Brand-Miller JC, Stitt PA. 2001. The effects of equal-energy portions of different breads on blood glucose levels, feeling and fullness and subsequent food intake. J. Am. Diet. Assoc. 101:767-773.

Juliano BO, Goddard MS. 1986. Cause of varietal differences in insulin and glucose responses to ingested rice. Qual. Plant Plant Foods Hum. Nutr. 36:35-41.

Juliano BO. 1990. Rice grain quality: problems and challenges. Cereal Foods World 35:245-253.

Juliano BO. 1992. Structure, chemistry, and function of the rice grain and its fractions. Cereal Foods World 37:772-779.

Juliano BO. 2001. Asian perspective on rice sensory quality. Cereal Foods World 46:531-535.

Kabir KA, Ferdous N, Dipti SS, Thilsted SH, Tetens I. 2001. The effect of ageing of rice on the rate of starch digestion. Ann. Nutr. Metab. 45(Suppl 1):75.

Larsen HN, Christensen C, Rasmussen OW, Tetens I, Choudhury NH, Thilsted SH, Hermansen K. 1996. Influence of parboiling and physico-chemical characteristics of rice on the glycaemic index in non-insulin-dependent diabetic subjects. Eur. J. Clin. Nutr. 50:22-27.

Larsen HN, Rasmussen OW, Alstrup KK, Biswas SK, Tetens I, Thilsted SH, Hermansen K. 2000. Glycaemic index of parboiled rice depends on the severity of processing: study in type 2 diabetic subjects. Eur. J. Clin. Nutr. 54:380-385.

Panlasigui LN, Thompson LU, Juliano BO, Perez CM, Yiu SH, Greenberg GR. 1991. Rice varieties with similar amylose content differ in starch digestibility and glycaemic response in humans. Am. J. Clin. Nutr. 54:871-877.

Raben A, Holst JJ, Christensen NJ, Astrup A. 1996. Determinants of postprandial appetite sensations: macronutrient intake and glucose metabolism. Int. J. Obes. 20:161-169.

Roberts SB. 2000. High-glycemic index foods, hunger, and obesity: Is there a connection? Nutr. Rev. 58:163-169.

Tetens I, Biswas AK, Glitsca LV, Kabir KA, Thilsted SH, Choudhury NH. 1997. Physico-chemical characteristics as indicators of starch availability from milled rice. J. Cereal Sci. 26:355-361.

Tetens I, Thilsted SH, Choudhury NH, Hassan N. 1998. The rice-based diet in Bangladesh in the context of food and nutrition security. Scand. J. Nutr. 42:77-80.

Unnevehr LJ, Duff B, Juliano BO. 1992. Consumer demand for rice grain quality. Manila (Philippines): International Rice Research Institute, and Ottawa (Canada): International Development Research Centre. 248 p.

WHO (World Health Organization). 1998. Obesity: preventing and managing the global epidemic. Report of a WHO consultation on obesity. Geneva (Switzerland): WHO. 276 p.

Wolever TMS, Jenkins DJA, Kalmusky J, Jenkins A, Giordano C, Giudici S, Josse RG, Wong GS. 1986. Comparison of regular and parboiled rices: explanation of discrepancies between reported glycaemic responses to rice. Nutr. Res. 6:349-357.

Notes

Authors' addresses: I. Tetens and S.H. Thilsted, Research Department of Human Nutrition, The Royal Veterinary and Agricultural University, 1958 Frederiksberg C, Denmark; K.A. Kabir, Grain Quality and Nutrition Division, Bangladesh Rice Research Institute (BRRI), Gazipur 1701, Bangladesh; S. Parvin, Research Division, Bangladesh Institute of Research and Rehabilitation in Diabetes, Endocrine and Metabolic Disorders (BIRDEM), Dhaka 1000, Bangladesh.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Crop management, climate change, and mechanization

Editor: S. Peng

Principles and practices of real-time nitrogen management: a case study on irrigated rice in China

S. Peng, R. Buresh, J. Huang, J. Yang, G. Wang, X. Zhong, and Y. Zou

Rice production consumes about 20% of the total N fertilizer used for agriculture in the world. This N fertilizer is often not effectively used by irrigated rice because of improper timing and rates of application. Excessive rates of N fertilizer can lead to losses of inorganic N from agricultural lands into surface water and groundwater, thereby threatening our environment. Traditional methods of fixed N fertilizer scheduling might be inappropriate for maximization of fertilizer N-use efficiency in current rice production systems because these practices do not consider the dynamic nature of N supply and demand in irrigated rice ecosystems. Real-time N management was developed on the basis of the physiology of rice leaf photosynthesis, tillering, and leaf area growth to optimize canopy development and maximize biomass accumulation and yield formation. A chlorophyll meter (SPAD) or leaf color chart (LCC) is used to monitor leaf N status and determine the timing of N application in real-time N management. Both SPAD and LCC measurements correlate closely with leaf area-based N content. A single critical value of SPAD and LCC can be used to determine the need for N topdressing throughout a growing season. The critical values of the SPAD reading and LCC score, however, differ depending on cultivar, location, and season. Real-time N management using SPAD or LCC has been tested in several countries and several sites in China. SPAD- or LCC-based N management improved fertilizer N-use efficiency by reducing total N input in most cases and by increasing grain yield in some cases. Results of the N-response curve, real-time N management using SPAD, and site-specific N management (SSNM) indicated that farmers in China overapplied N to the rice crop by at least 50%. The overapplication of N occurred mainly during the early vegetative stage (within 10 days after transplanting). Indigenous N supply capacity at Chinese sites was 54% higher than that at IRRI, but farmers did not adjust the N rate for the high N supply from soil in

China. The improper timing and rate of N application were largely responsible for poor agronomic N-use efficiency (AE) at Chinese sites. The poor AE was caused by low physiological N-use efficiency (PE). Nitrogen uptake ability was not the major limiting factor for fertilizer N-use efficiency of the rice crop in China. There is a great possibility to optimize the timing and rate of N application in irrigated rice in China through real-time N management and SSNM.

Nitrogen (N) is considered to be the most important input for rice production under irrigated conditions. This is because N fertilizer generally accounts for 35% of the total external input (including fertilizers, pesticides, seeds, and irrigation water) in the production of irrigated rice crops. Moreover, N management and solar radiation are the two major factors governing rice yield for a given cultivar in the favorable irrigated ecosystem.

Crop yields in the world have continuously increased to meet population growth, partly because of the increase in fertilizer nutrient input, especially N fertilizer. To maximize grain yield, farmers often apply a higher amount of N fertilizer than the minimum required for maximum crop growth. The relatively cheap price of N fertilizer has also stimulated excessive N application. Global use of N fertilizer increased over sevenfold, from 11.6 million tons (based on elemental N) in 1961 to 85.5 million t in 1999 (FAO 2001). Today, rice production consumes about 20% of the total N fertilizer used for agriculture in the world.

Fertilizer N-use efficiency is relatively low in irrigated rice because of rapid N losses from ammonia volatilization, denitrification, surface runoff, and leaching in the soil-floodwater system (Vlek and Byrnes 1986, De Datta and Buresh 1989). The magnitude and nature of N losses vary depending on the timing, rate, and method of N application, source of N fertilizer, soil chemical and physical properties, climatic conditions, and crop status. In general, ammonia volatilization is the major pathway of N loss in irrigated rice (Zhu 1997). Recovery efficiency (RE, i.e., uptake efficiency) of applied N fertilizer is usually 30-50% in the tropics (De Datta 1986). Zhu (1985) reported that RE was less than 30% for ammonium bicarbonate and 30-40% for urea in China. Cassman et al (1996) reported that agronomic N-use efficiency (AE) was 15 to 18 kg rough rice per kg applied N in the dry season in farmers' fields in the Philippines. In China, AE was 15-20 kg kg^{-1} N from 1958 to 1963 and declined to only 9.1 kg kg^{-1} N from 1981 to 1983 (Lin 1991).

Excessive N application and poor N management reduce the profit of rice farmers by increasing production costs and reducing grain yield. Furthermore, low fertilizer N-use efficiency with high N loss has many environmental consequences. Surface runoff and leaching may result in groundwater pollution and the eutrophication of surface waters in lakes and rivers. Denitrification contributes to global warming by emitting greenhouse gases such as nitrous oxide (N_2O).

The traditional practice of fixed N fertilizer scheduling might be inappropriate for maximization of fertilizer N-use efficiency in current rice production systems because these approaches do not consider the dynamic nature of N supply and demand in irrigated rice ecosystems. Real-time N management was developed based on the physiology of rice leaf photosynthesis, tillering, and leaf area growth to optimize canopy development and maximize biomass accumulation and yield formation.

Principles of real-time nitrogen management

Leaf N content is closely related to photosynthetic rate (Yoshida and Coronel 1976, Peng et al 1995a). Nitrogen application during the vegetative growth stage aims to promote growth by accelerating leaf area expansion and tiller production. Maintaining high leaf N content during the ripening phase improves grain filling by slowing down leaf senescence. During the reproductive phase, the goal of N management is to achieve a healthy canopy. A healthy canopy should have optimum leaf N content, leaf area index (LAI), and tiller number to maximize canopy photosynthetic rate, biomass accumulation, and yield formation. A healthy canopy should also have erect leaves, good light penetration and ventilation, and minimum disease and pest infestation. Jiang (1993) proposed to quantify healthy canopy using the canopy index. The canopy index is the product of LAI and leaf N concentration (N%). A canopy with a critical canopy index of 39.4 at heading was considered healthy (Jiang 1993). Within the critical canopy index, filled spikelets and yield were positively correlated with canopy index. When N is the major growth-limiting factor such as irrigated rice grown under favorable conditions, leaf N status positively correlates with LAI, tiller number, and canopy size. Under such conditions, optimum leaf N status is an indication of a healthy canopy. The objective of real-time N management is to achieve optimum leaf N status throughout the growing season. Real-time N management is also called crop need-based N management in which timing and rate of N application depend on crop N demand (Peng et al 1996). Because leaf N content is closely related to photosynthetic rate and biomass production, it is a sensitive indicator of the dynamic changes in crop N demand within a growing season. Therefore, the key for developing real-time N management is to establish a method for rapid diagnosis of leaf N status and to determine the critical leaf N content. The direct measurement of leaf N concentration by laboratory procedures is laborious, time-consuming, and costly. Such procedures have limited use as a diagnostic tool for optimizing N topdressing because of the extensive time delay between sampling and obtaining results.

The chlorophyll meter (SPAD) provides a simple, quick, and nondestructive method for estimating leaf chlorophyll content (Watanabe et al 1980). The ability to predict chlorophyll content on a leaf area basis from SPAD readings was demonstrated in several crops (Jiang and Vergara 1986, Takebe and Yoneyama 1989, Dwyer et al 1991). Since chlorophyll content in a leaf is closely correlated with leaf N concentration (Evans 1983, Blackmer and Schepers 1994), the measurement of chlorophyll provides an indirect assessment of leaf N status. However, the linear relationship between leaf N concentration on a dry weight basis (N_{dw}) and SPAD reading differs markedly depending on growth stage and rice cultivar. Differences in leaf thickness (reflected by specific leaf weight, SLW) are largely responsible for variations in the relationship between N_{dw} and SPAD values (Peng et al 1993). When leaf N was expressed on a leaf area basis (N_a), there was a similar linear correlation between SPAD values and N_a for all stages of development and genotypes tested (Peng et al 1995b). The most recent fully expanded leaf is usually considered as the index leaf to reflect rice leaf N status. Peng et al (1996) proposed that a single SPAD threshold value can be used to determine the need for N topdressing during the entire growing season of a cultivar, because N_{dw} of the index leaf decreases and SLW increases with plant age while SPAD values and N_a remain relatively constant throughout the growing season. Moreover, single-leaf photosynthetic rates were more closely correlated with N_a than with N_{dw}, and grain yields approaching yield potential levels could be achieved when N_a of the index leaf was maintained at or slightly above 1.4 g m^{-2} for IR72 (Peng et al 1996). Leaves with N_a at this critical level give a SPAD value of 35 regardless of developmental stage or genotype. In the SPAD-based N management, SPAD measurements were taken weekly on the most recent fully expanded leaves from 15 days after transplanting (DAT) to flowering. A topdressing of 30-45 kg N ha^{-1} during the dry season and 20-30 kg N ha^{-1} during the wet season was applied when the SPAD value fell below 35 for most modem indica cultivars. No basal N fertilizer was applied in the SPAD-based treatment if the zero-N plot produced more than 4 t grain ha^{-1}.

Instead of using an absolute SPAD value as the threshold, Hussain et al (2000) used a single SPAD sufficiency index to determine the timing of N topdressing. The sufficiency index was calculated as the percentage of the SPAD reading in the SPAD-based plot to the SPAD reading in the well-fertilized plot. To ensure that no N deficiency occurred in the reference treatment, the well-fertilized plot received 180% to 200% of the commonly recommended N rate in the fixed timing practice. When the sufficiency index fell below 90%, 30 kg N ha^{-1} was topdressed.

Huang et al (2003) compared six SPAD meters and determined the differences in SPAD readings among the meters. Correlations among the six SPAD meters were statistically significant ($P < 0.01$) with correlation coefficients *(r)* ranging from 0.971 to 0.990. The differences in SPAD readings were statistically significant among the six meters ($P < 0.05$) and the difference between two meters was as large as 2.7 units. When as many as 2.7 units of deviation could exist among different SPAD meters, users should consider the deviation when they use the suggested critical SPAD value from other sources. Otherwise, there is a possibility that the optimum timing of N application could be missed by 1 week or more. Therefore, it is desirable to use the same SPAD meter to determine the critical SPAD value and to take in-season SPAD measurements for real-time management. If several SPAD meters are used for multilocation trials on real-time N management, one should consider the possible variations in SPAD readings among different SPAD meters. If the difference is significant, one should standardize the SPAD meters.

The relatively high price of the SPAD meter limits its use by individual farmers. Another simple, quick, and nondestructive method for estimating leaf N status is a leaf color chart (LCC). Several types of LCC were developed to determine leaf greenness in rice. The most common ones are the LCC developed by the International Rice Research Institute (IRRI), Zhejiang Agricultural University (ZAU), China, and the University of California, Davis (UCD), USA. The gamut of green colors is visually different among the three LCC. Unlike the SPAD, which measures light absorption, an LCC measures leaf greenness and the associated leaf N by visually comparing light reflection from the surface of leaves and the LCC. Yang et al (2003) reported that strong correlations existed among the scores of the three types of LCC (*r* range of 0.93-0.99). There was a linear relationship between LCC scores and N_{dw} at each growth stage (R^2 range of 0.25-0.97) and across growth stages (R^2 range of 0.46-0.62). Adjusting LCC scores for SLW (LCC/SLW) greatly improved the prediction of N_{dw} across growth stages (R^2 range of 0.84–0.92), suggesting that leaf thickness affects LCC scores. LCC scores were closely related to SPAD values (R^2 range of 0.62–0.98). The SPAD value of 35 corresponded to an LCC-IRRI score of 3.2, an LCC-ZAU score of 4.8, and an LCC-UCD score of 5.2. An LCC score of 3.0 has been used with LCC-IRRI in the Long-Term Fertilizer Experiment at IRRI to guide in-season N management of modern indica cultivars (R. Buresh, personal communication).

Field testing of real-time nitrogen management

Real-time N management using SPAD was compared with fixed-timing N treatment in experiment station fields and farmers' fields in the Philippines (Peng et al 1996, Garcia et al 1996). In experiment station fields, AE was significantly higher in the SPAD-based N management than in the fixed-timing N treatment because of the reduction in N input. In farmers' fields, SPAD-based N management had a higher AE than the farmers' practice because of the increase in grain yield and decrease in N input.

Real-time N management using the SPAD and LCC was compared at the IRRI farm for four seasons in 2001 and 2002 (Buresh et al 2002, unpublished data). The leaf color or SPAD reading was determined at 7–10-day intervals from 14 days after transplanting (DAT) to flowering. The critical SPAD value was 35 and critical LCC reading was 3 with LCC-IRRI. In all four seasons, the timing of N application that was determined by the LCC was similar to that determined by SPAD. The LCC-based N treatment produced the same or higher grain yield and AE than the SPAD-based N treatment. Singh et al (2002) compared SPAD- and LCC-based N management for rice and wheat in northwestern India. They reported that real-time N management using the SPAD with the critical value of 37.5 reduced the N requirement of rice from 12.5% to 25%, with no loss in yield. Nitrogen management based on the critical LCC score of 4.0 with LCC-IRRI helped avoid overapplication of N to the rice crop. These results suggest that the LCC can substitute for the SPAD in real-time N management. The leaf color chart has been tested for real-time N

Table 1. Description of N treatments.

Code	N treatment
N1	Zero-N control (CK)
N2	Fixed N split with total N rate of 60 kg N ha^{-1}
N3	Fixed N split with total N rate of 120 kg N ha^{-1}
N4	Fixed N split with total N rate of 180 kg N ha^{-1}
N5	Farmers' fertilizer practice (FP)
N6	Modified farmers' fertilizer practice (MFP)
N7	Real-time N management using SPAD (SPAD)
N8	Site-specific N management (SSNM)

Table 2. Timing and proportion of N application in the fixed-N split treatments (N2-N4).

	Growth stage	Fixed split (%)
N application 1	Preplant	35
N application 2	Midtillering	20
N application 3	Panicle initiation	30
N application 4	Heading	15
Total		100

management in farmers' fields in several countries (Balasubramanian et al 1999). Results of using the LCC for real-time N management in farmers' fields are very promising.

In 2001, we evaluated the agronomic performance of fertilizer N strategies with different degrees of real-time N management (fixed → variable N rates) including reference treatments that were designed to obtain a fertilizer response curve in Jiangsu, Zhejiang, Hunan, and Guangdong. Experiments were conducted in farmers' fields using a randomized complete block with eight N treatments and four replicates. An indica/indica hybrid cultivar Shanyou 63 was used for all sites. Thirty-d-old seedlings were transplanted at 20 × 20 cm with one seedling per hill. Plot size was 30 m^2. Phosphorus at 40 kg ha^{-1}, potassium at 100 kg ha^{-1}, and zinc at 5 kg ha^{-1} were applied 1 day before transplanting. Continuous flooding was maintained throughout the growing season. The same experiment was repeated at the IRRI farm in the dry season of 2002. Phosphorus input was 30 kg ha^{-1} and potassium was 40 kg ha^{-1} at IRRI.

The eight N treatments are described in Table 1. The timing and proportion of N application for the three fixed N split treatments are listed in Table 2. The farmers' N fertilizer treatment was based on the common practice of the farmers near the sites (Table 3). At the four sites of China, the modified farmers' fertilizer practice was derived by reducing 30% of total N input in the farmer' N fertilizer treatment and the reduction in N input was restricted only within 10 DAT (Table 4). As result, the proportion of N applied in the first 10 DAT was reduced in the modified farmers'

Table 3. Rate (kg N ha^{-1}) and timing of N application in the farmers' fertilizer practice (N5).

Site	1st N application		2nd N application		3rd N application		4th N application		5th N application		Total N
	Rate	DAT[a]	Rate	DAT	Rate	DAT	Rate	DAT	Rate	DAT	
Jiangsu	144	0	24	4	36	46	36	66	-	-	240
Zhejiang	100	0	70	8	30	58	-	-	-	-	200
Hunan	100	0	35	19	25	35	20	64	-	-	180
Guangdong	70	0	65	5	30	24	20	37	15	59	200
IRRI	45	14	45	43	-	-	-	-	-	-	90

[a] Timing of N application is indicated as days after transplanting (DAT). Basal N application is indicated as DAT = 0.

Table 4. Rate (kg N ha^{-1}) and timing of N application in the modified farmers' fertilizer practice (N6).

Site	1st N application		2nd N application		3rd N application		4th N application		5th N application		Total N
	Rate	DAT[a]	Rate	DAT	Rate	DAT	Rate	DAT	Rate	DAT	
Jiangsu	74	0	24	4	36	46	36	66	-	-	170
Zhejiang	60	0	50	8	30	58	-	-	-	-	140
Hunan	50	0	35	19	25	35	20	64	-	-	130
Guangdong	40	0	35	5	30	24	20	37	15	59	140
IRRI	46	0	45	20	45	43	-	-	-	-	135

[a] Timing of N application is indicated as days after transplanting (DAT). Basal N application is indicated as DAT = 0.

Table 5. The amount of N applied (kg N ha^{-1}) in the first 10 days after transplanting in N5 and N6.

Site	Farmers' practice (N5)		Modified farmers' practice (N6)	
	N applied	% of total	N applied	% of total
Jiangsu	168	70	98	58
Zhejiang	170	85	110	79
Hunan	100	56	50	38
Guangdong	135	68	75	54
IRRI	0	0	45	33

fertilizer practice at the four sites in China (Table 5). In the real-time N management with the SPAD, if the SPAD reading was below 35, 30 kg N ha^{-1} was applied. If the SPAD was below 35 around the panicle initiation stage, 45 kg N ha^{-1} was applied (Table 6). There is no basal N application in this treatment. SPAD monitoring starts at 10 DAT and continues at weekly intervals until heading. In the site-specific N

Table 6. Rate (kg N ha^{-1}) and timing of N application in the real-time N management using SPAD (N7).

Site	1st N application		2nd N application		3rd N application		4th N application		Total N
	Rate	DAT[a]	Rate	DAT	Rate	DAT	Rate	DAT	
Jiangsu	30	10	45	40	–	–	–	–	75
Zhejiang	30	10	45	31	–	–	–	–	75
Hunan	30	10	30	17	30	31	–	–	90
Guangdong	30	39	–	–	–	–	–	–	30
IRRI	30	14	30	33	45	40	30	54	135

[a] Timing of N application is indicated as days after transplanting (DAT). Basal N application is indicated as DAT = 0.

Table 7. Method for determining the rate of N application in the site-specific N management (SSNM) treatment (NS) for experimental sites in China.

Application	Growth stage	% of total N	N rate (kg ha^{-1})	If SPAD
N application 1	Preplant	35	50	
N application 2	Midtillering	20	30 ± 10	* [a]
N application 3	Panicle initiation	30	40 ± 10	** [b]
N application 4	Heading	15	± 20	*** [c]
Total		100	100-160	

[a] If SPAD is greater than 36, apply 20 kg ha^{-1}; if less than 34, apply 40 kg ha^{-1}; if from 34 to 36, apply 30 kg ha^{-1}. [b] If SPAD is greater than 36, apply 30 kg ha^{-1}; if less than 34, apply 50 kg ha^{-1}; if from 34 to 36, apply 40 kg ha^{-1}. [c] In favorable season and if SPAD is less than 36, apply 20 kg ha^{-1}; otherwise, no need to apply N.

Table 8. Rate (kg N ha^{-1}) of N application in site-specific N management (SSNM) treatment (N8).

Site	Basal	Midtillering	Panicle initiation	Heading	Total N
Jiangsu	50	20	35	–	105
Zhejiang	50	20	40	–	110
Hunan	50	30	30	–	110
Guangdong	50	20	30	–	100
IRRI	35	50	35	15	135

management (SSNM) treatment, total N rate was predetermined based on the grain yield of the zero-N control and yield target. The timing of N application was fixed but the rate of in-season N application was variable depending on leaf N status (Table 7). Table 8 shows the rates of N application for SSNM treatments.

Soil samples were taken before transplanting. Plant samplings were done at midtillering, panicle initiation, and flowering. Yield components were determined

Table 9. Soil properties of the five sites.

Site	pH	Organic carbon (%)	Total N (%)	Available Olsen P (mg kg^{-1})	Extractable K (meq 100 g^{-1})	CEC (meq 100 g^{-1})
Jiangsu	6.3	1.27	0.13	13.3	0.10	13.8
Zhejiang	4.5	1.61	0.17	28.5	0.12	5.4
Hunan	5.8	1.99	0.19	10.3	0.09	11.7
Guangdong	4.6	1.89	0.21	43.3	0.07	8.3
IRRI	6.2	1.51	0.16	10.4	1.25	37.4

Table 10. Total N input, grain yield, total N uptake, N recovery efficiency, physiological N-use efficiency, and agronomic N-use efficiency of different N treatments at Jiangsu in 2001.

Treatment[a]	Total N input (kg ha^{-1})	Grain yield (t ha^{-1})	Total N uptake (kg ha^{-1})	Recovery efficiency (%)	Physiological efficiency (kg kg^{-1})	Agronomic efficiency (kg kg^{-1})
Control	0	7.50	94.0	–	–	–
Fixed split	60	8.94	135.5	69	34.7	24.0
Fixed split	120	9.69	190.1	80	22.8	18.2
Fixed split	180	8.89	218.9	69	11.1	7.7
FP	240	8.69	232.9	58	8.6	5.0
MFP	170	9.49	201.7	63	18.5	11.7
SPAD	75	8.98	152.7	78	25.2	19.7
SSNM	105	9.46	178.9	81	23.1	18.7

[a] See Table 1 for the details of N treatment description.

from 12 hills (0.48 m^2) at physiological maturity. All plant samples were separated into green leaf blades (leaf), culm plus sheath (stem), and panicles when present. Dry weight of each component was determined by oven-drying at 70 °C to constant weight. Tissue N concentration was determined by micro Kjeldahl digestion, distillation, and titration. Grain yield was determined from a 5-m^2 area at maturity and adjusted to a moisture content of 0.14 g H_2O g^{-1} fresh weight.

All five sites have ample available soil P (Table 9). Soil at the Zhejiang and Guangdong sites had a lower pH and CEC and higher available P content than the other three sites. Soil organic C and total N were not markedly different between IRRI and the Chinese sites. Soil at the Hunan and Guangdong sites contained more organic C and total N than the other sites. The Jiangsu site had the lowest soil organic C and total N contents. IRRI soil contained 12 times more extractable K than the Chinese sites. Its CEC was also significantly higher than that of all the sites in China.

Among the five sites, the highest grain yield was 9.69 t ha^{-1} at Jiangsu with 120 kg N ha^{-1} (Tables 10–14). Yield declined at an N rate greater than 120 kg ha^{-1} at Jiangsu and Hunan (Fig. 1). At Zhejiang and IRRI, yield decline occurred when the N rate was greater than 60 kg ha^{-1}. At Guangdong, yield reached a plateau at 120 kg N ha^{-1}. The zero-N control produced 6.41 to 7.50 t ha^{-1} at the four Chinese sites but

Table 11. Total N input, grain yield, total N uptake, N recovery efficiency, physiological N-use efficiency, and agronomic N-use efficiency of different N treatments at Zhejiang in 2001.

Treatment[a]	Total N input (kg ha^{-1})	Grain yield (t ha^{-1})	Total N uptake (kg ha^{-1})	Recovery efficiency (%)	Physiological efficiency (kg kg^{-1})	Agronomic efficiency (kg kg^{-1})
Control	0	6.68	104.1	-	-	-
Fixed split	60	7.17	137.3	55	14.8	8.0
Fixed split	120	6.54	162.6	49	-2.4	-1.1
Fixed split	180	6.72	174.6	39	0.6	0.2
FP	200	6.46	172.5	34	-3.2	-1.1
MFP	140	6.85	164.3	43	2.8	1.2
SPAD	75	6.69	143.4	51	0.3	0.2
SSNM	110	6.80	154.7	46	2.4	1.1

[a]See Table 1 for the details of N treatment description.

Table 12. Total N input, grain yield, total N uptake, N recovery efficiency, physiological N-use efficiency, and agronomic N-use efficiency of different N treatments at Hunan in 2001.

Treatment[a]	Total N input (kg ha^{-1})	Grain yield (t ha^{-1})	Total N uptake (kg ha^{-1})	Recovery efficiency (%)	Physiological efficiency (kg kg^{-1})	Agronomic efficiency (kg kg^{-1})
Control	0	6.57	91.1	-	-	-
Fixed split	60	7.65	133.7	71	25.4	18.0
Fixed split	120	7.91	169.8	66	17.0	11.1
Fixed split	180	7.41	211.3	67	7.0	4.7
FP	180	7.40	196.1	58	7.9	4.6
MFP	130	7.61	187.1	74	10.8	8.0
SPAD	90	7.68	151.0	67	18.5	12.4
SSNM	110	7.87	170.5	72	16.4	11.8

[a] See Table 1 for the details of N treatment description.

Table 13. Total N input, grain yield, total N uptake, N recovery efficiency, physiological N-use efficiency, and agronomic N-use efficiency of different N treatments at Guangdong in 2001.

Treatment[a]	Total N input (kg ha^{-1})	Grain yield (t ha^{-1})	Total N uptake (kg ha^{-1})	Recovery efficiency (%)	Physiological efficiency (kg kg^{-1})	Agronomic efficiency (kg kg^{-1})
Control	0	6.41	90.5	-	-	-
Fixed split	60	7.34	136.8	77	20.1	15.5
Fixed split	120	7.68	159.9	58	18.3	10.6
Fixed split	180	7.74	181.9	51	14.6	7.4
FP	200	7.74	184.9	47	14.1	6.6
MFP	140	7.33	171.9	58	11.3	6.6
SPAD	30	6.76	119.4	96	12.1	11.6
SSNM	100	7.62	156.3	66	18.4	12.1

[a] See Table 1 for the details of N treatment description.

Table 14. Total N input, grain yield, total N uptake, N recovery efficiency, physiological N-use efficiency, and agronomic N-use efficiency of different N treatments at IRRI in the dry season of 2002.

Treatment[a]	Total N input (kg ha^{-1})	Grain yield (t ha^{-1})	Total N uptake (kg ha^{-1})	Recovery efficiency (%)	Physiological efficiency (k kg^{-1})	Agronomic efficiency (kg kg^{-1})
Control	0	3.53	61.5	-	-	-
Fixed split	60	6.04	96.4	58	71.9	41.7
Fixed split	120	5.71	109.2	40	45.7	18.1
Fixed split	180	5.24	140.3	44	21.7	9.5
FP	90	5.89	110.8	55	47.9	26.2
MFP	135	5.76	121.5	44	37.2	16.5
SPAD	135	6.02	144.1	61	30.1	18.4
SSNM	135	5.82	130.3	51	33.3	17.0

[a] See Table 1 for the details of N treatment description.

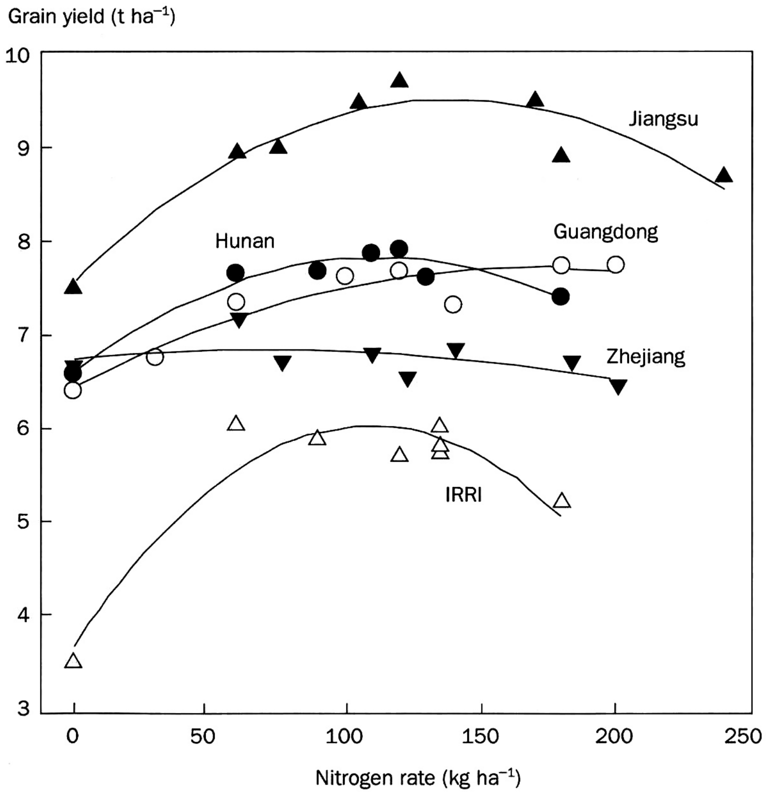


Fig. 1. Fertilizer-N response curve measured at Jiangsu, Zhejiang, Hunan, and Guangdong, China, in 2001 and at IRRI in the dry season of 2002.

only 3.53 t ha^{-1} at IRRI. Nitrogen uptake of the zero-N control was 90.5 to 104.1 kg ha^{-1} at the four Chinese sites vis-à-vis 61.5 kg ha^{-1} at IRRI. Therefore, the indigenous N supply capacity at Chinese sites was 54% higher than at IRRI. The farmers' practice had a lower RE, physiological N-use efficiency (PE), and AE than other N treatments at Chinese sites. The modified farmers' practice reduced N input by 30% but increased yield by 9% at Jiangsu, by 6% at Zhejiang, and by 3% at Hunan compared with the farmers' practice. At Guangdong, the modified farmers' practice reduced yield by 5% compared with the farmers' practice. Agronomic N-use efficiency was increased by the modified farmers' practice at all Chinese sites except for Guangdong, where AE was not different between the modified farmers' practice and the farmers' practice.

Real-time N management with the SPAD reduced grain yield by 3% to 13% compared with the maximum yield at each site in China (Tables 10–14). This was due to a heavy reduction in total N rate. The total N rate of real-time N management with the SPAD was only 30 to 90 kg ha^{-1} at the Chinese sites. At IRRI, however, the total N rate of real-time N management with the SPAD was 135 kg ha^{-1} and yield nearly reached its maximum in this N treatment (Table 14). The low N rate at the Chinese sites could be caused by the overestimation of leaf N status by the SPAD meters used at those sites. For example, the SPAD meter used at the Jiangsu site had 1.9 unit higher readings than the SPAD meter used at IRRI when they measured the same leaves. Another possibility is that the critical SPAD value for maximum grain yield could be 1-2 units higher at the Chinese sites than at IRRI for the same cultivar. Nevertheless, real-time N management with the SPAD confirmed that farmers applied excessive N to the rice crop in China.

Site-specific N management required an N input ranging from 100 to 110 kg ha^{-1} at Chinese sites and 135 kg ha^{-1} at IRRI (Tables 10–14). The grain yield under SSNM was greater than that under real-time N management with the SPAD and was very close to maximum at each site in China. SSNM had greater RE, PE, and AE than the farmers' practice at all four sites in China.

Yield increase because of N application was 2.25 t ha^{-1} averaged across all seven treatments with N input at IRRI (Table 14). The yield response to N is usually 3 to 4 t ha^{-1} at IRRI for IR cultivars. The low yield increase in this study occurred because Shanyou 63 was not adapted to tropical conditions. In China, the yield response to N application was 1.66 t ha^{-1} at Jiangsu, 0.07 t ha^{-1} at Zhejiang, 1.08 t ha^{-1} at Hunan, and 1.05 t ha^{-1} at Guangdong (Tables 10–13). Therefore, all Chinese sites had a poorer response to N fertilizer application than IRRI. Agronomic N-use efficiency was generally higher at IRRI than at the Chinese sites because of poor PE at the Chinese sites. The recovery efficiency of applied N was higher at the Chinese sites than at IRRI except for Zhejiang. These results suggest that poor AE of the rice crop in China is not associated with N uptake.

Conclusions

Both the SPAD and LCC estimate leaf area-based N content and significant correlation exists between SPAD and LCC readings. The LCC and SPAD are equally useful for improving N-use efficiency in real-time N management. When the SPAD or LCC is used in real-time N management, a single critical value can be used to determine the timing of N application during the entire growing season. Significant deviation in SPAD readings exists among different SPAD meters. Users should consider this deviation when they use the suggested critical SPAD value from other sources. It is unrealistic, however, to expect that the SPAD or LCC will be appropriate for every rice farmer, especially in rice-growing areas where labor is expensive or not available. In those areas, the principles of real-time N management can be used to optimize traditional fixed-schedule N management for a specific location, season, and cultivar. Results of the N response curve for real-time N management using the SPAD and SSNM indicate that farmers in China overapply N to the rice crop by at least 50%. The overapplication of N occurs mainly during the early vegetative stage (within 10 DAT). The indigenous N supply capacity at Chinese sites was 54% higher than that at IRRI, but farmers did not adjust the N rate for the high N supply from the soil in China. The improper timing and rate of N application are largely responsible for poor AE at the Chinese sites. The poor AE was caused by low PE, not by RE. There is a great possibility to optimize the timing and rate of N application in irrigated rice in China through real-time N management and SSNM.

References

Balasubramanian V, Morales AC, Cruz RT, Abdulrachman S. 1999. On-farm adaptation of knowledge-intensive nitrogen management technologies for rice system. Nutr. Cycl. Agroecosyst. 53:59-69.

Blackmer TM, Schepers JS. 1994. Techniques for monitoring crop nitrogen status in corn. Commun. Soil Sci. Plant Anal. 25: 1791-1800.

Cassman KG, Gines GC, Dizon MA, Samson MI, Alcantara JM. 1996. Nitrogen-use efficiency in tropical lowland rice systems: contributions from indigenous and applied nitrogen. Field Crops Res. 47: 1 - 12.

De Datta SK. 1986. Improving nitrogen fertilizer efficiency in lowland rice in tropical Asia. Fert. Res. 9:171-186.

De Datta SK, Buresh RJ. 1989. Integrated nitrogen management in irrigated rice. Adv. Soil Sci. 10:143-169.

Dwyer LM, Tollenaar M, Houwing L. 1991. A nondestructive method to monitor leaf greenness in corn. Can. J. Plant Sci. 71:505-509.

Evans JR. 1983. Nitrogen and photosynthesis in the flag leaf of wheat. Plant Physiol. 72:297-302.

FAO. 2001. Statistical databases, Food and Agriculture Organization (FAO) of the United Nations. www.fao.org.

Garcia FV, Peng S, Gines HC, Laza RC, Sanico AL, Visperas RM, Cassman KG. 1996. Chlorophyll meter-based nitrogen management improves nitrogen use efficiency of irrigated rice in farmers' fields. In: Ishii R, Horie T, editors. Crop research in Asia: achievements and perspectives. Proceedings of the 2nd Asian Crop Science Conference, 21-23 August 1995, Fukui, Japan. p 187-190.

Huang J, Peng S. 2003. Comparison among six chlorophyll meters in their readings on rice leaves. Commun. Soil Sci. Plant Anal. (Submitted.)

Hussain F, Bronson KF, Singh Y, Singh B, Peng S. 2000. Use of chlorophyll meter sufficiency indices for nitrogen management of irrigated rice in Asia. Agron. J. 92:875-879.

Jiang PY. 1993. Rice high-yielding crop management. Beijing (China): China Agricultural Tech Press.

Jiang XX, Vergara BS. 1986. Chlorophyll meter (SPAD-501) to quantify relative cold tolerance in rice. Int. Rice Res. Newsl. 11(3):10-11.

Lin B. 1991. Make the most efficient use of fertilizers in increasing crop production. In: Soil science in China: present and future. Soil Science Society of China, Jiangsu Science and Technology Press. p 29-36. (In Chinese.)

Peng S, Cassman KG, Kropff MJ. 1995a. Relationship between leaf photosynthesis and nitrogen content of field-grown rice in the tropics. Crop Sci. 35:1627-1630.

Peng S, Garcia FV, Laza RC, Cassman KG. 1993. Adjustment for specific leaf weight improves chlorophyll meter's estimate of rice leaf nitrogen concentration. Agron. J. 85:987-990.

Peng S, Garcia FV, Laza RC, Sanico AL, Visperas RM, Cassman KG. 1996. Increased N-use efficiency using a chlorophyll meter on high-yielding irrigated rice. Field Crops Res. 47:243-252.

Peng S, Laza RC, Garcia FV, Cassman KG. 1995b. Chlorophyll meter estimates leaf area based nitrogen concentration of rice. Commun. Soil Sci. Plant Anal. 26:927-935.

Singh B, Singh Y, Ladha JK, Bronson KF, Balasubramanian V, Singh J, Khind CS. 2002. Chlorophyll meter- and leaf color chart-based nitrogen management for rice and wheat in northwestern India. Agron. J. 94:821-829.

Takebe M, Yoneyama T. 1989. Measurements of leaf color scores and its implication to nitrogen nutrition of rice plants. Jpn. Agric. Res. Quart. 23:86-93.

Vlek PLG, Byrnes BH. 1986. The efficacy and loss of fertilizer N in lowland rice. Fert. Res. 9:131-147.

Watanabe S, Hatanaka Y, Inada K. 1980. Development of a digital chlorophyll meter. I. Structure and performance. Jpn. J. Crop Sci. 49(special issue):89-90.

Yang WH, Peng S, Huang J, Sanico AL, Buresh RJ, Witt C. 2003. Estimation of leaf nitrogen status using leaf color charts in rice. Agron. J. 95:212-217.

Yoshida S, Coronel V. 1976. Nitrogen nutrition, leaf resistance, and leaf photosynthetic rate of the rice plant. Soil Sci. Plant Nutr. 22(2):207-211.

Zhu Z. 1985. Research progresses on the fate of soil N supply and applied fertilizer N in China. Soil 17(1):2-9. (In Chinese.)

Zhu Z. 1997. Fate and management of fertilizer nitrogen in agro-ecosystems. In: Zhu Z, Wen Q, Freney JR, editors. Nitrogen in soils of China. Dordrecht (Netherlands): Kluwer Academic Publishers. p 239-279.

Notes

Authors' addresses: S. Peng, R. Buresh, J. Huang, International Rice Research Institute; J. Yang, Yangzhou University; G. Wang, Zhejiang University; X. Zhong, Guangdong Academy of Agricultural Science; Y. Zhou, Hunan Agricultural University, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Precision farming for site-specific crop and resource management

R.E. Plant and A. Roel

Site-specific crop management (SSCM) is the management of a crop at a spatial and temporal scale appropriate to that crop's own inherent variability. Precision agriculture has been defined as the application of modern information technologies to achieve SSCM. Concepts of precision agriculture have been developed primarily for application to large-scale production systems characteristic of Europe and North America, and have focused on the spatial dimension. Development of SSCM techniques in tropical regions has focused on the time dimension. Future research should permit these two approaches to be synthesized into a system that uses spatial relationships to optimize the efficiency of collecting information and that optimizes production in each year.

Site-specific crop management (SSCM) is a new name for an old concept. Modifying a bit the definition given by Plant (2001), we can define it as the management of a crop at a spatial and temporal scale appropriate to that crop's own inherent variability. That this is a new name is clear: the term achieved widespread usage only in the 1990s, and the first major international conference on SSCM was held in 1992. The focus of much SSCM research is on the application of information technologies to achieve something that had been lost in the process of agricultural mechanization.

It is in this sense that SSCM is an old concept. The development of mechanized agriculture led to increases in field size and in the uniformity of the application of inputs. Manual practices are better suited to detecting variations in crop condition and varying the rate of input application. The advent of mechanized agriculture in North America and Europe reduced labor and other costs to a degree that more than made up for the increased cost of inputs, which were uniformly applied at a rate that matched (or exceeded) the demand in all areas of the field. The increased cost of inputs and increased public concern about the environmental effects of inputs applied in excess have motivated research in SSCM to recover the more precise matching of inputs with field conditions that presumably existed before the advent of mechanized agriculture.

The new technological tools, such as the global positioning system (GPS), the yield monitor, variable rate chemical application, the geographic information system (GIs), and remote sensing, make it possible to quantify the crop's response to the environment, and to modify that environment by varying input levels, much more precisely than before. For this reason, the term "precision agriculture" has been used as a synonym for SSCM. A useful distinction defines precision agriculture to be the use of information technologies to achieve site-specific management (Lowenberg-DeBoer and Erickson 2000). These technologies are not widely available in many parts of the world, particularly those characterized by relatively small farms and a lower level of mechanization. An important question is whether the concepts of SSCM and precision agriculture can be used to improve farming practices in areas with a lower level of mechanization, and whether methods developed for small farmers to improve the precision with which they manage their crops can provide guidance in the development of SSCM strategies for large fields in high-technology systems. The objective of this paper is to consider these questions in the context of rice production. The overriding theme of the paper is that SSCM involves both a spatial and a temporal component, and that the most successful implementation of SSCM will be one that integrates these two components effectively.

Fundamental concepts of site-specific crop management

Plant (2001) and Miller et al (1999) provide a set of criteria (necessary, but not sufficient) that must be satisfied for SSCM to have a reasonable chance of successful implementation in a crop production system:

1. There must be a substantial spatial variation in yield.
2. The factors underlying this variation must be able to be identified and measured.
3. It must be possible to quantify an appropriate response to the factors underlying yield variability.
4. The technology must exist to apply the response at the appropriate spatial distribution of rates.
5. The increased cost of the site-specific management must be offset by increased economic yield or by reduced externalities or a combination of the two.

Figure 1 shows an example of yield maps from four successive years in a 38-ha California rice field that would normally be considered very uniform. The relatively high level of variability is readily apparent. Yield in the southwest corner of the field in Figure 1 was deficient in 1998. Roel et al (2001) identified the cause of this as excessively deep water in that part of the field. The field was laser-leveled in 1999 and yield in this area improved. The region of very poor yield in 2001 in the north-central portion of the field was caused by a stand of herbicide-tolerant watergrass that appears to be spreading. The figure illustrates an important property that is frequently observed in SSCM: in a large area, the primary yield-limiting factor will

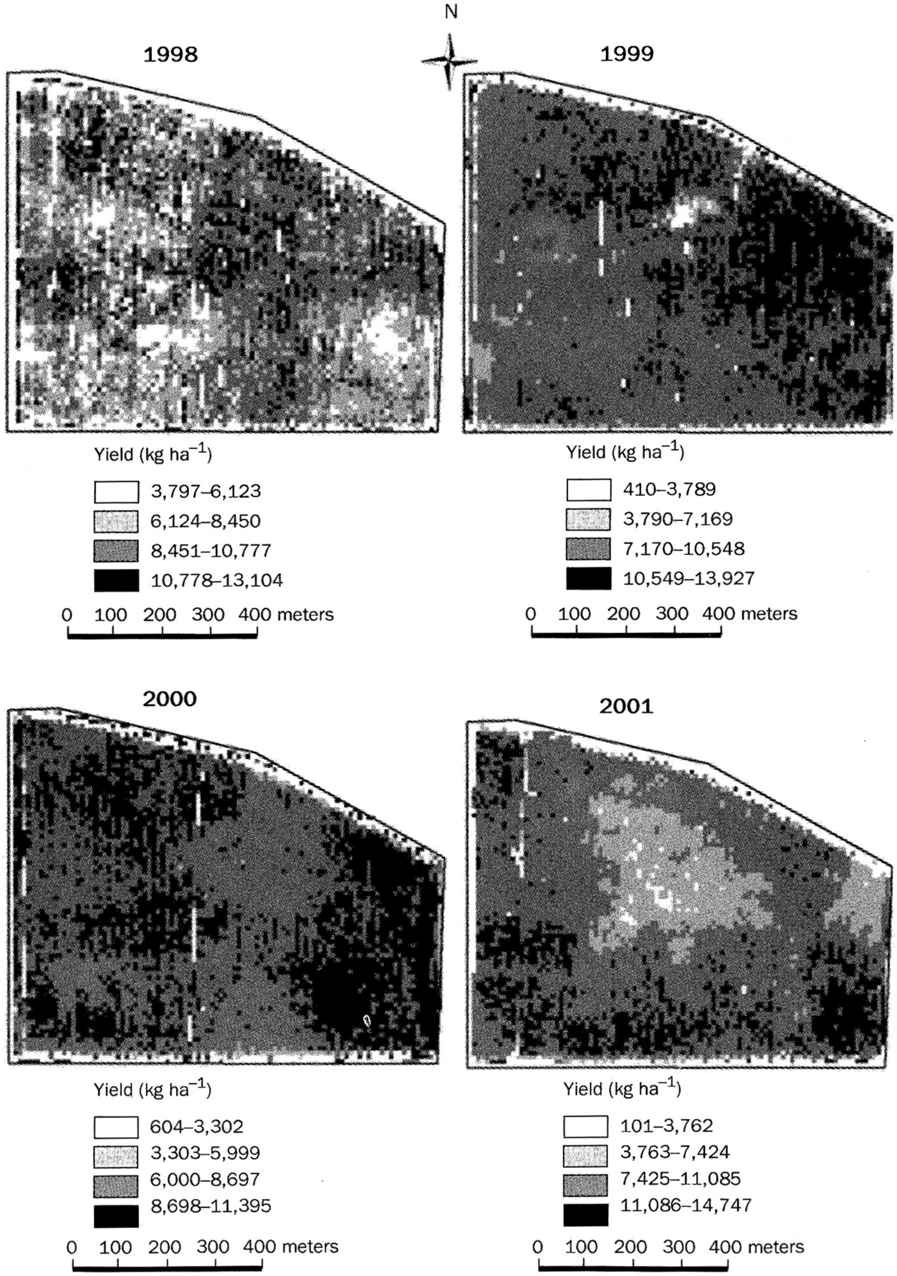


Fig. 1. Yield maps for 1998-2001 of a 38-ha field located in Marysville, California (USA). This field would normally be considered fairly uniform.

not be the same in every part of that area, nor will it necessarily be the same in every year. For example, Plant et al (1999) studied a wheat field in which, depending on the location in the field, weeds, aeration stress, phosphorus deficiency, or a combination of these were found to substantially limit yield.

Despite this multiplicity of yield-limiting factors, most research in SSCM has focused on managing a single factor, for example, fertilizer, insects, or weeds. This approach is certainly defensible: one has to start somewhere and to attempt to begin everywhere at once would be overwhelming. The area of most intense interest in both large- and small-scale agriculture has been fertilizer management. This has been the primary focus of research in tropical SSCM, which is discussed in the next section.

Site-specific rice management: the time dimension

The institutional leader in the development of SSCM strategies for small-scale tropical rice production has been the International Rice Research Institute. In a paper describing their approach, Dobermann et al (1996) assert that in many cases current management recommendations are based on a single production guideline for a whole region, an approach analogous to whole-field management in large-scale production systems. As an alternative, the IRRI researchers propose a field-based program consisting of an orderly sequence of steps in which to subdivide the SSCM process for nutrient management. These are (1) site-specific estimation of intrinsic soil nutrient supply for N, P, and K; (2) development of an initial recommended application rate and timing at each location based on information from step 1; (3) dynamic modification of the schedule developed in step 2 based on observations as the season progresses; (4) measurement of grain and straw yield and of nutrients in straw returned to the field; and (5) use of the information from step 4 together with a record of the fertilization program as carried out in step 3 to develop a revised estimate of soil N, P, and K status for step 1 of the following season.

Dobermann and Witt (2001) point out that a program such as this can serve as the basis for SSCM in large-field production systems as well as small-field systems. We therefore briefly examine the technologies available for carrying out each of these steps.

1. Estimating indigenous nutrient supply

One effective and yet relatively simple means of estimating indigenous nutrient supply is the use of small omission plots, that is, plots in which one of the nutrients, N, P, or K, is omitted. The intrinsic supply of N (or P or K) is estimated as the total N (P, K) uptake in the omission plot of that element. Mineral nutrient uptake can be estimated based on grain and tissue analysis, or based on empirical formulas relating nutrient concentration to grain yield (Witt et al 1999). Wang et al (2001) report on an application of this approach to the estimation of intrinsic nutrient supply in an experiment involving 21 farms located in Zhejiang Province, China. Omission plots have also been used in large-farm site-specific crop management experiments. Delin and Lindén (2001) used this method to estimate soil available N by measuring N content in plants collected from 34 60-m^2 omission plots in a 15-ha field. It is likely, however, that the use of multiple omission plots in large-scale commercial fields would be too complex logistically to be practical or widely used.

Dobermann et al (1996) discuss the possibility of using ion exchange resin capsules as an alternative to omission plots. These may be placed directly into flooded soil and then removed at a fixed later time. Laboratory analysis of exchanged cations provides a direct measure of ammonium concentration as well as that of other mineral nutrients (Dobermann et al 1996).

2. Interpretation of measurement results

Once the nutrient demand of the crop has been estimated, a decision must be made as to the fertilizer application rate necessary to meet this demand. Agronomists have studied few subjects more thoroughly than fertilizer rates, and a simplistic approach would be to incorporate the existing guidelines. However, as Hergert et al (1997) have pointed out, much of this early work may be of limited value in developing recommendations for site-specific nutrient management. Many of the recommendations are based on tests that were carried out a relatively long time ago using varieties no longer in use. Moreover, they are developed based on generalizations on soil properties, local climatic conditions, and so forth. To overcome these deficiencies, recommendations generally include a fairly large safety factor. Such imprecision, however, defeats the purpose of site-specific management. Thus, a guideline must be as closely matched as possible to the actual conditions that exist in the given field. Dobermann et al (1996) attempt to solve this problem by estimating crop nutrient demand directly using a semi-empirical model (Janssen et al 1990). Although this model does not represent an improvement in its incorporation of site-specific properties, it does provide more precision in the development of recommended rates based on the results of omission plot trials.

3. Within-season measurement of plant properties

One direct method of in-season measurement of plant nutrient status is leaf tissue analysis. In Australia, a rapid turnaround leaf tissue analysis service has been established to provide near-infrared spectroscopic analysis of leaf tissue for rice farmers (Batten et al 1994). In other systems, commercial analytical laboratories carry out tissue analysis for a fee. A second approach is to estimate plant N status through the spectral properties of its leaves. The Minolta SPAD (Soil Plant Analysis Development) meter measures the difference between transmittance in the infrared (940 nm) and red (650 nm) wavelengths of the electromagnetic spectrum (Turner and Jund 1991, Peng et al 1996). The SPAD reading is linearly related to leaf N concentration expressed on a leaf-area basis to take into account the effect of leaf thickness. As a less expensive but less precise alternative, color charts have been developed that permit rapid estimation of plant nitrogen status.

Plant tissue analysis and chlorophyll meter analysis both estimate the nitrogen status of individual plants. Aerial remote sensing provides a measure of crop status with a relatively high level of spatial resolution across the entire field. Most work on remote sensing in large-scale production systems has been devoted to the use of multispectral images, which constitute a set of measures of intensity of electromagnetic radiation in the green, red, and near-infrared portions of the spectrum. Wiegand et al (1989) and Leblon et al (1991) have investigated the use of multispectral remote sensing in rice fields. A serious drawback to the use of multispectral images in tropical climates, however, is that on many days there is sufficient cloud cover to make collecting an image impossible. This has motivated exploration of the use of synthetic aperture radar, or SAR, which can penetrate cloud cover. Several studies have been carried out examining the relationship of measures such as biomass with SAR measurements, for example, that of Rosenqvist (1999). This research, however, is still in the early stages.

4. Measurement of yield

The penultimate step of the cycle is the measurement of yield and incorporation of this information into the planning for SSCM in the following year. Technically, yield measurement is a relatively easy task for both small and large farmers. Small farmers, whatever means they use to harvest their crop, will have a measure of grain yield at the scale of their field. Large growers may use a yield monitor as described earlier in this paper. In either case, an important component of the yield measurement process is the mapping of the yield spatial distribution. This permits visualization and statistical analysis of the spatial patterns present in the yield distribution.

5. Modification of the next year's fertilizer strategy

In principle, the incorporation of additional information based on measured versus estimated yield can be carried out using dynamic optimization techniques discussed, for example, by Walters (1986). In practice, the modification may be simply a matter of computing the difference between estimated and realized yield and the corresponding surplus or deficit of each nutrient, and adjusting the next year's application rate accordingly. In tropical systems using omission plot data, these data are incorporated at this stage.

Site-specific rice management: the spatial dimension

Unlike the mosaic of small, individually managed fields that characterizes tropical rice production, the large fields of temperate growing regions generally have a history of uniform management. This simplifies the process of spatial analysis of field data and is perhaps one reason why SSCM research in temperate regions has focused more on the analysis of the spatial dimension. The four-year sequence of yield maps shown in Figure 1 is an example of a field in which there are no obvious major differences in soil properties. Figure 2 shows a four-year sequence of yield maps in a field on the same farm as the field in Figure 1. The field of Figure 2 has substantial variations in soil properties that result in easily identifiable variations in yield. The existence of a single dominant source of variability greatly simplifies the discussion of the statistical analysis of this variability.

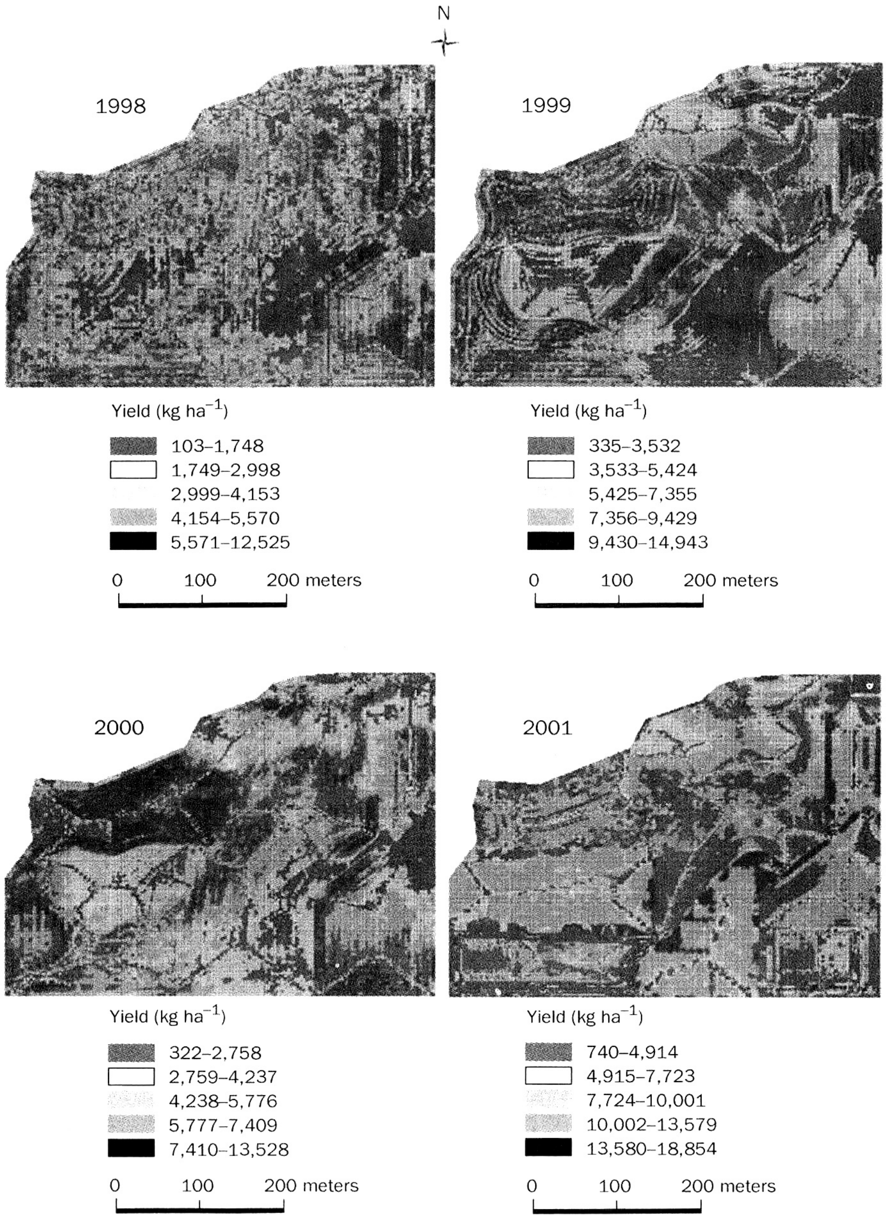


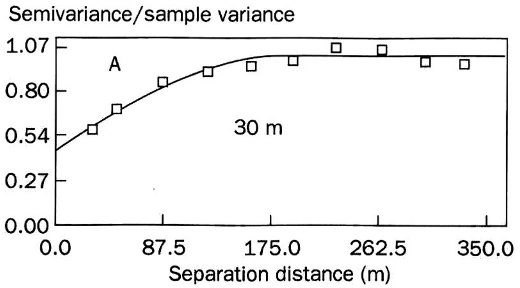
Fig. 2. Yield maps for 1998–2001 of a 52-ha field located in Marysville, California (USA). This field has substantial variation in soil properties, leading to persistent patterns in yield.

Spatial statistics makes use of the "first law of geography" (Tobler 1970), which states that "everything is related to everything else, but near things are more related than far things." Thus, a data value from a particular location conveys some information about the value of data from nearby locations. This is in contrast to classical statistics, in which a fundamental assumption is that data are independent. In our discussion of spatial statistics, we will keep the explanations on a strictly intuitive level. Readers who wish a more detailed and precise explanation are referred to books such as those of Isaaks and Srivastava (1989), Cliff and Ord (1981), and Cressie (1991). One of the key tools of much of spatial statistics is the variogram, which is a measure of the magnitude of spatial correlation. The variogram represents the average of the squared difference of values at a given distance apart. The smaller the variogram, the more spatially autocorrelated are the data. With the help of the variogram, one can model the effect of collecting data at different resolutions. Figure 3 shows the variograms of data collected from the field of Figure 2 on a 30-m, a 60-m, and a 90-m grid in 1998. Based on this figure, one can say that a 90-m resolution would be inadequate for sampling in that year. Further refinement of the optimal grid density can be obtained using the relative information criterion of Chen et al (1995).

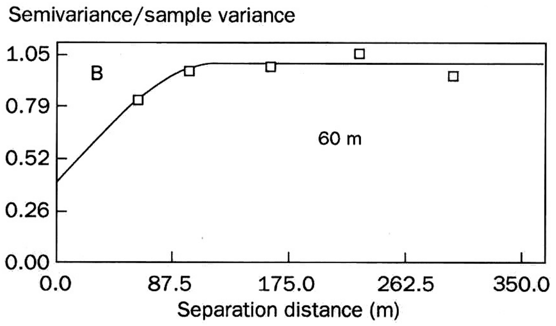
One of the problems in the analysis of spatiotemporal data such as these is their overwhelming volume and complexity. Exploratory analyses that simplify and organize the data are of great importance in making them understandable. One of the most useful is to assume that the spatial variability of the system is the sum of two components: a long-range trend, sometimes called the "deterministic" component, and short-range variation, sometimes called the "stochastic" component (Cliff and Ord 1981, Cressie 1991). Several analytical techniques exist for separating these components. One that is becoming more widely used is median polish (Cressie 1991). Figure 4 shows the results of a median polish of the yield data from Figure 2. A persistent trend is evident, but also considerable year-to-year variability.

One way to organize this variability is to search for clusters. K-means clustering is a widely used algorithm for this purpose (Jain and Dubes 1984). This algorithm searches for the K clusters (the value of K is specified at the start of the analysis) such that the within-cluster variance is minimized and the between-cluster variance is maximized. In carrying out the cluster analysis, we focused on data in the first three years. Examination of Figure 2 reveals that yield in the low-yielding area in the center of the field rose in 2001. This part of the field was quite visible, with a reduced plant population and stunted plants. A further characteristic of the area was that the plants matured more quickly. Therefore, the grower (implementing SSCM) harvested this portion of the field earlier than the rest in 2001 and obtained a relatively higher yield measurement, possibly because of a different yield monitor calibration. This scenario indicates a cautionary note that must be applied to field-based SSCM research. As the cooperating growers modify their management in a site-specific way, the act of carrying out the research may itself modify the results. Figure 5A shows the results of a K = 3 means cluster analysis applied to the first three years of data. The three clusters are consistent across years. Figure 5B shows the map of these clusters.

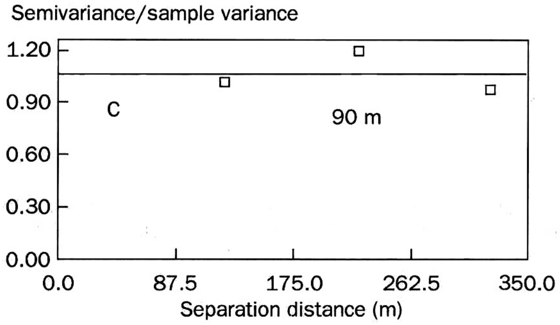
If a spatially referenced organizational structure can be established for a rice production system, the next task becomes one of identifying the factors underlying the observed yield variability. This is an active research area still in its early stages.



Spherical model (Co = 0.4500; Co + C = 1.0240; A_o = 185.00; r^2 = 0.944; RSS = 0.0135)



Spherical model (Co = 0.4000; Co + C = 1.0000; A_o = 120.00; r^2 = 0.786; RSS = 7.007E-03)



Linear model (Co = 1.0720; Co + C = 1.0720; A_o = 321.37; r^2 = 0.039; RSS = 1.150E +11)

Fig. 3. Experimental and fitted variograms of yield in the field in Figure 2 in 1998. Values of the fitted variogram sill, co + c_1, range, A_0, and model fitness, r^2, are given in the figures. (A) 30-m, (B) 60-m, and (C) 90-m sampling grid.

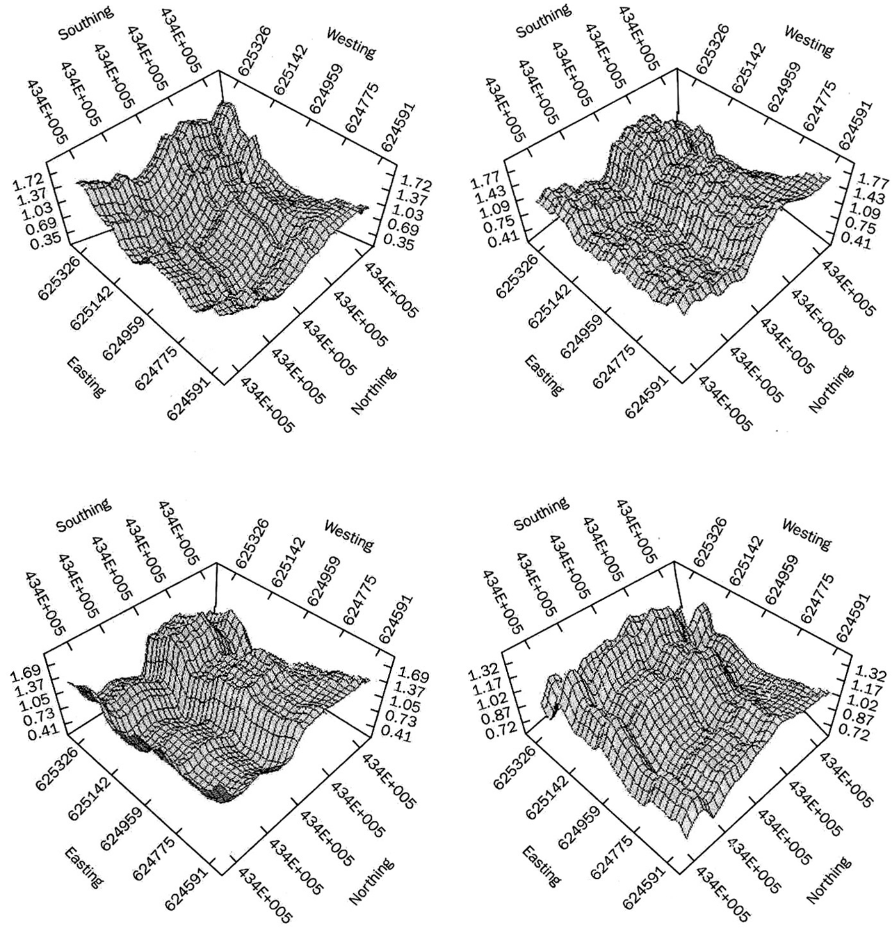


Fig. 4. Comparison of normalized trend surfaces estimated by the median polishing technique for the four years in the field in Figure 2: (A) 1998, (B) 1999, (C) 2000, and (D) 2001.

One promising approach, at least at the research level, is that of classification and regression trees (CART) (Breiman et al 1984). This is a nonparametric iterative classification method that recursively splits the data set into subsets that are as homogeneous as possible. Plant et al (1999) used CART to identify the factors underlying observed variability in two California wheat fields.

CART can be used to search for factors underlying the yield clusters created by K-means clustering. One advantage of this approach is that the K-means algorithm identifies regions that may show a commonality based on their dynamic yield behavior, and CART can then be used to search for possible field variations that underlie this

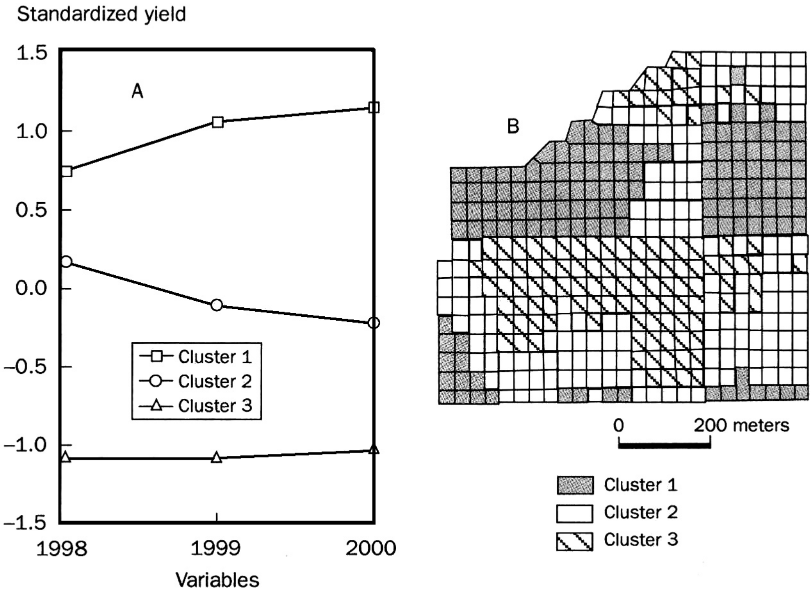


Fig. 5. (A) Cluster behaviors defined by standardized yields in three years. (B) Locations of the points making up the clusters shown in A.

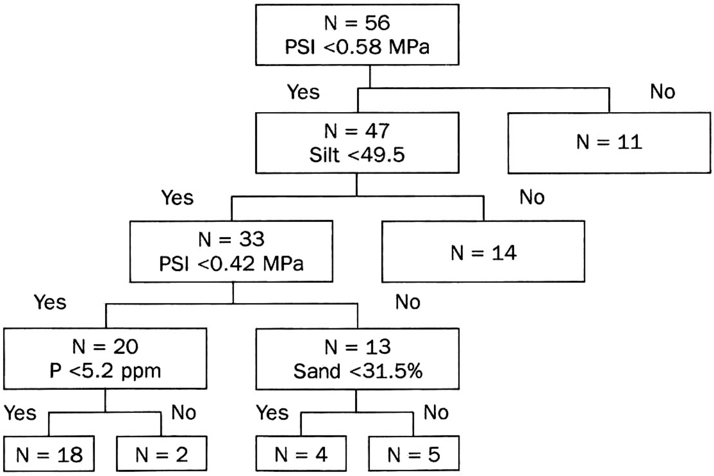


Fig. 6. CART analysis for yield-influencing factors in the field shown in Figure 2.

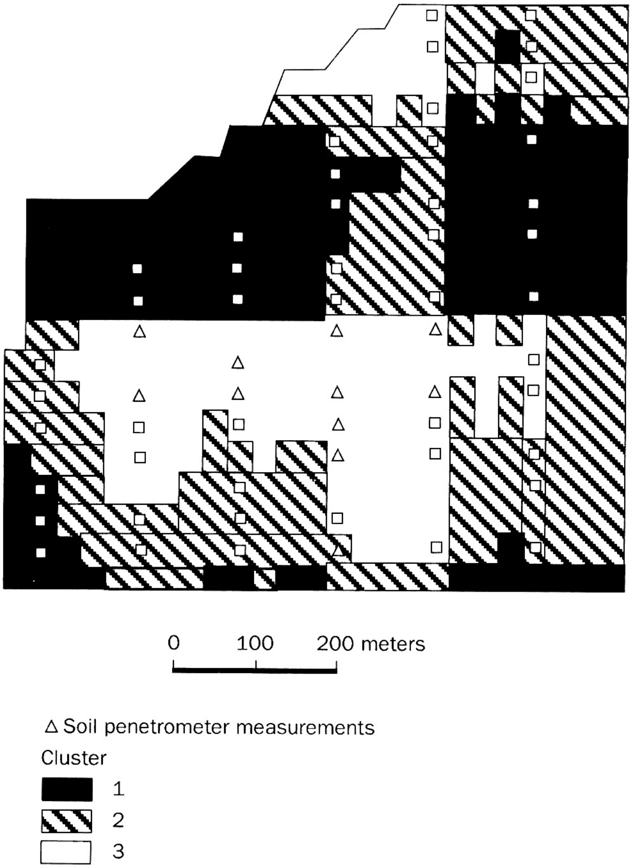


Fig. 7. Squares indicate location of the points with penetration resistance with lower than or equal to 0.58 MPa.

dynamic behavior. Figure 6 shows a regression tree generated by CART for the clusters of Figure 5. The splitting factor is soil impedance as measured by a soil penetrometer. Successive iterations of CART indicate that in this field soil variables correlated with soil texture and organic matter dominate yield variability. Figure 7 shows a map of those soil sample locations in the field having a penetration resistance greater than 0.58 MPa, the first splitting value identified by CART. All of the points are located in the central region of low yield.

Discussion: integrating spatial and temporal information

The process of managing a large field or a collection of small fields involves a complex interaction of spatial and temporal variability. Farmers have for thousands of years observed the way in which different parts of their fields responded to environmental and management fluctuations and used these observations to evolve highly efficient production systems. The introduction of technological changes such as short-statured rice and synthetic fertilizers has altered these production systems, and the process of regaining through observation an equivalent knowledge of the production system would take an unacceptably long time. The use of precision agriculture technology may help to speed up the process by incorporating more precise observations from more sources and a more efficient use of the data. The use of observation of a system's response to applied inputs as a means of learning more about the properties of that system has a long history in renewable resource theory, where it is called "adaptive management" (Walters 1986). These methods involve stochastic dynamic programming and may not be directly adaptable to crop management, but they do motivate the search for efficient ways to collect and use data.

The multistep management paradigm given by Dobermann et al (1996) and Dobermann and Witt (2001) provides an effective approach for dealing with the temporal component of SSCM. Because of the large quantities of data that must be gathered to carry out this program, it is essential to estimate as efficiently as possible the values of the parameters at unobserved locations in the field and at unobserved times. This in turn relies on an effective use of observed spatial structure in the field. Observations of values at individual locations must be scaled up to provide information about the distribution of those values across the landscape and observations about the landscape must be scaled down to provide information about values at unobserved locations. The process of integrating spatial and temporal information is made more complex by the spatially varying response of the farmer or farmers to field conditions. We have already seen the effect of this variability in the improved yield in the fourth year of the field in Figure 2. In the case of a large system of many independently acting small farmers, it will become necessary to have some information about the behavior of all of the individual farmers in response to management challenges. It may be possible to gain some of this information through indirect means such as synthetic aperture radar, or through information technologies yet to be commercialized. It is clear, however, that novel statistical and analytical methods will be required to make effective use of the new forms of data and information that precision agriculture will provide.

References

Batten GD, Blakeney AB, Lewin LG. 1994. A tissue testing service for rice producers. In: Humphreys E, Murray EA, Clampett WS, Lewin LC, editors. Proceedings of the Temperate Rice Conference. Yanco (Australia): Yanco Agricultural Institute.

Breiman L, Friedman JH, Olshen RA, Stone CJ. 1984. Classification and regression trees. New York, N.Y. (USA): Chapman and Hall.

Chen J, Hopmans JW, Graham EF. 1995. Sampling design for soil moisture measurements in large field trials. Soil Sci. 159:155-161.

Cliff AD, Ord K. 1981. Spatial processes: models and applications. London (UK): Pion Ltd.

Cressie NAC. 1991. Statistics for spatial data. New York, N.Y. (USA): Wiley.

Delin S, Linden B. 2001. Within-field variations in plant-available soil nitrogen: possibilities to predict an impact on optimum nitrogen fertilization. In: Robert PC, Rust RH, Larson WE, editors. Proceedings of the Fifth International Conference on Precision Agriculture. Madison, Wis. (USA): American Society of Agronomy. Unpaginated CD.

Dobermann A, Cassman KG, Peng S, Tan PS, Phung CV, Sta. Cruz PC, Bajita JB, Adviento MAA, Olk DC. 1996. Precision nutrient management in intensive irrigated rice systems. In: Proceedings of the International Symposium on Maximizing Sustainable Rice Yields Through Improved Soil and Environmental Management. Bangkok (Thailand): Soil and Fertilizer Society of Thailand. p 133-154.

Dobermann A, Witt C. 2001. A novel approach for managing plant nutrients and its application in irrigated rice systems. In: Robert PC, Rust RH, Larson WE, editors. Proceedings of the Fifth International Conference on Precision Agriculture. Madison, Wis. (USA): American Society of Agronomy. Unpaginated CD.

Hergert GW, Pan WL, Huggins DR, Grove JH, Peck TR. 1997. Adequacy of current fertilizer recommendations for site-specific management. In: Pierce FJ, Sadler EJ, editors. The state of site-specific management for agriculture. Madison, Wis. (USA): American Society of Agronomy. p 283-300.

Isaaks EH, Srivastava RM. 1989. An introduction to applied geostatistics. Oxford (UK): Oxford University Press.

Jain AK, Dubes RC. 1984. Algorithms for clustering data. Upper Saddle River, N.J. (USA): Prentice-Hall.

Janssen BH, Guiking FCT, van der Eijk D, Smaling EMA, Wolf J, van Reuler H. 1990. A system for quantitative evaluation of the fertility of tropical soils (QUEFTS). Geoderma 46:299-318.

Leblon B, Guerif M, Baret E 1991. The use of remotely sensed data in estimation of PAR use efficiency and biomass production of flooded rice. Remote Sensing Environ. 38:147-158.

Lowenberg-DeBoer J, Erickson K. 2000. Precision farming profitability. West Lafayette, Ind. (USA): Purdue University.

Miller RO, Pettygrove S, Denison RF, Jackson L, Cahn M, Plant R, Kearny T. 1999. Site-specific relationships among flag leaf nitrogen, SPAD meter values and grain protein in irrigated wheat. In: Proceedings of the Fourth International Conference on Precision Agriculture. Madison, Wis. (USA): American Society of Agronomy. p 113-122.

Peng S, Garcia FV, Laza RC, Sanico RM, Visperas KG, Cassman KG. 1996. Increased N-use efficiency using a chlorophyll meter on high-yielding irrigated rice. Field Crops Res. 47:243-252.

Plant RE. 2001. Site-specific management: the application of information technology to crop production. Computers Electronics Agric. 30:9-29.

Plant RE, Mermer A, Pettygrove GS, Vayssieres MP, Young JA, Miller RO, Lackson LF, Denison RF, Phelps K. 1999. Factors underlying grain yield spatial variability in three irrigated wheat fields. Trans. Am. Soc. Agric. Eng. 42:1187-1202.

Roel A, Plant RE, Young JA, Pettygrove GS, Deng J, Williams JF. 2001. Interpreting yield patterns for California rice precision farm management. In: Robert PC, Rust RH, Larson

WE, editors. Proceedings of the Fifth International Conference on Precision Agriculture. Madison, Wis. (USA): American Society of Agronomy. Unpaginated CD.

Rosenqvist A. 1999. Temporal and spatial characteristics of irrigated rice in JERS-1 L-band SAR data. Int. J. Remote Sensing 20:1567-1587.

Tobler W. 1970. A computer movie simulating urban growth in the Detroit region. Econ. Geog. 46:234-240.

Turner FT, Jund MF. 1991. Chlorophyll meter to predict nitrogen topdress requirement for semidwarf rice. Agron. J. 83:926-928.

Walters C. 1986. Adaptive management of renewable resources. New York, N.Y. (USA): McGraw Hill.

Wang G, Dobermann A; Witt C, Sun Q, Fu R. 2001. Performance of site-specific nutrient management for irrigated rice in southeast China. Agron. J. 93:869-878.

Wiegand C, Shibayama M, Yamagata Y, Akiyama T. 1989. Spectral observations for estimating the growth and yield of rice. Jpn. J. Crop Sci. 58:673-683.

Witt C, Dobermann A, Abdulrachman S, Gines HC, Wang GH, Nagarajan R, Satawathananont S, Son TT, Tan PS, Tiem LV, Simbahan GC, Olk X. 1999. Internal nutrient efficiencies of irrigated lowland rice in tropical and subtropical Asia. Field Crops Res. 63:113-138.

Notes

Authors' addresses: R.E. Plant, Department of Agronomy and Range Science and Biological and Agricultural Engineering, University of California, Davis, CA 95616, USA (email: replant@ucdavis.edu); A. Roel, Graduate Group in Ecology, University of California, Davis, CA 95616, USA, and Instituto Nacional de Investigación Agropecuaria, Treinta y Tres, Uruguay.

Acknowledgments: Research reported here was supported by the California Rice Research Board and the Fertilizer Research and Education Program. We are grateful to Charley Mathews, Marysville, California, for permitting us to collect data on his farm.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Environmental implications of nutrient use and crop management in rice-based ecosystems

Bijay-Singh and Yadvinder-Singh

To meet increasing human needs, rice-based ecosystems are under pressure to produce more but without some of the environmental implications associated with changing nutrient and crop management practices. Irrigated rice grown in low-permeability soils leads to the production of methane (CH_4) and nitrous oxide (N_2O). The contribution of rice cultivation to total greenhouse gas emissions in India and China is 8.5-10.1%. The application of organic matter/crop residues enhances CH_4 production, but water management practices such as creating additional drainage periods can effectively reduce CH_4 emissions. Drainage events lead to the production of more N_2O, but in quantities that produce substantially less greenhouse effect than that of CH_4 emissions with no drainage periods. Burning of rice residues is widely practiced. This produces relatively low CH_4 and N_2O emissions compared with those from rice fields, but smoke creates a serious nuisance.

Nutrients and agrochemicals applied to rice-based ecosystems in increasing amounts reach groundwater when soils are coarsetextured or rice is grown in rotation with well-fertilized upland crops. Concentrations of pesticides in shallow groundwater beneath rice ecosystems are generally below the World Health Organization critical limits. Major environmental problems associated with rice production are linked with irrigation water management. Under the emerging scenario of shrinking water resources, technologies being developed to increase/sustain rice production should lead to reduced adverse effects on the environment.

Nearly half the people on Earth, most of them concentrated in Asia, use rice as a staple food. More than 90% of rice is grown and consumed in Asia (Blake 1992). Rice is grown on 140 million ha of arable land, which constitutes about 10% of the arable land worldwide (IRRI 1993). Rice cultivation over thousands of years has sustained the Asian population, which is growing at 1.8% a year. But an additional 50-70% of the current rice supply will be needed in 1990-2025 (Pingali et al 1997).

Thus, with shrinking land resources, rice will be under even more pressure in the coming decades. As a consequence, several crop management practices have been changing to produce more rice within changing economic, social, and environmental frameworks of less irrigation water, less labor availability, more mechanization, and greater environmental considerations. Some of these changes, such as increasing fertilizer and pesticide use (particularly in the developing countries of Asia) and crop residue burning, have serious environmental implications and even have direct bearing on the sustainability of the ecosystems. Although less rice production will lead to widespread hunger in several developing countries in Asia—a catastrophe no less serious than any environmental implication of growing rice—sustainable rice-based cropping systems will have to ensure that environmental degradation because of intensive rice cultivation also remains under control.

Concern about global warming and its possible effects on sea level had been linked with rice farming, although now it is a matter of worldwide concern (Jones et al 1988). Besides carbon dioxide (CO_2), other significant greenhouse gases are methane (CH_4) and nitrous oxide (N_2O) and both of these are evolved from rice fields. Traditionally, rice straw and residues of other crops have been removed from fields for use as cattle feed and for several other purposes such as livestock bedding, thatching material for houses, and fuel. Recently, because of the advent of mechanized harvesting, farmers prefer to burn large quantities of rice residues left in the field *in situ* as these interfere with tillage and seeding operations for the next crop. This practice has important implications not only for recycling of nutrients contained in crop residues and for organic matter content of the soil but also in terms of air quality and emission of greenhouse gases. Since the appearance of the Brundtland report (Brundtland and Khalid 1987), concern about the effects that chemicals used in agriculture have on the environment has increased considerably. To ensure high yields, the amounts of fertilizer and pesticide used on rice have been increasing (Pingali et al 1997). As rice is grown in a wide variety of soils and environments, a possibility always exists that a portion of the applied nutrients and agrochemicals will end up in surface-water and groundwater bodies. Many of the rural poor in Asia obtain water for drinking and household use from shallow aquifers under agricultural land, generally under rice-based cropping systems (Kahnert and Levinne 1993, Pingali and Rogers 1995). Also, people in most of the rural areas in Asia can hardly afford treatment of water once it is polluted. We have confined the discussion to the environmental implications of emissions of greenhouse gases either directly from rice fields or because of crop residue burning and enrichment of natural waters with nutrients and agrochemicals applied to rice-based cropping sequences.

Greenhouse gas emissions from rice production

Next to CO_2, CH_4 and N_2O are the two most important radiatively active trace gases in the atmosphere. The current concentration of 1.7 ppm CH_4 and 310 ppb N_2O is increasing with time at 1% and 0.25%, respectively. As the rate of increase in atmospheric CH_4 exceeds that of CO_2 by a factor of 2, its effect on atmospheric chemistry and climate pattern may become even more important in the future (Bouwman 1990). The anthropogenic sources of CH_4 include rice fields, domestic ruminants, biomass burning, landfills, coal mining, oil and natural gas flarings, animal wastes, and domestic sewage. The 10% of the total cultivated land area used for rice cultivation is close to the land area covered by natural wetlands and thus constitutes a significant source of atmospheric trace gases, particularly methane. In China and India, the two largest rice-producing countries of Asia, the contribution of rice cultivation to total national greenhouse gas emissions is 8.5-10.1% (Table 1). Since Koyama (1964), who first estimated global source strength associated with rice paddies as 190 Tg CH_4 y^{-1}, annual global emission rates estimated from field measurements and from model calculations have been reported by several authors. Obviously, the database available for global calculations of CH_4 emissions from rice cultivation has improved considerably. The latest estimates as given by the IPCC (1996) and Lelieveld et al (1998) are 60 ± 40 and 80 ± 50 Tg CH_4y^{-1}. Although there are many known natural and anthropogenic sources, emissions of N_2O have been difficult to quantify on a global scale. Recently, Mosier and Zhu (2000) estimated N_2O emissions from Asian agricultural systems and, using the FAO database, found that N_2O-N emissions increased from 0.75 Tg in 1961 to 2.1 Tg in 1994. During this period, synthetic N input increased 18.9 times and total N input increased 4.5 times.

Among different rice ecosystems, irrigated rice has by far the highest CH_4 source strength. According to Wassmann et al (2000a), irrigated rice accounts for 97% of the CH_4 emissions from rice fields in East Asia and for 60% of the CH_4 emitted from South and Southeast Asian rice fields (Fig. 1). Rainfed and deepwater rice are negligible for East Asia and contribute only 24% and 16%, respectively, to CH_4 emissions in South and Southeast Asia. In large parts of northern India where rice is grown on coarse-textured soils with high percolation rates requiring frequent irrigation, low CH_4 emission rates are encountered because of the constant inflow of oxygen into the soil (Jain et al 2000).

Methane emissions from flooded rice fields differ markedly with climate, soil characteristics, rice cultivars, application of organic matter and mineral fertilizers, and other agricultural practices. Factors contributing to increases in rice production such as the application of organic matter (manures, crop residues) and inorganic fertilizer use also increase CH_4 emissions (Neue and Sass 1996), whereas fertilizer N applications (fertilizer N-use efficiency) regulate the production of N_2O. Of course, water management in rice holds the key for potential trade-off between rice production and CH_4 mitigation options. Irrigated rice is the largest source of CH_4 but it also offers the most options for mitigating these emissions. Optimizing irrigation patterns in the field by introducing practices such as additional midseason drainage accounted for 7–80% of CH_4 emissions (Wassmann et al 2000b).

Continuous flooding was found to emit more CH_4 than alternate flooding and drying (Mishra et al 1997). A single midseason drainage reduces seasonal CH, emissions from rice fields but increases the emission of N_2O (Bronson et al 1997). Studying CH_4 emissions from rice fields in China, India, Indonesia, Thailand, and the Philippines, Wassmann et al (2000b) worked out mitigation options for different

Table 1. **Contribution of rice farming and crop residue burning in the national inventories of greenhouse gas emissions In China and India in 1990 (ADB-GEF-UNDP, 1998a,b, as reported at www.ccasia.teri.res.in).**

Source	Net CO_2[a]	CH_4	N_2O	NO_x	CO	CO_2 equivalent [b]	Percent of total CO_2
			(Gg)				(%)
People's Republic of China							
Total	1,769,562	25,328-32,889	190–530			2,361,626–2,624,526	100
Agriculture		12,599–20,090	70-190			286,090- 480,790	12.1–18.3
Rice cultivation		9,661–12,648				202,881– 265,608	8.6–10.1
Crop residue burning			10-30			3,100–9,300	0.1-0.4
India							
Total	534,285	18,477	255	3,193	18.003	1,001,352	100
Agriculture		12,645	243	109	3,038	341,064	34.1
Rice cultivation		4,070				85,470	8.5
Crop residue burning		116	3	109	3,038	3,366	0.3

[a] CO_2 emissions from biomass burning are not included in the national totals. CO_2 equivalents are based on global warming potentials of 21 and 310 times that of CO_2 for CH_4 and N_2O, respectively.

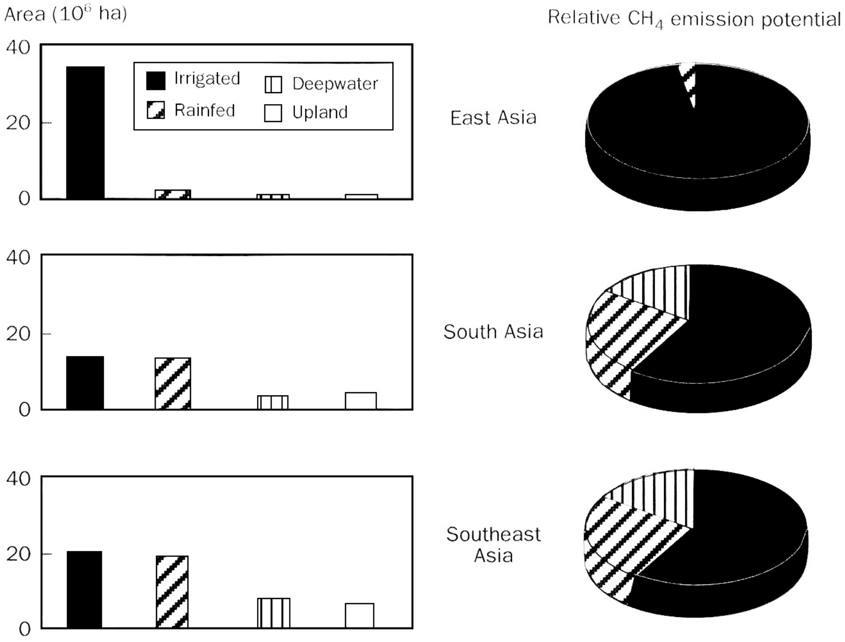


Fig. 1. Area and relative emission potential per season of different rice ecosystems in East, South, and Southeast Asia (source: Wassmann et al 2000a).

Table 2. Percent reduction in emissions of CH_4 by optimizing water management for rice grown with different baseline practices (adapted from Wassmann et al 2000b).

Baseline practice	Alternate water management practices	
	Midseason drainage	Alternate flooding/drying
Continuous flooding and organic amendments	7-44	59-61
Midseason drainage and organic amendments		21-46
Continuous flooding with no organic amendments	15-80	22

baseline practices of irrigated, rainfed, and deepwater rice. Table 2 summarizes results pertaining to the optimization of irrigation patterns. Modification of water regime appears to be a promising option to reduce CH_4 emissions when the baseline emissions are very high. Furthermore, based on global warming potential of 310 and 21 times that of CO_2 for N_2O and CH_4, respectively (IPCC 1996), reductions were more than greenhouse effects produced by increased emissions of N_2O caused by the introduction of drainage periods. It will not be possible to reduce CH_4 emissions to zero, but, in the vast area under rice cultivation located in South, Southeast, and East Asia, emissions are too high to be ignored for some reduction.

Encouraging incorporation of crop residues into the soil rather than burning may lead to increased CH_4 emissions (Sethunathan et al 2000). Substantial production of CH_4 occurs even in nonflooded soils amended with rice straw and abundant anaerobic microsites can create congenial conditions (Sextone et al 1985). However, it is interesting to note that emissions of CH_4 resulting from rice straw burning are 0.43-0.90% of the carbon content and this is similar to the range for straw application into the soil (Miura and Kanna 1997).

Effects of crop residue burning and management on air quality

Burning is perhaps the most common way of dealing with enormous quantities of crop residues produced in rice-based ecosystems. It is the easiest and cheapest way to remove large loads of crop residues produced by rice farmers worldwide. Besides saving time, it leads to reduced biotic stresses in terms of weeds, insects, and diseases and generally does not result in a decline in crop yield when compared with other crop residue management options (Samra et al 2002). Figures given by FAO in 1994 suggest that about 70% of all crop residues are burned globally. A survey carried out in 1996 and based on 237 farmers selected by stratified random sampling from the rice-wheat cropping area in the 11 districts of Indian Punjab revealed that 87% of rice and 52% of wheat was combine-harvested and burned. After four years, combine-harvested area under rice increased to 91% but, for wheat, it increased dramatically to 82% from 52% four years ago (Anonymous 1999). Another survey carried out during 2000-01 in different regions of the Indo-Gangetic Plain of India (more than 10 million ha under the rice-wheat system) revealed that a total of 72% of rice residues are burned *in situ,* 19% are incorporated in the soil, and the remaining 9% (manually harvested residues) are either used as fodder and industrial raw material or burned in heaps. This amounts to burning 10.7 Tg of rice residues per year (Table 3). These estimates do not include part of manually harvested residues burned in heaps (PR Gajri, Department of Soils, Punjab Agricultural University, Ludhiana, India, unpublished data).

During burning of crop residues, around 80% of carbon is lost as CO_2. A small fraction is lost as CO. It may be interesting to note that 70% of carbon contained in crop residues is lost via microbial respiration during decomposition anyway. Thus, incorporation of crop residues would reduce CO_2 by only 10%. Also, burning of crop residues does not constitute a net source of CO_2 because the carbon released to the atmosphere is reabsorbed during the next growing season. Burning involving incomplete combustion can also be a source of net emissions of many trace gases, including CH_4 and N_2O. The largest degree of uncertainty in estimating the emission inventories of CH_4 and N_2O from crop residue burning is the fraction of residue burned in the field. Nitrous oxide emissions from crop residue burning are calculated

Table 3. Estimates of burning of rice residues in different regions[a] of the Indo-Gangetic Plain in India (P.R. Gajri, Department of Soils, Punjab Agricultural University, Ludhiana, India, unpublished data).

Item	Punjab	Haryana	Uttranchal	Uttar Pradesh
		(million t)		
Total	15.0	6.6	3.3	13.5
Manually harvested (removed)	1.4	3.6	1.6	9.8
Machine-harvested	13.6	3.0	1.7	3.7
Completely burned	8.3	2.4	0.1	0
Completely incorporated	0	0	0	0.7
Partially burned	5.3	0.6	1.6	3.0
Total rice residues burned [b]	10.7	2.7	0.7	2.1

[a] Total area under the ricewheat system has been taken as 2.5 million ha in Punjab, 1.1 million ha in Haryana, 0.6 million ha in Uttranchal, and 2.7 million ha in Uttar Pradesh. Residue yield for each crop has been taken as 6.0 t ha^{-1} in Punjab and Haryana. 5.5 t ha^{-1} in Uttranchal, and 5.0 t ha^{-1} in Uttar Pradesh. [b] Assuming a burning component of 45% in the states of Punjab, Haryana, and Uttranchal and 70% in Uttar Pradesh for the partially burned rice residues.

Table 4. Greenhouse gas emissions (CO_2 equivalent) from burning of rice straw in northwestern India (N. Kalra, Department of Environmental Sciences, Indian Agricultural Research Institute, New Delhi, India, unpublished data).

State	CO_2	CO	CH_4	N_2O
		(Tg)		
Punjab	13.60	0.869	0.047	0.175
Haryana	1.56	0.099	0.005	0.013
Uttar Pradesh	11.10	0.706	0.038	0.090
Total	26.26	1.674	0.090	0.278

by first determining the amount of nitrogen released from the burned residues, then applying an emissions factor for nitrous oxide. Burning of rice and maize stubble in Australia releases more than 2 Tg of CO_2 and more than 21,000 t of NO_x (equivalent to 6.5 Tg of CO_2 in terms of greenhouse warming) (C.A. Kirkby, CSIRO Land and Water, Griffith, NSW, Australia, unpublished data).

The gaseous emissions from burning of rice straw were 70% CO_2, 7% CO, 0.66% CH_4, and 2.09% N_2O. Estimated emissions of greenhouse gases (Table 4) caused by burning of rice straw in three states in the Indo-Gangetic Plain of India are noteworthy. An idea of the relative contribution of crop residue burning to national emissions of greenhouse gases can be had from the data presented in Table 1. Although the data for only China and India, the two largest rice-producing countries in Asia, have been included, the trends are similar for other countries in Asia. Interestingly, crop residue burning contributed only 0.1% to 0.4% to the total emissions of greenhouse gases in both countries. The contribution of all agricultural sources was 12% to 18% in China and 34% in India.

Because of the large-scale burning of rice residues in the Indo-Gangetic Plain, a large patch of aerosol was detected by satellite during January-March 1999 in northwestern India. It resulted in a 30% reduction in biomass production and about a 15% reduction in grain yield because of aerosl-radiation-temperature-CO_2 interactions (N. Kalra, Department of Environmental Sciences, Indian Agricultural Research Institute, New Delhi, unpublished data). Smoke from crop residue burning pollutes the air with a mixture of gases and fine particles, which can lodge deep in the lungs when we breathe. Asthmatic people breathe with great difficulty under these conditions. In Griffith, New South Wales, Australia, the peak in asthma hospital admissions coincided with the annual burning of 30,000 t of rice stubble in the surrounding fields. Smoke can also create a haze that impairs visibility. As a matter of fact, smoke acts as a nuisance to people by preventing them from enjoying their own property and fresh air. The nuisance of smoke is perhaps one of the most important environmental problems associated with the large-scale burning of crop residues. Regulated rice residue burning seems a necessity if burning becomes essential.

Systematic studies to understand the role of rice straw burning in greenhouse gas emissions and air pollution in general are lacking in Asia. With the increase in mechanization, the amount of burned rice residues can increase conspicuously and may contribute substantially to air pollution. Of course, burning leads to the loss of organic matter and nutrients that otherwise can be returned to the soil by incorporating residues back into the soil, thereby leading to improvement in soil fertility (Samra et al 2002). The development of appropriate technologies and machinery to return residues to the soil is in progress.

Pollution of surface water and groundwater with nutrients and agrochemicals

Contamination of surface-water and groundwater bodies with nutrients and pesticides from routine agricultural practices is common and is a growing problem in the major agricultural regions of the world. To meet the long-term requirements of rice, a shift in the yield frontier of rice has been achieved, but it also involved a fundamental change in the way fertilizer and pesticide are used. The estimates of demand elasticity for fertilizer with respect to the adoption of modern varieties show that a 10% increase in the area under modern varieties increased fertilizer use by 24% for the Philippines, 14% for Indonesia, 13% for Thailand, and 10% for India (David and Otsuka 1994). In the 1990s, nitrogen application rates for the irrigated rice systems of South and Southeast Asia varied from 80 to 150 kg ha^{-1}. According to Rosegrant and Pingali (1994), fertilizer accounts for 20-25% of the total production cost in irrigated rice systems in Asia. Since the increase in nitrate and pesticides in drinking water, something about which the general public feels greatly concerned, seems to be the

Table 5. Leaching of fertilizer N under different land-use systems in China.

Site	Soil	Land use	N leaching as % of applied N	Reference
Saanxi	Stratified old manured loessial	Upland	1.2–3.5	Yi and Xie (1993)
Beijing	Fluvo-aquic soil	Upland	1–2	Yuan et al (1995)
Hebei	Fluvo-aquic soil	Upland	4.2	Dai and Zhao (1992)
Bejing	Fluvo-aquic soil	Rice	0.43-0.49	Wang et al (1996)
Liaoning	Fluvo-aquic soil	Rice	0.5	Zhang et al (1986)

Table 6. Statistics on nitrate-N in shallow groundwater in domestic wells under rice-based production systems in Laguna, Nueva Ecija, and Ilocos Norte provinces of the Philippines (adapted from Bouman et al 2001).

item	Laguna (1989-2000)		Nueva Ecija (1990-2000)		Ilocos Norte (1994–2000)	
	WS [a]	DS [a]	WS	DS	ws	DS
Cropping system	Rice-rice		Rice-rice		Rice-upland cash crops	
No. of observations	102	101	224	205	100	100
Mean (mg N L^{-1})	0.32	0.30	0.44	0.22	8.79	8.60
Maximum value	5.60	2.79	12.00	2.20	23.00	37.00

WS = wet season, DS = dry season.

most important environmental problem linked with agriculture, discussion in this section focuses on how significant the contributions of rice-based ecosystems are. Because of the paucity of data, phosphorus and herbicides are not discussed.

The problem of groundwater pollution by nitrate does not normally arise in areas where wetland rice is grown because nitrate is not normally formed under flooded conditions. Nitrate formed when soil is allowed to drain/dry may be promptly converted to nitrous oxide via denitrification. This is particularly true in the case of typical or ideal rice soils, which possess very low percolation rates after they are puddled. Data from different parts of China (Table 5) reveal that not more than 0.5% of the applied N is lost via leaching under rice. On the other hand, leaching losses can be more than 4% from soils under upland crops, where nitrates are readily formed because of aerobic conditions. Thus, in Laguna and Nueva Ecija provinces of the Philippines where the rice-rice cropping system is followed, very low nitrate-N concentrations in shallow groundwater in domestic wells were observed (Table 6). In sharp contrast, in Ilocos Norte Province (Magnuang), intensified rice-cash crop systems have evolved, with rice grown in the wet season and one or two nonrice food or cash crops (upland crops) in the dry season. Sweet pepper, the commonly grown cash crop in the region, receives high dosages of fertilizer N (340-450 kg N ha^{-1}) and about 10 times as much irrigation water as other crops. These conditions lead to the leaching of nitrate to groundwater bodies with the onset of rains (Tripathi

Table 7. ^{15}N balance in a field study for basal and topdressed applications of N individually to wheat grown on a porous soil (adapted from Katyal et al 1987).

N application	N source	^{15}N recovered (% of applied N)			
		Straw	Grain	Soil	Losses
Basal	Urea	7.2 b[a]	28.0 b	34.7 ab	30.1 b
	KNO_3	14.4 a	50.3 a	30.2 b	5.1 d
Topdressed after irrigation	Urea	6.7 b	23.8 b	27.4 b	42.2 a
Topdressed before irrigation	Urea	11.5 a	40.3 a	32.4 ab	15.8 c
	KNO_3	15.0 a	49.6 a	37.1 a	-1.7 d

[a] Numbers in the same column with a common letter are not significantly different (*P* = 0.05).

et al 1997) and very high nitrate-N content in groundwater is observed (Table 6). Inclusion of an N-catch crop during the dry-to-wet transition period has been shown to substantially reduce nitrate leaching to groundwater (Shrestha and Ladha 1998).

Soils in vast areas in Asia are porous, coarse in texture, and highly permeable. Depending upon the availability of irrigation water, these soils are used for raising both upland crops and wetland rice (Aulakh and Bijay-Singh 1997). Because of the plentiful availability of irrigation water, the rice-wheat system in the Indo-Gangetic Plain in northwestern India constitutes a typical example of highly productive nonideal rice soils. In this region, there hardly occurs any leaching of nitrate-N beyond the 2-m-deep rooting zone of the wheat crop. Data in Table 7 show that, even by supplying the whole requirement of wheat through $K^{15}NO_3$, all N could be recovered in the soil and plant, indicating no leaching losses. On the other hand, rice grown in the wet season receives around 150 cm of irrigation besides 33 cm of average rainfall. Under these conditions, a large part of the applied N is lost as nitrate via leaching to groundwater. Interestingly, because of the high percolation rates, soil under rice experiences alternating aerobic-anaerobic cycles that facilitate the production of nitrate, unlike in ideal rice soils. Thus, nitrate-N content in the groundwater in this region has been increasing consistently since 1975 when the first sampling was made (Table 8). In 1999, several samples of water drawn from shallow hand pumps contained nitrate-N levels much above the WHO limit of 10 mg N L^{-1} (Table 9). Enhancing fertilizer N-use efficiency in rice-based cropping systems by ensuring measures such as the balanced application of nutrients, proper coordination of N and irrigation management, and site-specific and need-based nutrient management can substantially control the leaching of nitrate-N beyond the root zone of crops (Bijay-Singh et al 1995).

Compared to nitrate, only a few studies have dealt with pesticide in groundwater beneath rice-based ecosystems. The leaching of agrochemicals to groundwater is governed by several transformation processes besides uptake by plants. In warm and humid conditions generally found under rice grown in tropical and subtropical climates, volatilization is a major process of pesticide loss, particularly when pesti-

Table 8. Nitrate concentration (mg NO_3-N L^{-1}) in water samples from shallow wells (4 to 10 m deep) located in agricultural land predominantly under the rice-wheat system in Ludhiana District (Punjab, India) during 1975 to 1988 (adapted from BijaySingh et al 1995).

Item	1975		1982		1988
	Jun	Sep	Jun	Sep	Nov/Dec
Number of observations	46	33	26	26	28
Range (mg NO_3- N L^{-1})	0.04-6.15	0.05-7.90	0.35-10.11	0.23-15.17	0.31-13.30
Geometric mean (mg NO_3-N L^{-1})	0.42	0.42	1.48	2.13	2.29
Correlation coefficient (r): fertilizer N applied vs NO_3^--N in well water	ns	0.51 [a]	ns	0.51 [a]	0.59 [a]

[a] Significant at 5% level of significance. NS = nonsignificant.

Table 9. Nitrate-N content (mg N L^{-1}) in tubewells and hand pumps located in agricultural land predominantly under the rice-wheat system in the four blocks of Ludhiana District (Punjab, India) in July 1999 (adapted from BIJaySingh et al 1995, Roopna Kaur 2000).

Block	Tubewells		Hand pumps	
	Range	Mean [a]	Range	Mean
High fertilizer use				
Jagraon	2.46-16.16	6.49	3.57-49.74	12.6
Samrala	1.44- 8.73	4.06	0.92-29.58	12.4
Low fertilizer use				
Pakhowal	1.67-4.41	2.82	2.95-13.19	6.75
Dehlon	1.32-9.25	4.29	0.15-20.64	8.67

[a] Mean values of nitrate-N in 1992 were tubewells = 3.62 ± 1.52 (n = 236), hand pumps = 5.72 ± 2.09 (n = 367).

cides are applied on wet soil or in standing water. The remaining pesticides are readily degraded through microbial or photochemical processes that are generally favored by high temperatures and solar radiation found in the tropics. Also, pesticides are less persistent under flooded than under upland conditions. Thus, relatively smaller amounts of pesticide will leach down to groundwater when applied to rice rather than to an upland crop. The data pertaining to the content of different pesticides in samples of shallow groundwater in Laguna and Nueva Ecija provinces of the Philippines (Table 10) show that values are generally lower and are one or two orders of magnitude below the WHO single (0.1 ppb) and multiple (0.5 ppb) pesticide limits for drinking water, although temporary peak concentrations of 1.14-4.17 ppb are observed. The mean use of pesticides in this study was 0.65–1.4kg ai ha^{-1} , and

Table 10. Statistics on pesticides in shallow groundwater in domestic wells under rice-based production systems in Laguna, Nueva Ecija, and Ilocos Norte provinces of the Philippines (adapted from Bouman et al 2001).

Pesticide	Nueva Ecija						Laguna			
	1990 WS[a]		1991 DS[a]		1991 WS		1989 WS		1990 DS	
	Mean	Max[b]	Mean	Max	Mean	Max	Mean	Max	Mean	Max
					(ppb)					
Azin	0.038	0.543	0.029	0.892	<dl	<dl	0.338	4.170	0.025	0.320
Butachlor	0.005	0.075	<dl[c]	<dl	0.001	0.018	0.142	1.140	0.036	0.380
Carbofuran	0.019	0.776	<dl	<dl	na[d]	na	0.015	0.440	0.098	1.150
DDT	0	0.010	<dl	<dl	na	na	0.010	0.140	0.003	0.020
Diazinon	0.047	0.510	0.012	0.052	0.015	0.040	0.038	0.460	0.004	0.072
Endosulfan	0.126	1.900	0.029	0.220	na	na	0.051	0.300	0.053	0.310
Endrin	0	0.004	<dl	<dl	na	na	0.006	0.101	0.002	0.060
Lindane	0.007	0.220	0.010	0.220	na	na	0.002	0.011	0.006	0.081
Malathion	0.004	0.132	0	0.020	0.029	0.060	0.004	0.070	0.004	0.072
MIPC	0.002	0.042	<dl	<dl	<dl	<dl	0.034	0.260	0.009	0.150
Parathion	0.006	0.250	0.001	0.038	0.001	0.010	0.023	0.130	0.010	0.234

[a] WS = wet season, DS = dry season. [b] Safe drinking water limit = 0.1 ppb for single pesticide. [c] Detection limit. [d] Data not available.

it was low compared with that in several other rice-producing countries in Asia. But, one should not expect that these small differences in pesticide use will lead to significantly higher pesticide levels in groundwater bodies.

Conclusions

To meet the food demand of the growing human population, rice productivity must continue to increase. Food shortages can lead to catastrophes no less serious than any of the environmental consequences linked with some of the nutrient and crop management practices associated with intensive rice-based cropping systems. Ecosystems based on irrigated rice are one of the main anthropogenic sources of CH_4 and N_2O. The trade-off between reducing greenhouse gas emissions and increasing rice yield can best be handled by manipulating water management practices. Introducing additional drainage periods can effectively mitigate CH_4 production to levels more than the greenhouse effects produced by increased emissions of N_2O as a result of midseason drainage. Crop residue incorporation into the flooded rice system does not result in the production of CH_4 more than that released by its burning.

Burning is still a preferred way to get rid of large amounts of residues from rice-based cropping systems, although, by not returning the residues to the soil, precious organic matter and nutrients are lost. The amounts of CO_2, CH_4, and N_2O that are produced by the burning of residues are very small in comparison with those produced in rice fields, but the production of huge amounts of smoke can create a variety of environmental hazards, such as smog, haze, and breathing problems. If absolutely necessary, large-scale crop residue burning needs to be strictly regulated to minimize the nuisance of smoke.

Nitrates are neither produced nor leached significantly beyond the root zone in wetland rice grown in puddled, low-permeability soils. It is only in coarse-textured soils or when rice is rotated with a well-fertilized upland crop that significant amounts of nitrate-N can leach to shallow groundwater and may eventually make it unfit for drinking. Enhancing fertilizer N-use efficiency can effectively reduce nitrate pollution of groundwater. Pesticide levels in shallow groundwater beneath rice-based ecosystems are generally lower than the critical drinking water standards.

References

ADB-GEF-UNDP (Asian Development Bank). 1998a. Asia least-cost greenhouse gas abatement strategy: India national report. Manila (Philippines): ADB. 5 p.

ADB-GEF-UNDP (Asian Development Bank). 1998b. Asia least-cost greenhouse gas abatement strategy: People's Republic of China. Manila (Philippines): ADB. 5 p.

Anonymous. 1999. Enhancing the biodegradation of rice residue in rice-based cropping systems to sustain soil health and productivity. Project Terminal Report. New Delhi (India): Indian Council of Agricultural Research.

Aulakh MS, Bijay-Singh. 1997. Nitrogen losses and N-use efficiency in porous soils. Nutr. Cycl. Agroecosyst. 47:197-212.

Bijay-Singh, Yadvinder-Singh, Sekhon GS. 1995. Fertilizer use efficiency and nitrate pollution of groundwater in developing countries. J. Contaminant Hydrol. 20:167-184.

Blake RO. 1992. Sustainable and increased food production. Agric. Syst. 40:7-19.

Bronson KF, Neue H, Singh U, Abao Jr EB. 1997. Automated chamber measurements of methane and nitrous oxide flux in a flooded rice soil. II. Fallow period emissions. Soil Sci. Soc. Am. J. 61:988-993.

Bouman BAM, Castañeda AR, Bhuiyan IS. 2001. Nitrate and pesticide contamination of groundwater under rice-based cropping systems: past and current evidence from the Philippines. Agric. Ecosyst. Environ. 1875:1-15.

Bouwman AF. 1990. Soils and the greenhouse effect. Chichester, Mass. (USA): Wiley.

Brundtland GH, Khalid M. 1987. Our common future. Report of the World Commission on Environment and Development. Oxford (UK): Oxford University Press.

Dai TS, Zhao ZS. 1992. Case study on chemical form conversion and leaching of nitrogen and phosphorus in the irrigated plain area of Haihe river basin. Acta Sci. Circumstantiae 12:497-501. (In Chinese.)

David CC, Otsuka K. 1994. Modern rice technology and income distribution in Asia. Boulder, Colo. (USA): Lynne Reinner Publishers, and Manila (Philippines): International Rice Research Institute.

IPCC (Intergovernmental Panel on Climate Change). 1996. Climate change 1995: the science of climate change. Cambridge (UK): Cambridge University Press. 572 p.

IRRI (International Rice Research Institute). 1993. IRRI rice almanac. Manila (Philippines): IRRI. 142 p.

Jain MC, Kumar S, Wassmann R, Mitra S, Singh SD, Singh JP, Singh R, Yadav AK, Gupta S. 2000. Methane emissions from irrigated rice fields in northern India (New Delhi). Nutr. Cycl. Agroecosyst. 58:75-83.

Jones PD, Wigley TML, Folland CK, Parker DE, Angell JK, Lebedeff D, Hansen JE. 1988. Evidence for global warming in the past decade. Nature 332:790.

Kahnert F, Levinne G. 1993. Groundwater irrigation and the rural poor: options for development in the Indo-Gangetic Basin. Washington, D.C. (USA): World Bank. 222 p.

Katyal JC, Bijay-Singh, Vlek PLG, Buresh RJ. 1987. Efficient nitrogen use as affected by urea application and irrigation sequence. Soil Sci. Soc. Am. J. 51:366-370.

Koyama T. 1964. Biogeochemical studies on lake sediments and paddy soils and the production of hydrogen and methane. In: Miyaki T, Koyama T, editors. Recent researches in the field of hydrosphere, atmosphere, and geochemistry. Tokyo (Japan): Maruzen. p 143-147.

Lelieveld J, Crutzen PJ, Dentener FJ. 1998. Changing concentration, lifetime and climate forcing of atmospheric methane. Tellus 50B: 128-150.

Mishra S, Rath AK, Adhya TKK, Rao VR, Sethunathan N. 1997. Effect of continuous and alternate water regimes on methane efflux from rice under greenhouse conditions. Biol. Fertil. Soils 24:399-405.

Miura Y, Kanna T. 1997. Emissions of trace gases (CO_2, CO, CH_4, and N_2O) resulting from rice straw burning. Soil Sci. Plant Nutr. 43:849-854.

Mosier AR, Zhu Z. 2000. Changes in patterns of fertilizer nitrogen use in Asia and its consequences for N_2O emissions from agricultural systems. Nutr. Cycl. Agroecosyst. 57:107-117.

Neue HU, Sass R. 1996. Trace gas emissions from rice fields. In: Prinn RG, editor. Global atmospheric biospheric chemistry. Environmental Science Research. Vol. 48. New York, N.Y. (USA): Plenum Press. p 119-147.

Pingali PL, Hossain M, Gerpacio RV. 1997. Asian rice bowls; the returning crisis? Oxon (UK): CAB International and Manila (Philippines): International Rice Research Institute. 341 p.

Pingali PL, Rogers PA, editors. 1995. Impact of pesticides on farmer health and the rice environment. Manila (Philippines): International Rice Research Institute. 664 p.

Roopna Kaur. 2000. Nitrate pollution of groundwater beneath soils under intensive loading. M.Sc. thesis. Ludhiana (India): Punjab Agricultural University.

Rosegrant MW, Pingali PL. 1994. Policy and technology for rice productivity growth in Asia. J. Int. Dev. 6:665-668.

Samra JS, Bijay-Singh, Kuldip Kumar. 2002. Management of crop residues in rice-wheat system of the Indo-Gangetic Plain. In: Improving the productivity and sustainability of rice-wheat systems: issues and impact. ASA Special Publication. Madison, Wis. (USA): American Society of Agronomy (ASA). (In press.)

Sethunathan N, Kumaraswamy S, Rath AK, Ramakrishnan B, Satpathy SN, Adhya TK, Rao VR. 2000. Methane production, oxidation, and emission from Indian rice soils. Nutr. Cycl. Agroecosyst. 58:377-388.

Sextone AJ, Revsbach NP, Parkin TB, Tiedje JM. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Sci. Soc. Am. J. 49:645-651.

Shrestha RK, Ladha JK. 1998. Nitrate in groundwater and integration of nitrogen-catch crop in rice-sweet pepper cropping system. Soil Sci. Soc. Am. J. 62:1610-1619.

Tripathi BP, Ladha JK, Timsina J, Pascua SR. 1997. Nitrogen dynamics and balance in intensified rainfed lowland rice-based cropping systems. Soil Sci. Soc. Am. J. 61:812-821.

Wang JY, Wang SJ, Chin Y, Li CY, Qi XJ. 1996. Study on nitrogen leaching in rice fields. Acta Pedol. Sin. 33:28-36. (In Chinese.)

Wassmann R, Neue HU, Lantin RS, Makarim K, Chareonslip N, Buendia LV, Rennenberg H. 2000a. Characterization of methane emissions from rice fields in Asia. II. Differences among irrigated, rainfed, and deepwater rice. Nutr. Cycl. Agroecosyst. 58:13-22.

Wassmann R, Lantin RS, Neue HU, Buendia LV, Corton TM, Lu Y. 2000b. Characterization of methane emissions from rice fields in Asia. III. Mitigation options and future research needs. Nutr. Cycl. Agroecosyst. 58:23-26.

Yi X, Xie CZ. 1993. Study on nitrogen fertilizer pollution by leaching in stratified old manured loessial. Agro-Environ. Prot. 12:250-253. (In Chinese.)

Yuan FM, Chen ZM, Yao ZH, Zhou CH, Fu GM, Song YL, Li XP. 1995. NO_3^--N transformation, accumulation and leaching loss in surface layer of Char-Soil in Beijing. Acta Pedol. Sin. 32:388-399. (In Chinese.)

Zhang FZ, Gao ZM, Xiong XZ. 1986. A dynamic ^{15}N study on the leaching of nitrogen in soil-plant system. In: Gao ZM, editor. Study of pollution ecology in soil-plant system. Beijing (China): China Science and Technology Press. p 490-502.

Notes

Authors' address: Department of Soils, Punjab Agricultural University, Ludhiana 141 004, India. E-mail: bjs_20@sify.com.

Citation: Mew TW, Bra DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Improving rice quality through crop and resource management

Fang Chen, Sam Portch, and Ji-yun Jin

Rice is one of the most important grain crops in the world. Obtaining both high yield and high-quality rice is becoming more and more important. Rice quality includes processing quality as well as appearance, cooking, eating, and nutritional quality factors. Many factors can affect quality.

Up to now, much research on the application of new technology to rice growing and the influences of the ecological environment on rice quality has been done in China, the Philippines, and Japan. Much research focused mainly on a single factor or evaluated currently planted varieties. Thus, it is hard to have a common understanding of some problems. Many environmental and man-made factors influence rice quality. To improve rice quality, natural factors such as climate cannot be changed, but manmade factors such as fertilization, irrigation, and breeding can be controlled.

We briefly discuss the effects of nine main factors: temperature, illumination, water and irrigation, soil, fertilization, planting density, field organisms, grain processing, and breeding selection for rice quality. For natural factors, temperature regulation and control by planting dates and locations are a key, and, for man-made factors, irrigation and balanced fertilization are the most important. Good regulation and control of these factors will increase rice yield and quality greatly.

Rice quality can be improved by increasing rice grain filling, unpolished and polished grain ratios, grain protein content, grain transparency, amylose content, nutrient uptake and use efficiency, nutrient element content, elongation, the ratio of filled to unfilled grain, taste, and breeding selection and by decreasing grain chalkiness, percent unfilled grain, disease and insect damage, and weed influence.

Rice is one of the most important grain crops in the world, Twenty years ago in China, persuading farmers to use modern rice varieties and their accompanying inputs was easy because the farmers benefited from yield and income increases. Today, however, to persuade farmers to use modern rice varieties and their accompanying planting practices is not so easy because both yield and quality have become an important factor contributing to the price that farmers receive. In addition, to achieve high yield and high quality of rice, more reliance on "knowledge-based" farming is needed.

Today, because of their increase in living standard, Chinese consumers like to, and can afford to, eat good-quality rice. Rice quality is expressed as the essential characteristics of rice in the commodity market. It mainly has five aspects—processing, appearance, cooking, eating, and nutritional quality (Gu De-fa et al 1995). In rice production, many factors other than genetic control of the rice variety can affect rice quality, including climate, sowing dates, fertilization, soil, irrigation, and other cultural practices.

Up to now, much research on rice quality has been done in China, the Philippines, and Japan. The research in Japan focused mainly on applying new techniques and new measures, whereas in China the research focused mainly on the relationship between ecological environment and rice quality (IRRI 2000). In this paper, we would like to briefly discuss the main factors in crop and resource management that relate to rice quality.

Temperature

Of all the environmental factors, temperature, especially in the stage of grain filling, is the most important one affecting rice quality. High temperature in the tassel to maturity stage would speed up the grain-filling rate and shorten the grain-filling period, resulting in lower grain filling and decreased unpolished and polished grain ratios, with grain chalkiness becoming bigger and transparency lower. Low temperature will also result in bigger grain chalk spots and an increased percent unfilled grain. So, both high and low temperature would decrease the processing and appearance quality of rice (Sao Dong-sheng and Tang Jian 1987, Li jun and Gu De-fa 1995, Tang Tiang-ru and Yu Zie-fiao 1991). High temperature would increase the temperature of grain gelatinization and vice versa. The highest amylose content of rice grain will be obtained only in an optimum temperature condition. Both high and low temperature reduced the accumulation of grain amylose (Resurreccion 1997).

It was reported that, after the tassel stage, high temperature would influence the nutritional quality (protein content) of rice. In the heading stage, if daily average temperature increased from 20 to 30 °C, the total polished grain ratio would decrease 24-35% (He 1992). To keep a high polished grain ratio, japonica rice needs a lower temperature than indica rice (Yang Hua-long et al 2001). For example, Da Yan village in Gong Zhu Ling, Jilin Province, can produce high-quality rice that has good transparency and a low chalkiness ratio because the average temperature of the village in August is 19 °C. This temperature is 1 °C lower than that of other areas and the grain-filling stage of local rice is precisely in August (Zhang Shan-yuan 1996).

Compared with that of high temperature, the negative effect on rice from low temperature is much smaller. It was reported that, to obtain good rice quality, the optimum temperature should be in the range of 20-s30 °C in the tassel and maturity stages. This is the main reason why the quality of late rice, ratooning rice, and rice planted in high-altitude regions is better than that of early rice, middle rice, and rice planted in low-altitude regions (Wu Guan-ting and Xia Ying-wu 1994).

Illumination

Illumination is an important factor related to rice quality, just after temperature. If illumination is low in the late growing stage, rice photosynthesis is restrained. In contrast, high illumination results in high temperature, thus shortening the heading stage. Therefore, both high and low illumination will make grain chalkiness larger and the ratio of chalky grain higher than normal. It was reported that there is a positive correlation between sunshine and gelatinization temperature and consistence, and a negative correlation between sunshine and amylose content. In tropical areas, rice protein content was reduced by strong radiation of sunlight (Li Jun et al 1997).

The effect of different sowing times on rice quality is mainly caused by climatic factors such as temperature and illumination. The same rice variety at the same location but sown at different times of the season will show significant differences in quality. Usually, late-season rice has better quality than early-season rice (Zhu Xu-dong et al 1993).

Water

Both water quantity and quality can affect rice quality. Soil water content mainly influences processing quality and amylose and protein content of rice. In the heading stage, reducing soil water content properly could increase the polished grain ratio and decrease the percent unfilled grain. But if soil water content is too low for a long period, rice processing quality would decrease significantly, grain chalkiness would be larger, and amylose content in polished grain would decrease. Research results indicated that, when soil water content was low and drought occurred, protein content in unpolished grain was higher than normal.

Relative humidity and/or rainfall can also affect rice quality. Results from field experiments on sowing time and planting in different locations indicated that relative humidity has a positive correlation with gelatinization temperature, consistence, and chalkiness size, and a negative correlation with amylose content. Different rainfall amounts have a significant effect on grain elongation and amylose and protein content in unpolished grain (Wu Guan-ting and Xia Ying-wu 1994).

Irrigation water quality also has a notable effect on rice quality. Usually, rice irrigated by river water has better quality than that irrigated by pool water when comparing the same rice variety.

Soil

Usually, rice planted on soil developed from granite parent material has a better taste than that planted on soil developed from volcanic parent material. Rice planted in wet fields is better than rice planted in dry fields. In terms of land form, rice planted on plains has a better taste than that planted in mountainous areas and basins. There is a significant difference in rice quality such as protein content and grain chalkiness size when the same rice variety using the same farming practices is planted on different soils (Qian Qian et al 1998).

Research results indicated that, with intensive soil improvement and deep plowing practices, the plowing layer and root zone of high-yielding and high-quality paddy fields were considerably deeper than those of neighboring paddy soils. Soil hardness and bulk density of the high-yielding paddy fields were lower than those of the neighboring paddy soils (Sung Bae Kim 1990).

It was reported that total soil nitrogen (N) and available N content have a positive correlation with rice protein content and a negative correlation with amylose content, especially in late rice. Scented rice is usually grown on soils with higher phosphorus (P) content. Soil total and available P content also have a significant positive correlation with rice protein content. Soil available sulfur (S) content has a positive correlation with polished grain ratio and protein content. Soil available manganese (Mn) content has a significant negative correlation with rice quality. With higher soil-available Mn content, grain chalkiness size is bigger. Soil available zinc (Zn) content is significantly higher in scented rice-planting areas than that in nonscented rice-planting areas (Huang Shu-zhen 1990). Zn deficiency is the most widespread micronutrient disorder in rice. Its occurrence has increased with the introduction of modern varieties, crop intensification, and increased Zn removal (Dobermann and Fairhurst 2000). Rice soil and plant Zn deficiency will result in plant stunting, reduced tillering, severely affected growth, and some dusty brown spots appearing on upper leaves. This deficiency will not only reduce rice yield but also affect grain quality.

Fertilization

The quick development of modern science and the fertilizer industry made it possible to produce many kinds of fertilizer. These fertilizers supply many kinds of plant nutrients essential for plant growth, They provide sufficient nutrition to support plant growth when the soil nutrient supply is not sufficient for high yield and high quality.

The relationship between fertilization and crop yield and quality can be summarized as: (1) When a plant nutrient is deficient, fertilization can increase crop yield and quality. (2) When all plant nutrients are in excess because of overfertilization, the crop may maintain a high yield but the quality would be lower. When overfertilization with one kind of plant nutrient occurs, both crop yield and quality would decrease significantly.

Rice quality can be affected greatly by nitrogen and potassium (K). Other fertilizers such as P, Zn, S, silicon (Si), magnesium (Mg), and calcium (Ca) can

Table 1. The effect of applying N at the full-heading stage on rice quality.

Variety	Treatment	Stem and leaves		Unpolished grain	
		N (%)	Protein (%)	N (%)	Protein (%)
Early rice, V1136	Topdressing N	1.00	5.96	1.53	9.11
	Check	0.85	5.04	1.18	7.02
Late rice, Gui 99	Topdressing N	0.93	5.53	1.33	7.93
	Check	0.69	3.98	1.03	6.10

Table 2. Relationship between potassium and rice fungal diseases.

Disease name	Report number			
	Positive effect	Zero effect	Negative effect	Subtotal
Brown leaf spot	50	11	5	66
Cercospora leaf spot	2	—	–	2
Dustbrand	–	3	2	5
Rice blast	34	14	45	93
Sheath blight	6	–	–	6
Sheath rot	3	–	1	4
Stem rot	32	2	–	34
Sclerotiniosis	1	–	–	1
Total	128	30	53	211

affect rice quality as well, but not as significantly as N and K. N fertilizer applied at a rational rate increases polished grain ratio and protein content and decreases chalkiness ratio and size and amylose content. Split N applications can increase the unpolished and polished grain ratio, grain transparency, and protein content, whereas amylose content would be lowered when N is applied at one time. If N is applied in excess, especially at the rice grain-filling stage, taste would be negatively affected by increased protein content (Qian Qian et a1 1998). Research results indicated that topdressing N at the full heading stage for both early and late rice increased both grain filling and grain protein content (Table 1).

Potassium can promote N metabolization and the transportation of photosynthetic product to grain. It was reported that K application increased the ratio of winnowed paddy 1.3-1.7% and increased the protein content of unpolished grain 2.8-6.8%. Late rice has a tendency similar to that of early rice (He Dian Yuan et a1 1994). Potassium application can also reduce rice fungus diseases. Data (Table 2) show that the positive effect (reduced diseases) of K application was 61%, the zero effect is 14%, and the negative effect is 25%. The negative effect was mainly with rice blast (Huang-Xiao Lan 1998).

Of course, it should not be thought that only the practice of fertilizer application can control the damage from rice diseases and insects. Usually, the increase in plant resistance by K application cannot compare with the effect of pesticide use. But it should be understood that optimum fertilization, especially sufficient K application, will reduce the risk of crop yield losses because of diseases and insects as well as support the plant through other climatic stresses such as drought or cold weather. With improvements in the plant's nutritional condition, it will grow well and resist diseases and insects better. This will produce a higher yield and quality.

Planting density

For a selected variety, planting density has a notable effect on rice quality. With an increase in planting density, the unpolished and polished grain ratio, protein content, and transparency of rice decrease, whereas the chalkiness ratio, percent unfilled grain, amylose content, and consistency of rice grain increase. These will reduce the quality of rice appearance and processing greatly.

Although high planting density may negatively affect rice quality, it is often necessary in many countries to use limited land resources efficiently to achieve high yields and production. Studies on the "optimum planting density" for local rice varieties based on yield and quality factors are always necessary.

Organisms

Field organisms are mainly related to diseases, insects, and weeds. For example, rice sheath blight will result in poor rice quality as the stem withers away, grain filling is low, and black spots appear on the grain. Grain smut will affect rice taste and may cause poisoning to humans and animals. Some rice insects such as the rice planthopper and rice stinkbug affect rice quality by reducing grain filling. Weeds such as cockspur grass and cluster Chinese sprangletop can affect rice quality by competing for plant nutrients and water, thus reducing rice grain size.

Processing

All the essential plant nutrients for rice growth are also essential nutrients for humans and animals, except boron. Cultivated crops provide humans with not only organic nutrition but also with many essential macronutrients (N, P, K), secondary nutrients (Ca, Mg, S, sodium [Na]), and micronutrients such as copper (Cu), iron (Fe), Mn, Zn, etc. Rice is the main grain food for humans and its nutritional quality can affect human health directly.

Most of the nutritional value such as vitamins, minerals, and high-lysine-content protein are located in the exterior and embryo of rice grain, whereas the interior of the grain contains less nutrition. Thus, during processing of the grain, some nutrition will be lost. The finer the processing, the higher will be the loss of nutritional value,

Table 3. Nutritional change in different ratio of filled to unfilled grains (per 100 g).

Nutrition	Ratio of filled to unfilled grains (%)					
	88.8	90.2	91.9	94.0	96.6	100
Protein (g)	8.03	7.88	8.21	8.09	7.79	7.60
Fat (g)	0.75	0.82	0.98	1.55	2.02	2.89
Carbohydrate (g)	90.56	90.57	89.95	89.22	88.89	87.95
Water (g)	12.78	12.65	12.44	12.77	12.30	13.18
Ash (g)	0.66	0.73	0.86	1.14	1.30	1.55
Vitamin B_1 (mg)	1.25	1.49	1.64	2.46	3.11	4.00
Nicotinic acid (mg)	25.1	34.7	37.5	44.5	53.1	67.0
Ca (mg)	5.85	5.87	6.85	7.4	8.45	9.25
P (mg)	84.5	94.0	105.0	141.5	152.0	200.5
Fe (mg)	0.7	0.58	0.95	1.15	1.05	1.40

especially the vitamin-B family. Data (Table 3) show that different ratios of winnowed paddy have different nutrition content (Li Jing 1993).

Breeding

Breeding selection for modern high-nutrition rice varieties combined with proper fertilization is an efficient way to improve both rice yield and nutritional value. It is well established that differences in nutrient uptake rate, quality, and nutrition-use efficiency exist in different plants and varieties. Thus, these differences can be used to select high-quality varieties to satisfy both the quality and nutritional needs of humans.

References

Dobermann A, Fairhurst T. 2000. Rice nutrient disorders & nutrient management. Singapore: Phosphorus and Potash Institute and International Rice Research Institute. p 84-86.

Gu de-fa, Cai yi-zhong, Li Jun et al. 1995. Research and development for special rice. Beijing (China): Chinese Agricultural Science and Technology Publishing House. p 70-81. (In Chinese.)

He Dian Yuan et al. 1994. Soil fertility and planting crop fertilization in south China. Beijing (China): Science Publishing House. p 335-339. (In Chinese.)

He KY. 1992. Grain quality characteristics for brown rice. Korea J. Crop Sci. 39(1):38-44.

Huang Shu-zhen. 1990. Relationship between soil characteristics and rice quality in Hunan scented rice planting area. Hunan Agric. Sci. 4:10-13. (In Chinese.)

Huang Xiao Lan. 1998. Potassium and plant health. Agricultural Science and Technology Publishing House of China. p 22. (In Chinese.)

IRRI (International Rice Research Institute). 2000. IRRI library and documentation service. Rice Lit. Update 8(1):68-71.

Li Jing. 1993. Human and social nutriology. Beijing (China): Light Industrial Publishing House of China. p 274-275. (In Chinese.)

Li Jun, Gu de-fa. 1995. Effect of different sowing time and fertilization rates on two high-quality rice varieties. J. Shanghai Agric. College 13(1):63-67. (In Chinese.)

Li Jun, Gu De-fa, Li Lin-feng. 1997. Research advances on the effect of environment and planting factors on rice quality. J. Shanghai Agric. 13(1):94-97. (In Chinese.)

Qian Qian, Liu Xiou-yan, Zeng Da-li. 1998. Introducing research on the factors that affect rice taste quality in Japan. Rice China 234-37. (In Chinese.)

Resurreccion AP, 1997. Effect of environment on rice amylose content. Soil Sci. Plant Nutr. 23(1):109-112.

Sao dong-sheng, Tang Jian. 1987. Relationship between grain milk filling and rice quality. Guizhou Agric. Sci. 2:12-14. (In Chinese.)

Sung Bae Kim. 1990. Maximum yield research for paddy rice in Korea. Proceedings of the symposium on maximum yield research. p 78-86.

Tang xiang-ru,Yu tie-qiao. 1991. Effect of temperature on rice quality and related biochemistry characteristics in milk filling and maturity stages. J. Hunan Agric. College 17(1):1-8. (In Chinese.)

Wu Guan-ting, Xia Ying-wu. 1994. Effect of environment and cultivation on rice quality. Rice China 4:37-39. (In Chinese.)

Yang Hua-long, Yang Zhe-ming, Lu Bi-lin. 2001. Effect of ecological environment on rice quality. Hubei Agric. Sci. 6:14-16. (In Chinese.)

Zhang Shan-yuan. 1996. Discussion on high-quality rice production in Jilin province: Research papers on a highly efficient agriculture with great and better yields. Beijing (China): Business Publishing House of China. p 428-430. (In Chinese.)

Zhu Xu-dong, Xiong Zheng-ming, Luo Yu-kuen. 1993. Effect of different sowing seasons on rice quality. Rice Sci. China. 7(3):172-174. (In Chinese.)

Notes

Authors' address: Fang Chen, Sam Portch, Ji-yun Li, PPI/PPIC China Program; Fang Chen, also Wuhan Botanical Garden/Wuhan Institute of Botany, Chinese Academy of Sciences. E-mail: FChen@ppi-ppic.org.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Interaction of nutrients with rice diseases and insect pests existing knowledge and research directions

N.P. Castilla and S. Savary

We discuss the linkages between integrated disease and insect pest management on the one hand and integrated nutrient management on the other. This analysis involves three levels of integration: (1) at the plant level, the direct path linking plant morphology and physiology and injury; (2) at the crop or population level, the paths linking nutrients and damage via plant physiology, crop growth and development, and crop microenvironment; and (3) at the systems level, the overall interaction between plant nutrients and injury profiles. A review of the literature shows that most existing knowledge pertains to the first level of integration only, in which the effects of the rate, timing of application, and form of nutrients on injuries are studied via the changes in plant anatomy and physiology. Information at the population level is available only in a few examples—such as studies that analyze the relationships between the timing of nitrogen application and leaf blast, nitrogen rate and sheath blight, and nitrogen rate and leaffolders. Little information is available concerning the third level of integration.

Although the existing knowledge base is essential, there is a need for a shift from a reductionist to a systems approach to develop strategies to manage both nutrients and rice pests. A systems approach, involving controlled experiments, on-farm studies, and simulation modeling, can help in understanding and predicting the outcome of nutrient management strategies on injuries and yield, incorporating nutrient management in integrated pest management methods, and identifying research priorities for optimized nutrient management.

Consideration of plant nutrition is an integral part of disease and insect pest management (Zadoks 1974, Zadoks and Schein 1979). In this review, we examine the linkages between integrated disease and insect pest management and integrated nutrient management. Ideally, optimized nutrient management should achieve, or at least facilitate, disease and insect pest management, thus yielding two results: an increased attainable yield caused by a better physiological crop performance and a stabilized actual yield caused by reduced damage from pathogens and insect pests. Our review will show that achieving both objectives can, in general, be contemplated for rice, but that the congruence of the two cannot always be guaranteed because of the specific requirements of pathogens or insect pests and the nature of pest interactions with the growing crop. In this review, we shall refer to pathogens and insect pests collectively as "pests."

Much of the current interest in optimizing the nutrition of a growing rice crop is production-oriented; thus, new approaches to improve nutrient management are being developed to fully exploit the yield potential of rice. Instead of blanket fertilizer recommendations, the International Rice Research Institute (IRRI) is now promoting site-specific nutrient management (SSNM) to increase yield, profit, plant nutrient uptake, and nitrogen-use efficiency (Dobermann et al 2002). Another essential reason for optimizing plant nutrition is to stabilize yields and maximize agricultural resources and farmers' benefits. Optimized plant nutrition, just like integrated disease and pest management, is then considered a key component of sustainable rice production (Greenland 1997).

In as much as crop management operations must be guided by the crop's requirements and the expected benefits of farming, pest management actions must be directed toward reducing risks that actually threaten a yield target or expected benefits. Although crop management may be based on the crop environment, pest management must be based on both the crop environment and the growing crop itself. A key step toward an integrated view of nutrient and pest management is therefore an understanding of the linkages that exist among the status of the crop, its susceptibility to pests, its nutrient requirements, and its vulnerability to injury. Any production situation—which includes several components of an agroecosystem's attributes, including farmers' management practices, inputs, and environmental factors (De Wit 1982, 1986, Rabbinge 1993, Savary et al 2000a)—corresponds to a given attainable yield (the yield of an uninjured crop) and is often closely related to a fairly precise pest injury profile, leading to actual yields. Even though much research is still necessary to establish this hypothesis, it can be assumed that a specific nutrient management strategy exists that can be associated with any production situation and that would both maximize attainable yield and minimize damage.

As Figure 1 shows, the relationship between plant nutrition and pests can be considered at two levels of integration: (1) the individual plant level with a direct path linking plant anatomy and physiology with pest injury and (2) the population level with paths linking nutrients and damage via plant physiology, crop growth and development, crop microenvironment, and damage. The first two levels can be defined for each individual nutrient-by-pest combination. The third level of integration, the systems level, considers plant nutrition as a whole and the injury profile, that is, the combination of pathogens and insects that may affect a rice crop (Savary et al 2000a). This level of integration can be defined in specified production situations (De Wit 1982), and it allows us to consider both the system's behavior and its management.

This review follows the structure of available knowledge, which has been mostly produced by considering the interaction between individual macronutrients and

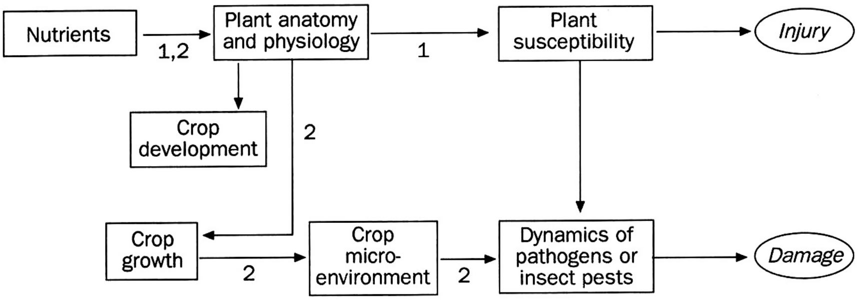


Fig. 1. Relationships among plant nutrients, injury, and damage. Uptake of nutrients by plants triggers a series of events leading to decreased or increased injury and damage. Two paths of relationships can be distinguished. At the individual plant level, a direct path (path 1) links the physiology of the plant and the level of injury. At the crop or population level, a much more complex path links plant nutrient uptake and damage (or crop loss) via plant physiology, crop development and growth, and crop microenvironment. While knowledge exists concerning the effects of some nutrients on susceptibility and injury (path 1), little is known about path 2, the population level (crop growth and pest dynamics). Knowledge concerning overall plant nutrition and injury profiles (combinations of pathogens and insects) is lacking.

specific rice pests. This classical reductionist approach is a necessary step toward the goal of integrated nutrient and pest management. This review will show that most existing knowledge on the interaction between nutrients and insect pests and diseases pertains to the plant level of integration.

Interaction between nutrients and rice pests

This review will focus on the most important nutrients of rice: nitrogen (N), phosphorus (P), and potassium (K). Some of the mechanisms by which these nutrients affect insect pests and diseases are outlined below. Related studies on rice pests are limited, but they will be used as examples when applicable. Each mechanism is classified based on the level of integration, where L1 and L2 refer to the first and second levels of integration.

Nitrogen

The interaction of N with rice pests has been studied more extensively because of its apparent effects on crop growth and yield. It is a common view that N fertilizers favor the development of rice pests. This is true for some rice pests only, and quite the contrary for others. A well-documented contrast is that of rice blast and brown spot, whose dynamics are favored and hampered, respectively, by an excessive supply of N to the crop (Zadoks 1974, Ou 1985).

Rate of nitrogen. The most common consequences of a high amount of N are

- Formation of loose tissues with large and thin-walled cells, large intercellular spaces, and widely open stomata (Grossmann 1970 as cited by Palti 1981).

These changes may facilitate the entry and development of foliar pathogens, which usually enter the host plant through the stomata (Agrios 1997). [L1]

- Reduction in the amounts of cellulose and lignin. N increases the susceptibility of the plant by reducing cellulose and lignin, which provide a mechanical barrier against pathogens and insect pests. For example, Matsuyama (1975) found that N application reduced hemicellulose and lignin in cell walls, thus reducing the plant's mechanical resistance to leaf blast. The reduction in lignin content in plants receiving high N may also explain why more stem borer larvae penetrate the stems and require less time for penetration (Koyama 1955). [L1]
- Decrease in the amount of phenols. The activity of some key enzymes that are involved in phenol metabolism (Matsuyama and Dimond 1973) and the amount of phenol (Kiraly 1964) are lower in plants supplied with high N. Phenols are among the defensive substances in plant cell walls that inhibit the progress of invading pathogens (Agrios 1997). [L1]
- Increase in amino acid concentration in and sugar content of the leaves. According to Sogawa (1982), increases in amino acids in N-fertilized plants may account for the increased ingestion rates of the brown planthopper. Increased amino acid concentration also influences the germination and growth of conidia of some fungal pathogens (Robinson and Hodges 1981). Soluble sugars are used principally as sources of energy or may form the sole source of food of pathogens and insect pests (Uexkull 1987). [L1]
- Synthesis of insect attractants. According to Sasamoto (1961), N fertilizer may favor the synthesis of olfactory and gustatory substances that attract the larvae of the yellow stem borer. [L1]
- Development of dense canopies and creation of crop canopy structure and microclimate that favor pests. The increase in bacterial leaf blight with increased nitrogen supply is a well-documented example (Reddy et al 1979). Similarly, N indirectly favors the spread of sheath blight by creating a dense canopy structure that increases the frequency of tissue contacts and canopy wetness (Savary et al 1995, Fig. 2). Detailed studies showed that these indirect effects cancel the small, negative, direct effect of N content on the susceptibility of the plant to sheath blight (Castilla et al 1996). Rice plants with a high amount of N have droopy leaves (Yoshida et al 1969, Pangga 1995). Leaf wetness duration was longer (Friedrich et al 1991) and more spores were deposited (Ono 1965, Mohanty et al 1983) on cultivars with droopy leaves than on those with erect leaves. Kawamura and Ono (1948) observed that dew on the leaves of plants receiving high N stimulates the germination and appressorium formation of the spores of the blast pathogen. Excessive N fertilizer can create a favorable microclimate for some insect pests and their natural enemies (Teetes 1981). The closed canopy created by high N provides environmental conditions suitable for planthoppers and leafhoppers (Reissig et al 1986). It may also reduce the searching efficiency of natural enemies. De Kraker et al (2000) explained that the increased survival of the rice leaffolder

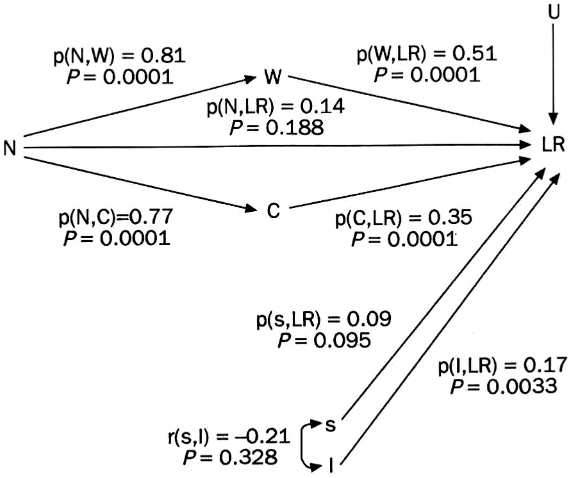


Fig. 2. A diagram showing the integration at the population level of the relationship between the rate of nitrogen and sheath blight (Savary et al 1995). This path diagram shows the direct and indirect effects of N content in the leaves (N), area under the leaf-to-leaf and leaf-to-sheath contact curve (C), area under the leaf wetness curve (W), and initial sheath blight severity on the sheaths (s) and leaves (I) of the source hill on the log-transformed average rate of expansion of sheath blight foci caused by *Rhizoctonia solani* (LR). U represents the unexplained source of variation. A cause-and-effect relationship between two variables is measured by a path coefficient [p(X,Y)]. A single-headed arrow points from cause to effect. A double-headed curved arrow indicates that variables are merely correlated; no causal relations are assumed. The significance level (P) of the path and regression coefficients (r) are indicated.

at high N could be due to the reduced searching efficiency of the natural enemies. [L2]

- Prolonged vegetative stage of the crop. One effect of an excess amount of N, which has often been overlooked, is a prolonged vegetative stage of the crop. At this stage, the proportion of young to mature tissues is higher than during later crop stages, thereby increasing the infectious period of pathogens and favoring insect pests that normally attack young tissues (Marschner 1995). [L2]
- Better plant compensation and tolerance of injury. A high N supply to rice plants may also result in a higher capacity to compensate for injury (Marschner 1995). Ishikura et al (1953) found that the addition of N helps rice plants to compensate for stem borer injury. An excessive amount of N fertilizer has been found to retard the expression of typical symptoms of tungro (Shastry et

al 1972, Chawdhury and Mukhopadhyay 1974, Gopalakrishna Pillai et al 1978) probably because the plants outgrow the disease (Chawdhury and Mukhopadhyay 1974). According to Shastry et al (1972), plants that recovered after high N application transmitted less virus, suggesting that virus multiplication may have been hampered and/or the enhanced growth of the host may have a diluting effect on the virus. N application is one method commonly recommended to manage the disease in its expression, and it has been found to mitigate the effect of the disease on damage, at least in the case of late infection of the plants. [L2]

Forms of nitrogen. Two forms of N fertilizer are commonly used: ammonium nitrogen (NH_4-N) or nitrate nitrogen (NO_3-N). Disease intensity frequently depends on the form rather than the amount of nitrogen available (Huber and Watson 1974). A study showed that an increase in NH_4-N increased blast severity (Kawai 1952 as cited by Ou 1985), although a more recent study (Osuna-Canizalez et al 1993) showed that plants grown in solution with NO_3-N were more susceptible than plants receiving NH_4-N. NH_4-N was found to increase the intensity of diseases caused by *Rhizoctonia solani* in other crops (Huber and Watson 1974). It also favored sheath rot (Alagarsamy and Bhaskaran 1986a). On the other hand, NO_3-N favored brown spot (Chattopadhyay and Dickson 1960, Dasgupta and Chattopadhyay 1977). The form of nitrogen affects pests mainly through the biochemical and physiological changes in the plant (Huber and Watson 1974). [L1]

The effect of NH_4-N on the infestation of some insect pests may be indirectly caused by its effect on crop growth. According to Michael and Morachan (1973), NH_4-N may have resulted in luxuriant crop growth that favors leaffolder infestation. [L2] However, the effects of the form of N are not known for most insect pests and diseases.

Timing of fertilizer application. Split application of N reduced the intensity of several diseases, such as bacterial leaf blight (Mizukarni and Wakimoto 1969, Sharma et al 1991), leaf blast (Amin and Venkatarao 1979, Alagarsamy and Baskaran 1986b, Kurschner et al 1992, Long et al 2000), and stem rot (Keim and Webster 1974). Basal application or the application of an excessive amount in the early stage of crop development may prolong the vegetative period and would therefore extend the infectious period of foliar pathogens that occur early in the cropping season. By creating dense canopies, basal application or application of N early in the cropping season may, in turn, create a microclimate favorable for disease development (Kurschner et al 1992). Under irrigated conditions, Amin and Venkatarao (1979) and Long et al (2000) found that leaf blast decreased when N fertilizer was applied in splits rather than when a full dose was applied early in the cropping season. However, the timing of N application did not affect the intensity of collar blast and neck blast (Long et al 2000). [L2]

Split application of N is often recommended as a strategy to manage several insect pests of rice (e.g., Reissig et al 1986, Pathak and Khan 1994). However, the mechanisms leading to the reduction in insect pests when N is applied in splits are not well understood. Split application of N may minimize insect pests by shortening the vegetative stage of the crop or by preventing dense crop growth. It may prevent an abrupt increase in insect pests and, consequently, allow natural enemies to effectively regulate the pest population. [L2]

Phosphorus

The interaction between P and rice pests is not clearly understood and is sometimes contradictory. In general, P may either enhance or suppress diseases (Datnoff 1994). P may affect insect pests and diseases through the following mechanisms:

- Reinforcement of the plant tissues. P helps provide a mechanical barrier to penetration by pathogens by reinforcing plant tissues (Huber 1981). Abdel-Hak et al (1973) attributed the decrease in blast and brown spot with the application of P to this mechanism. [L1]
- Increase in N content and decrease in silica content of the host. As described previously, an increase in N content appears to increase the susceptibility of the host to rice pests. Paik (I 975) found that an excessive amount of P fertilizer resulted in an increase in both total N and P and a decrease in silicate content of the leaves, thus making them more susceptible to leaf blast. [L1]
- Enhanced susceptibility to virus diseases. Since P is essential for virus multiplication, excesses may increase susceptibility to virus diseases (Huber 1980). [L1]
- Promotion of root development. Application of P is most beneficial in reducing insect pests and diseases where vigorous root development permits the plants to escape disease (Huber 1980). By improving root development, P increases tolerance of root pests, such as root weevil (Tirumala Rao 1952). [L2]
- Shortening of the vegetative period. By shortening the vegetative period, the application of P counteracts the effects of high levels of N (Huber 1980, 198 I). [L2]

Potassium

K seems to affect insect pests and diseases mainly through biochemical changes that alter the interaction between the host plant and pests (Huber and Amy 1985). More studies are done on the effect of K on plant pathogens than on insect pests (Perrenoud 1977). K may affect rice pests through the following:

- Promotion of the closure of the stomata. K minimizes the entry of pathogens through the stomata by promoting stomatal closure (Uexkull 1982). [L1]
- Increase in the concentration of inhibitory amino acids, phenols, phytoalexins. and auxins (Huber and Amy 1985). By promoting membrane permeability, K predisposes the host to pathogen infection by allowing increased concentrations of phenolic compounds and other toxic substances. According to Reddy and Sridhar (1975), the decrease in bacterial leaf blight with the addition of potassium may be a result of the accumulation of phenolic compounds. K also suppressed stem rot by increasing the level of phenol content in tissues (Velazhahan and Ramabadran 1992). Phenols are also toxic to insect pests

and may increase the resistance of plants to sap feeders, such as green leafhoppers and brown planthoppers (Vaithilingam and Baskaran 1985). [L1]

- Decrease in sugar levels in tissues. Vaithilingam and Baskaran (1985) showed that K depleted soluble sugars in rice by depositing them in nonavailable forms. By increasing K, the level of sugar in the tissues decreased and, consequently, induced resistance to bacterial leaf blight (Reddy and Sridhar 1975) and brown planthopper (Vaithilingam and Baskaran 1985, Uexkull 1987). [L1]
- Impairment of the synthesis of high-molecular-weight compounds, such as proteins, starch, and cellulose, and the accumulation of low-molecular-weight compounds (e.g., total nonprotein N compounds, free amino acids, and amides) (Perrenoud 1977). This reduces the infection of many plant pathogens whose source of food is amino acids and amines. The results of Akai (1962, as cited by De Datta and Mikkelsen 1985) suggested that high K content could reduce dibasic amino acids in rice plants and, in turn, reduce the lesion size of brown spot. [Ll]
- Reduction in the amount of N. By reducing the amount of N in the plant, K reduces the favorable effects of excess N on rice pests. According to Perrenoud (1977), the balance between N and K is as important as their absolute rate of application since both the relative N excess and relative K deficiency appear to increase susceptibility to pests. [Ll]
- Hardening of plant tissues. K hardens plant structures by increasing the lignin content of the culm (Noguchi and Sugawara 1966), the thickness of the sclerenchymatous layer (Vaithilingam and Balasubramanian 1976), and the amount of silica (Noguchi and Sugawara 1966, Vaithilingam 1975, Subramanian and Balasubramanian 1976, Vaithilingan and Baskaran 1985). These changes improve the mechanical resistance of the rice plant to diseases and insect pests. [L1]
- Better ability to recover from injuries. K can increase the ability of the plant to recover from injuries caused by pests (Perrenoud 1977). Since K promotes the production of new tissues, it indirectly affects the level of injury by facilitating the healing of infected tissues (Uexkull 1982, Huber and Amy 1985). [L1]

The effects of N, P, K, and silicon on insect pests are found in Table 1. Datnoff (1994) has summarized the effects of these nutrients on diseases. Although silicon is not considered a macronutrient, recent studies suggest that it can play an important role in integrated insect pest and disease management. Additional information on interactions between silicon and rice pests is provided by Savant et al (1997) and Alvarez and Datnoff (2001).

Knowledge gaps and research directions

Our review shows that much research has focused on describing or quantifying the effects of the rate and form of nutrients on the injury level of a specific pest via

Table 1. Influence of nitrogen, phosphorus, potassium, and silicon on insect pests of rice. [a]

Common name	Scientific name	Effects				References
		N	P	K	Si	
Armyworm	*Mythimna separata*	↑				Koyama (1966)
Brown planthopper	*Nilaparvata lugens*	↑				Uthamasamy et al (1983), Heinrichs and Medrano (1985)
				↓		Vaithilingam (1975), Subramanian and Balasubramanian (1976), Ittyavirah et al (1979), Vaithilingam and Baskaran (1985)
					↓	Sujatha et al (1987)
Gall midge	*Orseolia oryzae*	↑				Chelliah and Subramanian (1972), Narayanan et al (1973)
		↓	↓	-		Nanda and Satapathy (1979)
				↓		Israel and Prakasa Rao (1967)
Gall midge	*Orseolia oryzivora*	↑				Ukwungwu and Badeggi (1985), Ukwungwu (1987)
Green leafhopper	*Nephotettix virescens*	↑				Prasad and Misra (1983)
				↓		Subramanian and Balasubramanian (1976), Samiayyan and Janarathanan (1988)
Leaffolder	*Cnaphalocrocis medinalis*	↑				Regupathy and Subramanian (1972), Chandragiri et al (1974), Chandramohan and Jayaraj (1977), Subbaih and Morachan (1974), Saroja et al (1981, 1987), Balasubramanian et al (1983), Jaswant Singh and Shahi (1984)

continued on next page

Table 1. continued

Common name	Scientific name	Effects				References
		N	P	K	Si	
					↓	Michael and Morachan 1973, Vaithilingam (1975), Narayanasamy et al (1976), Subramanian and Balasubramanian (1976)
Root weevil	*Echinocnemus oryzae*	↑				Bowling (1963)
			↓			Tirumala Rao (1952)
Striped stem borer	*Chilo suppressalis*	↑				Ishii and Hirano (1958, 1959)
				–		Hirano and Ishii (1961)
Thrips	*Stenchaetothrips biformis*			↓		Subramanian and Balasubramanian (1976)
			–			Israel and Veda Moorthy (1963)
					↓	Jones and Handreck (1967)
White stem borer	*Maliarpha separatella*	↑				Ukwungwu and Badeggi (1985)
Whitebacked planthopper	*Sogatella furcifera*	↑				Yein and Das (1988), Salim and Saxena (1992)
					↓	Salim and Saxena (1992)
Whorl maggot	*Hydrellia philippina*			↓		Vaithilingam (1975), Subramanian and Balasubramanian (1976), Ittyavirah et al (1979), Vaithilingam and Baskaran (1985)

continued on next page

Table 1. continued

Common name	Scientific name	Effects				References
		N	P	K	Si	
				↑		Saroja and Raju (1981)
Yellow stem borer	*Scirpophaga incertulas*	↑				Koyama (1955), Ghosh (1962), Israel and Veda Moorthy (1963), Varadharajan and Nagaraja Rao (1965), Saha and Saharia (1970), Saroja et al (1987), Thakur and Mishra (1989)
			-			Israel and Veda Moorthy (1963)
				↓		Narayanasamy et al (1976), John and Thomas (1980)
					↓	Savant et al (1997)

[a] ↑ = = increase in growth, population, or injury, ↓= = decrease in growth, population, or injury, - = no effect on growth, population, or injury.

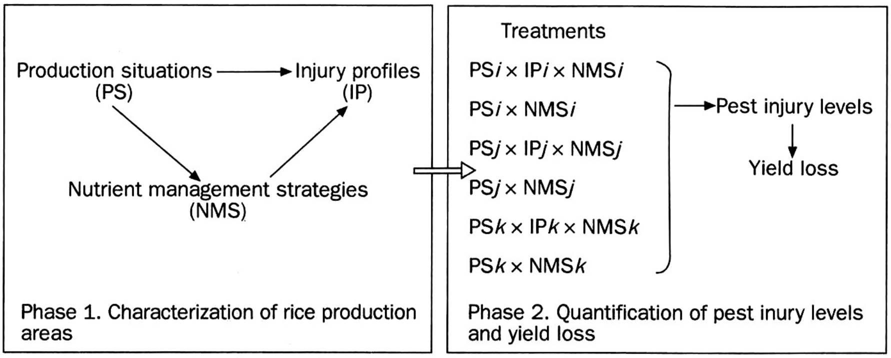


Fig. 3. Methodology for analyzing the relationship among plant nutrition, profiles of pest injuries, and yield loss. Phase 1 involves surveys of farmers' fields at selected sites to characterize production situations (PS), injury profiles (IP), and nutrient management strategies (NMS) and analyze their relationships. Phase 2 involves the manipulation of characterized PS, IP, and NMS in field experiments to quantify their combined effects on pest injury levels and yield loss.

changes in plant anatomy and physiology. At the individual plant level of integration, it appears that nitrogen, especially when applied excessively at the start of the cropping season, would increase most injuries, whereas potassium would have an opposite effect. However, these effects cannot be directly extrapolated to higher levels of integration because of the various interacting factors that could affect the interaction between nutrients and pests. The effect of the rate of N has been documented at both the individual and population levels of integration for leaf blast (Kurschner et al 1992), sheath blight (Savary et al 1995, Castilla et al 1996) and leaffolder (De Kraker et al 2000). In general, little is known about the interaction between nutrients and rice pests at this level of integration. An integrated approach to the analysis of the relationship among nutrients, injury, and damage needs to be considered. Aside from the study conducted by Sta. Cruz et al (2001), which involved the characterization of pest injury profiles at varying input levels, no study that specifically examines the third level of integration has been conducted. Methodologically, the techniques required to address level 1—monocyclic experiments—and level 2—polycylic experiments—are well established (Zadoks 1972, Zadoks and Schein 1979). The methodology required to address level 3 involves three phases: (1) characterization of rice production situations, current nutrient management strategies, and the combination of rice pest injuries (injury profiles) and the analysis of their relationships, (2) manipulation in holistic field experiments of characterized production situations, nutrient management strategies, and injury profiles and quantification of their effects on injury levels and yield loss (Fig. 3), and (3) analysis of the behavior of the plant nutrient and pest injury profile system. Nutrient management strategies should include the form, rate, and timing of application of different macro- and micronutrients. In field experiments, the effects of improved nutrient management strategies, such as the SSNM, should also be quantified. While part of the methodology can be derived from past experiences (Sta. Cruz et al 2001, Savary et al 2000a,b), several aspects remain largely to be developed, and thus represent a scientific challenge of their own.

Analysis of the plant nutrient × pest system

To understand the behavior of the plant nutrient × pest system, and to predict the future outcome, foreseeable scenarios, and yet untested hypotheses, a systems approach involving simulation modeling is desirable. Validated rice crop growth models are now available (e.g., Willocquet et al 2000, Bouman et al 2001), to which models of pest population dynamics can be coupled. A first step of modeling would be to modify the selected crop growth model so that it can account for different nutrient management strategies. A second step would be to develop a generic model of the injury dynamics of rice pests. Although insect pests and pathogens (viruses, bacteria, and fungi) of rice are extremely diverse, an attempt might be made to use simple population ecology concepts, and take into account a reasonable fraction of their diversities. A third step would be to couple the crop model with the injury model(s). The above steps should be based on available data from the literature on biological cycles, from stimulus-response experiments, and from field experiments in which the effects of nutrient management strategies in different production situations on pest injuries and yield loss are quantified. Before simulating pest effects by means of crop models, coupling points, that is, processes and pathways where these effects specifically take place, have to be identified. A last stage of model development would consist of comparing the modeled dynamics with empirical observations, especially those from the above conventional field experiments (validation). This modeling approach could then be used to predict the outcome of improved nutrient management strategies, to incorporate nutrient management in integrated pest management methods, and to identify research priorities for optimized nutrient management.

References

Abdel-Hak TM, Siny AR, Kamel SM, Ashour WA. 1973. Effect of different fertilizers on the incidence of blast and brown spot diseases of rice in A.R.E. Agric. Res. Rev. 51:45-62.

Agrios GN. 1997. Plant pathology. San Diego, Calif. (USA): Academic Press. 635 p.

Alagarsamy G, Bhaskaran R. 1986a. Effect of form and level of N fertilizers on sheath rot (ShR) incidence and yield. Int. Rice Res. Newsl. 11(6):18.

Alagarsamy G, Bhaskaran R. 1986b. Effect of time of application of nitrogen and potassium in combination with nutrients and fungicide spray on sheath rot incidence and grain yield of rice. Philipp. Agric. 69(1):99-105.

Alvarez J, Datnoff LE. 2001. The economic potential for integrated management and sustainable rice production. Crop Prot. 20:43-48.

Amin KS, Venkatarao G. 1979. Rice blast control by nitrogen management. Phytopathol. Z. 96:140-145.

Balasubramanian P, Palaniappan SP, Gopalan M. 1983. Effect of carbofuran and nitrogen on leaffolder incidence. Int. Rice Res. News]. 8(5):13-14.

Bouman BAM, Kropff MJ, Tuong TP, Wopereis MCS, ten Berge HFM, van Lax HH. 2001, ORYZA2000: modeling lowland rice. Los Baños (Philippines): International Rice Research Institute, and Wageningen (The Netherlands): Wageningen University and Research Centre. 234 p.

Bowling CC. 1963. Effect of nitrogen levels on rice water weevil populations. J. Econ. Entomol. 56:826-827.

Castilla NP, Leaño RM, Elazegui FA, Teng PS, Savary S. 1996. Effects of plant contact, inoculation pattern, leaf wetness regime, and nitrogen supply on inoculum efficiency in rice sheath blight. J. Phytopathol. 144:187-192.

Chandragiri KK, Velusamy R, Janaki IP, Ramakrishnan MS. 1974. Effect of different levels of nitrogen on rice leaf roller (*Cnaphalocrocis medinalis* Guenee) incidence. Madras Agric. J. 61:717.

Chandramohan N, Jayaraj S. 1977. Effect of different levels of nitrogen and age of the crop on the incidence of rice leaf roller. Madras Agric. J. 64:684-685.

Chattopadhyay SB, Dickson JG. 1960. Relation of nitrogen to disease development in rice seedlings infected with *Helminthosporium oryzae.* Phytopathology 50:434-438.

Chawdhury AK, Mukhopadhyay S. 1974. Effect of different dosages of nitrogen fertilization upon some morphological characters of RTV infected rice varieties. Indian Phytopathol. 27:571-574.

Chelliah S, Subramanian A. 1972. Influence of nitrogen fertilization on the infestation by gall midge, *Pachydiplosis oryzae* (Wood-Mason) Mani, in certain rice varieties. Indian J. Entomol. 34(3):255-256.

Dasgupta MK, Chattopadhyay SB. 1977. Effect of different doses of N and P on the susceptibility of rice to brown spot caused by *Helminthosporium oryzae.* Z. Pflanzenkr. Pflanzenschutz 84:276-285.

Datnoff LE. 1994. Influence of mineral nutrition of rice on disease development. In: Teng PS, Heong KL, Moody K, editors. Rice pest science and management: selected papers from the International Rice Research Conference, Manila (Philippines): International Rice Research Institute. p 89-100.

De Datta SK, Mikkelsen DS. 1985. Potassium nutrition and rice. In: Munson RD, editor. Potassium in agriculture. Madison, Wis. (USA): American Society of Agronomy, Crop Science Society of America, Inc., and Soil Science Society of America, Inc. p 665-699.

De Kraker J, Rabbinge R, Van Huis A, Van Lenteren JC, Heong KL. 2000. Impact of nitrogenous-fertilization on the population dynamics and natural control of rice leaffolder (Lep.: Pyralidae). Int. J. Pest Manage. 46:225-235.

De Wit CT. 1982. Simulation of living systems. In: Penning de Vries FWT. van Laar HH, editors. Simulation of plant growth and crop production. Wageningen (Netherlands): PUDOC. 308 p.

De Wit CT. 1986. Introduction. In: van Keulen H, Wolf J, editors. Modelling of agricultural production: weather, soils and crops. Wageningen (Netherlands): PUDOC. 479 p,

Dobermann A, Witt C, Dawe D, Abdulrachman S, Gines HC, Nagarajan R, Satawathananont S, Son TT, Tan PS, Wang GH, Chien NV, Thoa VTK, Phung CV, Stalin P, Muthukrishnan P, Ravi V, Babu M, Chatuporn S, Sookthongsa J, Sun Q, Fu R, Simbahan GC, Adviento MAA. 2002. Site-specific nutrient management for intensive rice cropping systems in Asia. Field Crops Res. 74:37-66.

Friedrich S, Kuerschner E, Schloesser I, Bonman JM. 1991. A simple method for measuring dew in upland rice canopies. J. Plant Prot. Trop. 8:69-79.

Ghosh BN. 1962. A note on the incidence of stem-borer (*Schoenobius incertulas* Wlk.) on boro paddy under nitrogen fertilizers. Cum. Sci. 38:472-473.

Gopalakrishna Pillai K, John VT, Kondaiah A, Reddy NV. 1978. Effect of nitrogen fertilization on tungro disease of rice. Indian J. Agric. Sci. 48:413-418.

Greenland DJ. 1997. The sustainability of rice fanning. Wallingford (UK): CAB International, and Manila (Philippines): International Rice Research Institute. 273 p.

Heinrichs EA, Medrano FG. 1985. Influence of nitrogenous fertilizer on the population development of brown planthopper. Int. Rice Res. Newsl. 10(6):20-21.

Hirano C, Ishii S. 1961. Effect of fertilizers on the growth of larvae of the rice stem borer, *Chilo suppressalis* Walker. IV. Growth responses of larvae to the rice plant applied with potassium fertilizer at different levels. Jpn. J. Appl. Entomol. Zool. 5:180-184.

Huber DM. 1980. The role of mineral nutrition in defense. In: Horsfall JG, Cowling EB, editors. Plant disease: an advanced treatise. Vol. V. New York (USA): Academic Press, Inc. p 381-406.

Huber DM. 1981. The use of fertilizers and organic amendments in the control of plant disease. In: Pimentel D, editor. CRC handbook of pest management in agriculture. Volume I. Boca Raton, Fla. (USA): CRC Press, Inc. p 357-394.

Huber DM, Arny DC. 1985. Interactions of potassium with plant disease. In: Munson RD, editor. Potassium in agriculture. Madison, Wis. (USA). American Society of Agronomy, Crop Science Society of America, Inc., and Soil Science Society of America, Inc. p 467-488.

Huber DM. Watson RD. 1974. Nitrogen form and plant disease. Annu. Rev. Phytopathol. 12:139-165.

Israel P, Prakasa Rao PS. 1967. Influence of potash on gall fly incidence in rice. Oryza 495-86.

Israel P, Veda Moorthy G. 1963. Influence of fertilisers on the incidence of the yellow stem borer of rice, *Tryporyza incertulas* Wlk. Part I. Oryza 1:112-118.

Ishii S, Hirano C. 1958. Effect of fertilizers on the growth of larvae of the rice stem borer, *Chilo suppressalis* Walker. I. Growth response of larvae to the rice plant cultured in different nitrogen level soils. Jpn. J. Appl. Entomol. Zool. 2:198-202.

Ishii S, Hirano C. 1959. Effect of fertilizers on the growth of larvae of the rice stem borer, *Chilo suppressalis* Walker. II. Growth of the larvae on the rice plants cultured in nutrient solutions of different nitrogen level. Jpn. J. Appl. Entomol. Zool. 3:16-22.

Ishikura H, Tamura I, Watanabe Y. 1953. Analytical studies on the infestation of rice crop by borer insect. I. The relation of the amount of fertiliser and the degree of infestation by borers. Bull. Shikoku Natl. Agric. Exp. Stn. 1:217-227.

Ittyavirah PJ, Nair KPV, Thomas MJ. 1979. Effect of potash application on the incidence of brown plant hopper. Agric. Res. J. Kerala 17: 118-1 19.

Jaswant Singh, Shahi HN. 1984. Effect of nitrogen on leaffolder, *Cnaphalocrocis medinalis* (Guen.), incidence in rice. J. Res. Punjab Agric. Univ. 21(4):629-630.

John PS, Thomas MJ. 1980. Effect of potash nutrition on infestation by the yellow stem borer *Tryporyza incertulas.* Agric. Res. J. Kerala 18:107-108.

Jones LHP, Handreck KA. 1967. Silica in soils, plants and animals. Adv. Agron. 19:107-149.

Kawamura E, Ono K. 1948. Studies on the relation between the preinfection behaviour of rice blast fungus, *Pyricularia oryzae,* and water droplets on rice plant leaves. Bull. Natl. Agric. Exp. Stn. 4:l-12.

Keim R, Webster RK. 1974. Nitrogen fertilization and severity of stem rot of rice. Phytopathology 64:178-183.

Kiraly Z. 1964. Effect of nitrogen fertilization on phenol metabolism and stem rust susceptibility of wheat. Phytopathol. Z. 51:252-261.

Koyama J. 1955. Studies on the paddy borer (*Schoenobius incertulas*). Wakayama-Ken. Agric. Res. Stn. 53:169-174.

Koyama J. 1966. The relation between outbreak of armyworm (*Leucania separata* Walker) and the richly nitrogenous manured cultivation of rice plant. Jpn. J. Appl. Entomol. Zool. 10:123-128.

Kurschner E, Bonman JM, Garrity DP, Tamisin MM, Pabale D, Estrada BA. 1992. Effects of nitrogen timing and split application on blast disease in upland rice. Plant Dis. 76:384-389.

Long DH, Lee FN, TeBeest DO. 2000. Effect of nitrogen fertilization on disease progress of rice blast on susceptible and resistant cultivars. Plant Dis. 84:403-409.

Marschner H. 1995. Mineral nutrition of higher plants. London (UK): Academic Press Limited. 889 p.

Matsuyama N. 1975. The effect of ample nitrogen fertilizer on cell wall materials and its significance to rice blast disease. Ann. Phytopathol. Soc. Jpn. 456-61.

Matsuyama N, Dimond AE. 1973. Effect of nitrogenous fertilizer on biochemical processes that could affect lesion size of rice blast. Phytopathology 63:1202-1203.

Michael Raj S, Morachan YB. 1973. Incidence of stem-borer and leaf-roller on ‘IR8’ rice as influenced by fertilization and diazinon application. Indian J. Agric. Sci. 43:290-294.

Mizukami T, Wakimoto S. 1969. Epidemiology and control of bacterial leaf blight. Annu. Rev. Phytopathol. 751-72.

Mohanty CR, Gangopadhyay S, Sahoo K. 1983. Correlation and path-coefficient analysis study between some leaf characters and blast incidence at seedling stage of rice. Indian Phytopathol. 36:508-515.

Nanda UK, Satapathy JM. 1979. Effect of varying levels of N, P and K on the incidence of gall midge and stem borers. Andhra Agric. J. 26(1/2):52-55.

Narayanan K, Chandrasekaran J, Meerzainudeen M, Jayaraj S. 1973. Effect of graded levels of nitrogen on the incidence of gall midge. Madras Agric. J. 60:572.

Narayanasamy P, Baskaran P, Balasubramaniam M, Adaickalam V. 1976. Different levels of N, P and K on the incidence of rice insect pests. Rice Entomol. Newsl. (Final) 4:37.

Noguchi J, Sugawara T. 1966. Potassium and japonica rice. Bern (Switzerland): International Potash Institute. 102 p.

Ono K. 1965. Principles, methods, and organization of the blast disease forecasting. Proceedings of a symposium at the International Rice Research Institute, July 1963. Baltimore, Md. (USA): Johns Hopkins Press. p 173-194.

Osuna-Canizalez FJ, De Datta SK, Bonman JM. 1993. Nitrogen form and silicon nutrition effects on resistance to blast disease of rice. Plant Soil 135:223-231.

Ou SH. 1985. Rice diseases. Surrey, England (UK): Commonwealth Mycological Institute. 380 p.

Paik SB. 1975. The effects of silicate, nitrogen, phosphorus and potassium fertilizers on the chemical components of rice plants and on the incidence of blast disease of rice caused by *Pyricularia oryzae* Cavara. Korean J. Plant Prot. 14:97-109.

Palti J. 1981. Cultural practices and infectious crop diseases. Berlin (Germany): Springer-Verlag. 243 p.

Pangga IB. 1995. Blast development on the new rice plant type in relation to canopy structure, microclimate, and crop management practices. Master's thesis. University of the Philippines at Los Baños, Laguna, Philippines. 163 p.

Pathak MD, Khan ZR. 1994. Insect pests of rice. Manila (Philippines): International Rice Research Institute, and Nairobi (Kenya): International Centre of Insect Physiology and Ecology. 89 p.

Perrenoud S. 1977. Potassium and plant health. Bern-Worblaufen (Switzerland): International Potash Institute. 204 p.

Prasad J, Misra DS. 1983. Influence of different levels of N, P and K on the population of leafhoppers and planthoppers. In: Chelliah S, Balasubramanian M, editors. Pest management in rice. Coimbatore (India): Tamil Nadu Agricultural University. p 245-254.

Rabbinge R. 1993. The ecological background of food production. In: Chadwick DJ, Marsh J, editors. Crop protection and sustainable agriculture. Chichester, England (UK): John Wiley & Sons. p 2-29.

Reddy PR, Sridhar R. 1975. Influence of potassium nutrition and bacterial blight on phenol, soluble carbohydrates and amino acid contents in rice leaves. Acta Phytopathol. Acad. Sci. Hung. 10:55-62.

Reddy APK, Katyal JC, Rouse DI, MacKenzie DR. 1979. Relationship between nitrogen fertilization, bacterial leaf blight severity, and yield of rice. Phytopathology 69:970-973.

Regupathy A, Subramanian A. 1972. Effect of different doses of fertilizers on the mineral metabolism of IR8 rice in relation to its susceptibility to gall fly *Pachidiplosis oryzae* (Wood-Mason) and leaf roller, *Cnaphalocrocis medinalis* Guenee. Oryza 9:81-85.

Reissig WH, Heinrichs EA, Litsinger JA, Moody K, Fiedler L, Mew TW, Barrion AT. 1986. Illustrated guide to integrated pest management in rice in tropical Asia. Manila (Philippines): International Rice Research Institute. 411 p.

Robinson PW, Hodges CF. 1981. Nitrogen-induced changes in the sugars and amino acids of sequentially senescing leaves of *Poa pratensis* and pathogenesis by *Dreschlera sorokiniana.* Phytopathol. Z. 101:348-361.

Salim M, Saxena RC. 1992. Iron, silica, and aluminum stresses and varietal resistance in rice: effects on whitebacked planthopper. Crop Sci. 32:212-219.

Samiayyan K, Janarathanan R. 1988. An appraisal of potash fertilization in controlling the incidence of leaf and plant hoppers in some rice varieties. J. Potassium Res. 4(2):61-66.

Saroja R, Raju N. 1981. Effect of potash on the incidence of rice whorl maggot. Int. Rice Res. Newsl. 6(3):15.

Saroja R, Nazeer Peeran S, Raju N. 1981. Effects of methods of nitrogen application on the incidence of rice leaffolder. Int. Rice Res. Newsl. 6(4):15-16.

Saroja R, Jagannathan R, Raju N. 1987. Effect of N nutrition and rice variety on leaffolder (LF), yellow stem borer (YSB), and grain yield. Int. Rice Res. Newsl. 12(5):11-12.

Sasamoto K. 196 I. Resistance of the rice plant applied with silicate and nitrogenous fertilizers to the rice stem borer *Chilo suppressalis* Walker, Proc. Fac. Lib. Arts Educ. Yamanashi Univ. 3:l-73.

Savant NK, Snyder GH, Datnoff LE. 1997. Silicon management and sustainable rice production. Adv. Agron. 58:151-199.

Savary S, Castilla NP, Elazegui FA, McLaren CG, Ynalvez MA, Teng PS. 1995. Direct and indirect effects of nitrogen supply and disease source structure on rice sheath blight spread. Phytopathology 85:959-965.

Savary S, Willocquet L, Elazegui FA, Teng PS, Du PV, Zhu DF, Tang QY, Huang SW, Lin XQ, Singh HM, Srivastava RK. 2000a. Rice pest constraints in tropical Asia: characterization of injury profiles in relation to production situations. Plant Dis. 84:341-356.

Savary S, Willocquet L, Elazegui FA, Castilla NP, Teng PS. 2000b. Rice pest constraints in tropical Asia: quantification of yield losses due to rice pests in a range of production situations. Plant Dis. 84:357-369.

Sharma NR, Hossain MA, Haque MA, Mondal AH, Rahman MM, Nahar NS, Miah SA. 1991. Effect of rate and split application of nitrogen on bacterial leaf blight incidence in rice. Bangladesh J. Plant Pathol. 7:17-20.

Shastry SVS, John VT, Seshu DV. 1972. Breeding for resistance to tungro virus in India. In: Rice breeding. Los Baños (Philippines): International Rice Research Institute. p 239-252.

Sogawa K. 1982. Studies on the feeding habits of the brown planthopper. I. Effects of nitrogen-deficiency of host plant on insect feeding. Jpn. J. Appl. Entomol. Zool. 14:101-106.

Sta. Cruz PC, Simbahan GC, Hill JE, Dobermann A, Zeigler RS, Du PV, dela Peña FA, Samiayyan K, Suparyono, Tuat NV, Zheng Z. 2001. Pest profiles at varying nutrient input levels. In: Peng S, Hardy B, editors. Rice research for food security and poverty alleviation. Proceedings of the International Rice Research Conference, 31 March-3 April 2000. Makati City (Philippines): International Rice Research Institute. p 431-440.

Subbaih KK, Morachan YB. 1974. Effect of nitrogen nutrition and rice varieties on the incidence of leaf roller (*Cnaphalocrocis medinalis* Guen.). Madras Agric. J. 61:716.

Subramanian R, Balasubramanian M. 1976. Effect of potash nutrition on the incidence of certain insect pests of rice. Madras Agric. J. 63:561-564.

Sujatha G, Reddy GPV, Murthy MMK. 1987. Effect of certain biochemical factors on expression of resistance of rice varieties to brown planthopper (*Nilaparvata lugens* Stål). J. Res. APAU 15:124-128.

Teetes GL. 1981. The environmental control of insects using planting times and plant spacing. In: Pimentel D, editor. CRC handbook of pest management in agriculture. Volume I. Boca Raton, Fla. (USA): CRC Press, Inc. p 209-221.

Thakur RB, Mishra SS. 1989. Effect of different levels of nitrogen and some granular insecticides on stem borer and leaffolder incidence in rice. J. Entomol. Res. 13:121-124.

Tirumala Rao V. 1952. The paddy root weevil (*Echinocnemus oryzae* Mshll.)—a pest in the deltaic tracts of the northern Circars. Indian J. Entomol. 14:31-37.

Uexkull HR von. 1982. Potassium nutrition and plant diseases. In: Heong KL, Lee BS, Lim TM, Teoh CH, Ibrahim Y, editors. Proceedings of the International Conference on Plant Protection in the Tropics, 1-4 March 1982. Kuala Lumpur (Malaysia): Malaysian Plant Protection Society. p 141-151.

Uexkull HR von. 1987. Potassium helps reduce damage of brown planthopper in rice. Better Crops Int. 3(1):8-9.

Ukwungwu MN. 1987. Effects of spacing and nitrogen fertilizer on infestation by the rice gall midge *Orseolia oryzivora* Harris and Gagné (Diptera: Cecidomyiidae) in Nigeria. Trop. Pest Manage. 33:164-165.

Ukwungwu MN, Badeggi PMB. 1985. Effect of nitrogen and carbofuran on gall midge (GM) and white stem borer (SB) infestation in Nigeria. Int. Rice Res. Newsl. 10(6):19-20.

Uthamasamy S, Velu V, Gopalan M, Ramanathan KM. 1983. Incidence of brown planthopper *Nilaparvata lugens* Stål on IR50 at graded levels of fertilization at Aduthurai. Int. Rice Res. Newsl. 8(5):13.

Vaithilingam C. 1975. Effect of potash nutrition on the incidence and severity of different pests of rice. Rice Entomol. Newsl. 3:23-34.

Vaithilingam C, Balasubramanian M. 1976. Effect of potash on sclerenchyma thickness and silica content in rice. Indian Potash J. 1:17-23.

Vaithilingam C, Baskaran P. 1985. Induced resistance to insect pests in rice with enhanced potassium application. In: Role of potassium in crop resistance to insect pests. Gurgaon, Haryana (India): Potash Research Institute of India. p 43-51.

Varadharajan G, Nagaraja Rao PR. 1965. The influence of nitrogen and phosphoric acid on the incidence of rice stem borer, *Tryporyza incertulas* Wlk. Rice News Teller 13(4):105-106.

Velazhahan R, Ramabadran R. 1992. Influence of potassium fertilization on sheath rot incidence and phenolic content of rice. Madras Agric. J. 79:294-298.

Willocquet L, Savary S, Fernandez L, Elazegui F, Teng PS. 2000. Development and evaluation of a multiple-pest, production situation specific model to simulate yield losses of rice in tropical Asia. Ecol. Model. 131:133-159.

Yein BR, Das GR. 1988. Effect of spacing and nitrogen levels on the incidence of insect pests of rice. Pesticides 22:37-40.

Yoshida S, Navasero SA, Ramirez EA. 1969. Effects of silica and nitrogen supply on some leaf characters of the rice plant. Plant Soil 31:48-56.

Zadoks JC. 1972. Methodology of epidemiological research. Annu. Rev. Phytopathol. 10:253-276.

Zadoks JC. 1974. The role of epidemiology in modern phytopathology. Phytopathology 64:918-923.

Zadoks JC, Schein RD. 1979. Epidemiology and plant disease management. New York (USA): Oxford University Press, Inc. 427 p.

Notes

Authors' addresses: N.P. Castilla, Entomology and Plant Pathology Division, International Rice Research Institute, Philippines; S. Savary, ENSAR/BiO3P, 65 rue de Saint-Brieuc 35042 Rennes cedex, France; email: n.castilla@cgiar.org.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Strategies for managing water scarcity in rice production areas in China

Li Yuanhua, Ni Wenjin, and Chen Chongde

Demand for freshwater for industrialization and domestic urban needs is growing rapidly throughout Asia. Less water will be available for agriculture and for rice, the crop that consumes the largest amount of freshwater. With one of the most intensive rice irrigation systems and the most rice production in the world, the need for more rice with less water is more urgent in China than in many other countries. Increasing attention has been paid to improving irrigation water management of paddy fields, because of both their importance for food production and their huge water use. First, China has made significant efforts in developing and applying on-farm water-saving irrigation (WSI) practices in rice-based systems aiming at increasing field-level water and land productivity. The widespread adoption of WSI techniques provides an opportunity for efficient water use on a large scale because it impels every farmer to use water carefully, capture the return flow, harvest rainfall water, and control percolation losses. Second, China's high-level policymakers have implemented water-saving policies and promoted research on and dissemination of new technologies. Sound water-pricing mechanisms have brought about reduced demand, an increased supply, facilitation of reallocation among water-use sectors, and increased managerial efficiency. Third, the modernization and rehabilitation of irrigation schemes result in improvements in water-use efficiency and irrigation reliability.

China also finds that it is difficult to produce more rice with less water, and many scientific issues remain to be studied. Reducing institutional friction among various administrative levels is another critical problem. This paper, however, focuses on the successful experiences and presents the research and practices of the WSI techniques for paddy in China, and introduces policies and incentives for water savings in rice-based systems,

The Chinese farm is the largest rice area in the world. Rice planting area is about 31 million hectares and makes up 30% of the total grain crop planting area throughout the country, from tropical Hainan Island in the south to the frigid-temperature zone

Table 1. Forecasting of water supply capacity and water available for agriculture.

Item	2000	2010		2030	
		Supply	Demand	Supply	Demand
Total water supply capacity (billion m^3)	559.1	605.7	613.4	699.0	711.9
Water available for agriculture (billion m^3)	386.9	397.9	418.6	420.0	463.4
Water available for irrigation (billion m^3)	360.0	366.0	381.9	378.0	417.1
Ratio of agricultural water use (%)	69.2	65.7	68.2	60.1	65.0
Ratio of irrigation water use (%)	64.3	60.4	62.3	54.1	58.6

in Heilongjiang Province in the north, and from Taiwan Island in the east to the Xinjiang Uygur Autonomous Region in the west. Rice production per year is around 195 million tons and accounts for 38% of the total grain in China. About 60% of the Chinese eat rice as a staple food (Denning and Mew 1998). Not only is rice an important element in China's history and culture, but rice production is also the most important factor influencing China's food security.

China is also severely water short (see Table 1); per capita freshwater availability in China is among the lowest in Asia. There are only 2,260 m^3 of freshwater per year per capita on average, which is less than a quarter of the average value in the world. Furthermore, the country-level data hide massive regional differences in water scarcity behind the average figures, and the basic situation in China is that the distribution of precipitation in seasons and years in most parts of the country is quite uneven and water resources do not match with the distribution of farm land. Though it is wet in South China, where traditional paddy-field agriculture is dominant, about 90% of the freshwater is used for rice production and industrial and domestic water requirements increase sharply in this region. Both population and income growth have been influencing the demand-supply balances of staple grain and freshwater and will remain a major force in the future. Along with development of the national economy and improvement of people's living standards, irrigation is not likely to have more water and the water shortage will be the "bottleneck" for future agricultural development in China (Brown 1995, Brown and Halweil 1998, DRWM 2001, Qian and Zhang 2001, Seckler et al 1999, Serageldin 1999).

China has been taking measures to increase the availability of water resources, but the ratio of irrigation water consumption to total water use has been declining because of industrialization and urbanization. Since a huge amount of water is used for land preparation, adequately meeting the water needs of rice and an efficient supply of nutrients to the crop (Liang 1983), it is assumed that a great deal of water could be saved if farmers were encouraged to grow crops other than rice. Hence, rice is most likely to become the “victim” of water shortage.

On the other hand, most authorities would agree that rice must play a greater proportionate role in meeting future food needs than many other crops (Barker et al 2001, Denning and Mew 1998). To guarantee food security, sustainable economic development, and sound ecosystems and environments, there is a more urgent need for China to produce more rice with less water than for many other countries in the world. In recent years, China has pioneered some water-saving policies and water-saving irrigation (WSI) techniques for rice production, aiming at increasing water and land productivity. This paper presents the strategies for managing water scarcity in rice production areas in China. Research on and implementation of efficient water-use techniques for paddy are presented. Physical and institutional measures leading to increasing water and land productivity are discussed.

Research on and implementation of on-farm WSI techniques for paddy

Since the mid-1980s, many studies have indicated that significant savings in quantities of water used in traditional rice culture were possible without a distinct reduction in rice yield (Li et al 1994, 1999, Peng et al 1997, Tabbal et al 1992, Wang 1992). Some WSI techniques have been adopted widely in China (Li 1999, Mao 1997, Peng et al 1997, Wang 1992). Farmers have further adapted these practices. Evidence indicates that the traditional practice of irrigating rice has changed.

Developing on-farm WSI techniques for paddy

To control the ineffective tillering of rice, improve the illumination and heat conditions of paddy fields, use rainfall more effectively, and save pumping energy, attempts were made to control the ponded water level in paddy fields and use less irrigation water. Table 2 shows that the practice of WSI allows paddy fields to become dry before receiving further water, thereby retaining more water after rainfall. As a result,

Table 2. Water regimes for different rice cultures with alternate wet and dry irrigation.

Growth stages	Early rice		Middle rice		Late rice	
	Irrigation (mm)	Spilling (mm)	Irrigation (mm)	Spilling (mm)	Irrigation (mm)	Spilling (mm)
Revival of green	0-30	50	5-40	50	0-40	50
Early stage of tiller	0-30	50	0-40	60	0-40	60
Late stage of tiller	70%SMC[a]-20	50	70%SMC-20	60	80%SMC-20	60
Booting	80%SMC-30	80	80%SMC-30	80	80%SMC-30	80
Shooting	90%SMC-30	80	90%SMC-30	80	80%SMC-30	80
Milk ripening	70%SMC-20	50	70%SMC-20	50	70%SMC-20	50
Yellow ripening	Dry field	20	Dry field	0	Dry field	0

[a] SM = saturated moisture content.

the use of rainfall is facilitated, irrigation water management of the canal system is easy, irrigation events are reduced greatly, and percolation and seepage losses from paddy fields are reduced (Feng 1998, Li 1999, Li et al 1999, Wu et al 1995).

Theoretical research on WSI for paddy

The systematical research on WSI techniques for rice in China began and was emphasized in the mid-1980s (Fang 1989, Zhu and Gao, 1987) to avoid a reduction in rice yield or other negative effects resulting from WSI practices. This research has been giving priority to obtaining funds from the ministries of sciences and technology, water resources, education, and agriculture, and provincial governments and irrigation agencies since then. Experiments at more than 150 stations involve collaboration with professional institutes and are proposed in line with the requirements of national or local governments. Research on drought tolerance of rice in Hubei and Anhui provinces at the beginning of the 1980s (Fang 1989, Li 1999) could not bring to light the relationship between water input and rice yield but indicated that a slight water stress did not reduce rice yield (Fang 1989, Li 1999, Zhu and Gao 1987), which encouraged more people to study improvements in rice irrigation.

It was indicated that it is necessary to keep shallow ponded water until the middle stage of rice tillers, and then alternate wet and dry (AWD) irrigation does not have negative effects on rice growth if water content in the root zone is not lower than 70% to 80% of the saturated moisture (Li 1999, Li et al 1994, Zhang et al 1994). Li et al (1994) and Peng et al (1997) reported that neither continuous flooding nor a long time drying controlled weeds effectively, and that alternate wetting and drying was good for weed control in paddy fields. The recommended WSI practices were always advantageous for improving the ecological conditions of rice.

To save irrigation water in rice production without a distinct yield reduction, the sensitive indices of rice to water deficit have to be obtained. Based on the experimental data, rice water production functions (RWPF) for different rice varieties (early, middle, or late rice) and in different regions have been recommended, and the regularity of the variation in water sensitivity parameters in various models has been analyzed (Cui et al 1998, Li 1999, Mao and Cui 1998). This makes it possible to model the optimum irrigation regime for rice and the optimum allocation of water resources among crops and regions with a limited water supply.

Implementation of WSI for paddy

The research on WSI techniques should be carried out for more than three years in plot experiments, and then be demonstrated in typical fields. What has been applied successfully in paddy fields will be spread in an orderly manner. Training courses are given to representatives of farmers and irrigators from the townships and villages. Technicians give on-site direction in rice production areas. Meanwhile, guidebooks for WSI practices are disseminated widely. From experiences in Guangxi, Hubei, Jiangsu, Zhejiang, and Shandong provinces, farmers should not only understand the technical essentials of WSI practices but should also be convinced of the benefits from WSI practices. It is generally perceived that the AWD irrigation technique does not reduce rice yield but reduces irrigation water compared with continuous flooding. When the AWD irrigation practice is adopted, farmers pay less for water that is charged based on the volumetric water used and they have more time to work in cities or townships because irrigation events are reduced (Barker et al 2001).

Impacts of on-farm WSI techniques

Theoretically, on-farm WSI practices would result in only modest real water savings for an entire rice production area (Nyberg and Rozelle 1999, Seckler et al 1999); however, they are a prerequisite for efficient water use because they impel every farmer to use water carefully, capture return flow, harvest rainfall water, and control percolation losses. Therefore, deliveries from water sources will decrease and overall water productivity will increase with the wide implementation of on-farm WSI techniques (Barker et al 2001).

Water scarcity also has a qualitative dimension in rice production areas. Under AWD conditions, the average ponded water depth decreases and so does the infiltration water head. In addition, the slow drainage flux after water vanishes from the soil surface is much lower than the percolation under submerged conditions. Many reports claimed that percolation losses could decrease by 30% to 40% with AWD techniques (Mao 1997, Tabbal et al 1992, Wu et al 1995). Therefore, less polluted water goes into the surface water body or recharges groundwater. As mentioned above, AWD practices prevent paddy fields from keeping continuous flooding and induces an oxidized condition of soils. Thus, soil aeration is improved, poisonous matters within the rice root zone resulting from anaerobic conditions are reduced, and the water quality from percolation losses is better compared to continuous flooding (Li et al 1999).

From Table 2, the limits for spilling with AWD techniques are similar to those with traditional irrigation, but the upper limits for irrigation with the improved practice are much lower than those for the traditional irrigation method. The capacity of paddy fields to store rainfall is increased greatly, and precipitation is fully used without hindering rice growth under AWD conditions. The heavier the rainfall is, the higher the use ratio of rainfall is. Efficient rainfall use makes irrigation water requirements decrease; meanwhile, drainage water is reduced, which implies that pressure for waterlogging and flood control in the main rice-growing area of China in the flooding season could be alleviated to some extent with the introduction of AWD practices.

Modernization of irrigation schemes

The statistics on water diversions to irrigation indicate very low efficiency, and irrigation water productivity changes from 0.39 to 1.44 kg m^{-3} in different regions in China. This implies that opportunity exists for large real water savings in this sector. It is necessary to reduce water losses from conveyance, distribution, and application during irrigation, and to improve the efficiency with which precipitation and irrigation water are used. In the wake of water scarcity, the Ministry of Water Resources was asked to develop irrigation agriculture without taking more freshwater in 1995

(DRWM 2001). According to values of the irrigation water diversion and irrigation area from 1996 to 2000, irrigation water consumption per unit area decreased by 555 m^3 ha^{-1} and effective irrigation area increased by 4.3 million ha without an increase in water supply (DRWM and NCIDD 2001). With the initiation of the irrigation scheme modernization program aiming at increases in water and land productivity, the reliability of the irrigation water supply improved, which gave support to diversified cropping and ensured that total grain production reached 500 million t in a normal year. The achievements in the past five years also indicate that great potential exists for efficient water use.

Modernizatlon of large-sized irrigation systems

China has 402 large-sized irrigation schemes with more than 20,000 ha of designed irrigation area for each. Rice grows in almost half of them. The total irrigation area of the large-sized irrigation schemes is more than 15.7 million ha, which accounts for about 11.3% of total cultivated area. Grain production from the area makes up 22% of national grain output and yield is as high as 6.75 t ha^{-1}, which is 1.5-3.0 t ha^{-1} higher than the average value (DRWM 2001). So, this is the main force of agricultural production, the national grain commodity base, and a major component of agriculture and the agricultural economy of China. However, most of those irrigation systems were constructed in the 1950s and ’60s and had low design standards, aged structures, and imperfect field works, resulting in low irrigation water-use efficiency. Starting in 2001, the program of modernization and rehabilitation of the existing large-sized irrigation schemes, leading to higher water-use efficiency and higher water productivity, went into effect. After the modernization and rehabilitation of the 402 irrigation schemes in 15-20 years, 33 billion m^3 of irrigation water will be saved compared with existing water consumption. Then, real water savings would support the expansion of effective irrigation area, the improvement of irrigation reliability, and an increase in multiple cropping indices. Grain production from the large-sized irrigation districts will be more than 160 million t per year and account for 27% of national grain output. According to the program, not only will the irrigation guarantee probably be improved, but also the effective irrigation area will be increased to 19.3 million ha. In addition, experiences from the modernization of large-sized irrigation systems will be introduced to the modernization of medium and small-sized irrigation schemes, which will form the foundation for sustainable water use and agricultural development.

Funding policy

Not only does this program improve facilities of irrigation systems, it also pays great attention to capacity building and institutional development. To ensure the success of the ambitious program and the most cost-effective option of the high investment, priority is given to those with wider adoption of WSI practices, more incentives for water savings, and better institutional management. Equal attention should be paid to infrastructure and on-farm systems, project and institutional measures, irrigation practices and agro-techniques, modern techniques, and traditional experiences.

Otherwise, local governments and agencies could not obtain funds. Irrigation agencies should search for technical support from universities and professional institutes for planning the protection and use of water resources, the design of the irrigation system, research on and implementation of comprehensive measures for real water savings, capacity building, and institutional management.

Meanwhile, financial support from the central government is available each year for three programs. First, 60 counties are selected as "key counties" for developing efficient water use in agriculture. Second, 30 medium-sized irrigation schemes are to be improved, focusing on increasing conveyance efficiency. Third, 120 demonstration projects serve as examples of the implementation of comprehensive measures for efficient water use. Local governments have to compete for the budget according to the research on and dissemination of WSI techniques, incentives for water savings, and planning for achieving sustainable economic development and sound ecosystems and environments.

Institutional development

Many reports mentioned institutional development as the "core problem" that China needs to address to solve its water problems (Barker et al 2001, Heilig et al 2000, Nyberg and Rozelle 1999). On the other hand, in response to increased competition for water and the importance of rice production, the Chinese have invested in research on WSI practices and supported policies and practices that promote real water savings. Institutional development has gone beyond the traditional narrow concept of organizational and manpower strengthening and training. Experience, especially the post-1978 reforms, demonstrates the importance of incentives and a conducive institutional framework in maximizing the effects of agricultural infrastructure, and of successful research on and dissemination of new technologies.

High-level policy support

Nevertheless, it is necessary to recognize that China already has relatively sound laws and institutions. Institutional "software" deserves equal attention with physical "hardware" for irrigation systems. A series of policies has been drawn up, such as the Water Law, Water Resources Protection Law, Water Charge Rules, etc. Pursuing WSI and creating a water-saving society is one of the basic national policies that is the highest law in China. Not only is the water shortage the key problem in economic development, but also it has been one of the most important political topics. The central government asked that WSI be promoted as a revolutionary approach and that political leaders at the provincial and county level be responsible for building advanced agriculture. The achievement in developing sustainable agriculture and lightening the burden on farmers is one of the most important indices for checking on cadres at different levels, which spurs leaders to bring into line the benefits of farmers, irrigation agencies, the region, and the state.

Theory and technology on strategies for management of water scarcity are included in education and students who are working with irrigation pay a much lower tuition fee than others. The Ministry of Water Resources has authorized the unified administration and management of water resources at the national and basin levels to promise "a better life for all" and to avoid repeating the tragedy of the Yellow River drying up, which was common before 1997.

Water pricing

Most people agree that water pricing has effects on reduction in demand, increased supply because marginal projects become affordable, facilitation of reallocation among water-use sectors, and increased managerial efficiency. But, the mechanisms are more important than the pricing. Water measurement provides an opportunity for volumetric water charge, but, in China, water consumption is not usually measured at the level of individual farms. Instead, the measurements are typically taken for groups of farm households, with the size of these groups being quite variable over space within an irrigation system and across different irrigation systems, which creates potential free-rider problems. To solve this problem, on the one hand, farmers should be convinced that WSI techniques do not reduce rice yield but do reduce the use of irrigation water and thus water charges. Demonstrations, training, and dissemination of the techniques are necessary. On the other hand, decisions on water consumption require some degree of collective action. As collectivized agriculture was practiced for many years in China, farmers still understand the importance of collective action for irrigation, land reclamation, flood control, etc., even after the wave of great reforms. A study indicates that group or village heads prorate the charge to farmers based on area, but farmers are well aware that, if the village or group uses less water, the charge is reduced (Barker et al 2001).

Though the water price has increased in nominal terms in the past two decades, the water price for irrigation should not simply reflect its costs to cover all development, operation, and management at the moment because Chinese farmers are still poor. The effective pricing mechanisms should focus on incentives for farmers to value water resources and use water carefully. Under the macroscopic control of the state, the Provincial Finance and Pricing Control Bureau determines the price per unit of water for each alternative use—irrigation, industry, municipal, and hydropower. In some regions, the water price is not constant in different seasons and for different quantities. When water is short, the price increases, and the price for extra delivery is much higher than the standard price.

It should be remembered that water pricing is a double-edged sword. Sometimes, the benefits of farmers, irrigation agencies, and the government could not be well coordinated with the WSI practices. If the agency is not able to transfer the water savings from irrigation to more beneficial water-use sectors, the agency would send as much water as possible to the water measurement points. If farmers worry that they will not get their fair share of water in the group, they might take too much water. Therefore, the pricing mechanism, combined with new institutional frameworks involving participation by farmers, promises incentives for both farmers and the agency to save water.

Farmer irrigation association (FIA)

Recently, it has been very popular for governments to transfer greater responsibility to user groups for irrigation system management and performance to improve irrigation efficiency (Nyberg and Rozelle 1999). The model of a self-financing irrigation and drainage district (SIDD) has been introduced to developing countries by the World Bank and other institutions over the past several years, and experimental institutions have successfully piloted this for several years in China. This model constitutes a water supply corporation (WSC) and water user associations (WUAs). In practice, the WUAs have been highly satisfactory in improving water management efficiency (reducing water use while increasing production), but the establishment of WSCs appears to be more difficult because of the existing systems. Alternatively, the FIAs are recommended. The size of FIAs varies over space. The chairman of the FIA, who is elected by "one family, one vote," appoints an irrigator to measure the volume of "inflow" together with people from the agency and allocates water within the group. The chairman organizes the "collective action" of building and maintaining on-farm irrigation systems and tanks, protecting irrigation facilities, purchasing irrigation water and storing extra deliveries, catching return flow, and harvesting rainwater. The water fee is paid directly to the irrigation agency and the farmers see what they pay and are happy to minimize water use.

Changing of agency's role

Starting in 1980, irrigation agencies were asked to be self-financing except for infrastructure construction. The irrigation agencies had to pay equal attention to maintenance and operation of the irrigation system, institutional management, team building, financial management, and environmental protection in the irrigation district based on both current and future benefits. In addition, the reform of the water charge provided a basis for irrigation agencies to change the water allocation policy. Though the water rate for irrigation is the lowest, irrigation normally has a top priority. The irrigation agency has to improve irrigation water management to transfer more water for other purposes and provide more benefits with the same water quantity. After more water is transferred to more profitable sectors, irrigation agencies have the financial capacity for perfecting the irrigation system, especially the distribution systems, and strengthening maintenance and operations, which provide an opportunity to improve the reliability of the irrigation water supply and irrigation water efficiency. Therefore, a virtuous circle for the application of WSI techniques has been formed.

Conclusions

Demand for freshwater for industrialization and domestic urban needs is growing rapidly throughout Asia. Less water will be available for agriculture and for rice, the crop that consumes the largest amount of freshwater. In addition, China will find that it is more difficult to sustain producers' interest in rice farming with the progress of its joining the WTO because of the "free trade" in agricultural production. To find incentives for rice farming and to produce more rice with less water, China has established some strategies for managing water scarcity in rice production areas. However, many scientific issues remain that need to be studied. The application of WSI techniques in some regions is still very difficult because of physical problems. Institutional frictions remain among various administrative levels concerning planning, financing, constructing, and maintaining water-related infrastructure. Not only should water consumers be aware of water scarcity, but the incentives for water savings should also be given to water users. Broad cooperation of water and agricultural scientists is requested in the research on and practice of WSI techniques, and forceful support from the government is required.

References

Barker R, Loeve R, Li YH, Tuong TP, editors. 2001. Water-saving irrigation for rice: Proceedings of an International Workshop held in Wuhan, China, 23-25 March 2001. Colombo (Sri Lanka): International Water Management Institute. 123 p.

Brown LR. 1995. Who will feed China? New York (USA): W. W. Norton & Company.163 p.

Brown LR, Halweil B. 1998. China's water shortage could shake world food security. World Watch 11(4):10-21.

Cui YL, Li YH, Mao Z. 1998. Models of crop water production function with consideration of influence of the reference evapotranspiration frequency. J. Hydraulic Eng. (Beijing) 4:48-51.

Denning GL, Mew TW, editors. 1998. China and IRRI: improving China's rice productivity in the 21st century. Manila (Philippines): International Rice Research Institute. 104 p.

DRWM (Department of Rural Water Management). 2001. Program for irrigation development. Beijing (China): Ministry of Water Resources of China. 55 p. (In Chinese.)

DRWM and NCIDD (National Center of Irrigation and Drainage Development). 2001. Water saving irrigation: a review of the "Ninth-Five Year Plan." Beijing (China): Ministry of Water Resources of China. 405 p. (In Chinese.)

Fang XJ. 1989. The physiological reaction of rice to drought. Irrig. Drainage Small Hydropower Stn. 1:16-18. (In Chinese, with English abstract.)

Feng GZ. 1998. On developing overall thought of water saving irrigation in China. China Rural Water Hydropower 11:1-6. (In Chinese, with English abstract.)

Heilig GK, Fischer G, Velthuizen H. 2000. Can China feed itself? An analysis of China's food prospects with special reference to water resources. Int. J. Sustain. Dev. World Ecol. 7:153-172.

Li YH (chief editor). 1999. Theory and techniques of water saving irrigation. Wuhan (China): Wuhan University of Hydraulic and Electric Engineering Press. 310 p. (In Chinese.)

Li YH, Cui YL, Xie LG, Zhao CM. 1994. Experimental study of water saving irrigation model for rice. Irrig. Drainage Small Hydropower Stn. 12:5-9. (In Chinese, with English abstract.)

Li YH, Dong B, Yu F. 1999. Improved irrigation management of paddy fields for sustainable increases in water productivity. In: Musy A, Pereira LS, Fritsch M, editors. Emerging technologies for sustainable land use and water management. Lausanne (Switzerland): EPFL Press. p 36.

Liang GS. 1983. Rice ecology. Beijing (China): Agricultural Publishers 250 p. (In Chinese.)

Mao Z. 1997. Water saving irrigation for rice. China Rural Water Hydropower 4:45-47. (In Chinese, with English abstract.)

Mao Z, Cui YL. 1998. Water-yield function of rice and its temporal and spatial variation. In: Pereira LS, Gowing JW, editors. Water and the environment. London and New York: E & FN Spon. p 213-220.

Nyberg A, Rozelle S. 1999. Accelerating China's rural transformation. Washington, D.C. (USA): The World Bank. 86 p.

Peng SZ, Yu SE, Zhang HS. 1997. Water saving irrigation techniques for paddy. Beijing (China): China Water and Hydro Publishers. 154 p. (In Chinese.)

Qian ZY, Zhang GD (chief editors). 2001. Strategy study on water resources for China's sustainable development. Beijing (China): China Water Publishers. 340 p. (In Chinese.)

Seckler D, Barker R, Amarasinghe U. 1999. Water scarcity in the twenty-first century. Water Res. Dev. 15(1-2):29-42.

Serageldin I. 1999. Looking ahead: water, life and the environment in the twenty-first century. Water Res. Dev. 15(1-2):17-28.

Tabbal DF, Lampayan RM, Bhuiyan SI, 1992. Water efficient irrigation technique for rice. In: Murty VVN, Koga K, editors. Soil and water engineering for paddy field management. Bangkok (Thailand): Asian Institute of Technology. p 146-159.

Wang GT. 1992. High-yield and water-saving irrigation method: deep-thin-alternate dry and wet. Irrig. Drainage Small Hydropower Stn. 8: 18-19. (In Chinese, with English abstract.)

Wu DP, Wu TE, Wu YX. 1995. Experimental study of irrigation techniques and water requirement of rice. Img. Drainage Small Hydropower Stn. 11:11-15. (In Chinese, with English abstract.)

Zhang MZ, Li YH, Cui YL, Wu LC, Fang RJ. 1994. Studies on the growth and physiological mechanism of rice cultivated under the condition of deficit irrigation. Irrig. Drainage 13:6-11. (In Chinese, with English abstract.)

Zhu TY, Gao PW. 1987. Shallow-wet irrigation techniques for rice. Beijing (China): China Water and Hydro Publishers. 110 p. (In Chinese.)

Notes

Authors' addresses: Li Yuanhua, professor, deputy director general, National Center of Irrigation and Drainage Development, Beijing 100053, China, tel. 0086-10-6320-3727, fax 0086-10-6320-3374, email yuanhli@yahoo.com; Ni Wenjin, senior engineer, National Center of Irrigation and Drainage Development, Beijing 100053, China, email wenjinni@yahoo.com.cn; Chen Chongde, deputy chief engineer, Zanghe Irrigation Agency, Hubei Province, 434556, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Examining the water-shortage problem in rice systems: water-saving irrigation technologies[1]

B.A.M. Bouman

Rice production in Asia needs to increase to feed an ever-growing population. More than 75% of the rice produced comes from irrigated land. However, the water crisis threatens the sustainability of the irrigated system. The supply of water for irrigation is endangered by declining water quality, declining resource availability, increased competition from other users, and increasing costs. Rice is especially sensitive to declining water availability since it requires more water than any other food crop and it has a relatively low water-use efficiency. At the farm level, water inputs can be reduced by decreasing the relatively large and unproductive losses from seepage, percolation, and evaporation. Water-saving irrigation technologies such as saturated soil culture and alternate wetting and drying can drastically diminish these losses. Under these technologies, yields also decline, though to a lesser extent than the water inputs; hence, water productivities increase. A new concept of growing rice using less water is aerobic rice: high-yielding rice grown in nonpuddled aerobic soil using supplementary irrigation just like upland crops. Farmers in Brazil, China, and India are pioneering this system where water is scarce or costly. However, new aerobic rice varieties and specially designed management strategies are needed if this system is going to be successful. Through the adoption of water-saving irrigation technologies, rice land will shift away from being continuously anaerobic to being partly or even completely aerobic. This will have major consequences for other aspects of sustainability, such as weed, pest, and disease ecology and nutrient and soil organic matter dynamics.

Food security in Asia is challenged by increasing food demand and threatened by declining water availability. Rice is the most important staple in Asia, where it provides

---

[1] This paper is an updated and expanded version of a short paper published earlier in *International Rice Research Notes:* Bouman BAM. 2001. Water-efficient management strategies in rice production. *International Rice Research Notes* 26(2):17-22 (IRRI, Los Baños, Philippines).

35-80% of total calorie uptake (Maclean et al 2002). More than 75% of the rice supply comes from 79 million ha of irrigated land. Thus, the present and future food security of Asia depends largely on the irrigated rice production system. However, the water-use efficiency of rice is low, and to grow rice requires large amounts of water. In Asia, irrigated agriculture accounts for 90% of total diverted freshwater, and more than 50% of this is used to irrigate rice (Barker et al 1999). Until recently, this amount of water has been taken for granted, but now the global "water crisis" threatens the sustainability of irrigated rice production. The available amount of water for irrigation is increasingly becoming scarce (Postel 1997). The reasons are diverse and location-specific, but include decreasing quality (chemical pollution, salinization), decreasing resources (e.g., falling groundwater tables, silting of reservoirs), and increased competition from other sectors such as urban and industrial users.

In Asia, rice is mostly grown under supplementary irrigation in the wet season and under full irrigation in the dry season. Irrigated wet-season rice mostly grows in the subtropical regions of North and Central China, Pakistan, and northwest India. Dry-season irrigated rice is concentrated in South China, southern and eastern India, and the whole of Southeast Asia. Among them, China, India, and Pakistan have 120 million hectares of (supplementary) irrigated farmland upon which they depend for about half their domestic food production. Salinization has already damaged up to 17% of it through mismanagement of irrigation schemes (Postel 1997). China's Yellow River, which flows 4,600 kilometers through some of Asia's richest farmland, has run dry nearly every year since 1972. Such is the demand on its water that, in 1997, its final 600 kilometers were dry for more than 4 months (Postel 1997). The Ganges and Indus rivers have virtually no outflow to the sea in the dry season and, in inland India, in the intensively cultivated states of Punjab and Haryana, groundwater tables fall about 70 cm per year. In the Philippines, some 61 % of the 3.4 million ha of rice land is under irrigation, with the majority of the production coming from the rice bowl in Central Luzon (Maclean et al 2002). Irrigation is provided by gravity systems and, increasingly, by shallow and deep tubewells. Water availability, however, is being threatened from various sources. Water from the Angat reservoir in Bulacan Province is increasingly diverted toward Greater Manila at the expense of irrigation (Bhuiyan and Tabbal, as referenced in Pingali et al 1997, p 196-197), water in the Agno River in Pangasinan Province is polluted with sediments and chemicals from mining activities upstream (Castañeda and Bhuiyan 1993), and many irrigation systems were destroyed and clogged by the earthquakes of 1990 and the Mount Pinatubo eruption in 1991 (NIA 1996). Moreover, water is always scarce in the dry season, in which the lack of rainfall makes cropping impossible without irrigation.

Overlaying the International Water Management Institute's water scarcity atlas (IWMI 2000) with IRRI's rice area maps, Tuong and Bouman (2002) estimated that a total of 2 million ha of Asia's dry-season rice and 13 million ha of its wet-season rice will experience "physical water scarcity" by 2025. The increasing scarcity of water means that the costs of its use and resource development are increasing dramatically (Postel 1997, Rosegrant 1997). Most of the approximately 22 million ha of dry-season rice in South and Southeast Asia fall in IWMI's defined "economic water scarcity" zone. Therefore, farmers and researchers alike are looking for ways to decrease water use in rice production and increase its use efficiency. Though water use can be optimized at scale levels from the field to the farm, irrigation system, watershed, and entire river basin, a fundamental approach is to look at water use at the field level where water and the rice crop interact. This is also the scale level that concerns rice farmers most. For farmers with no control over the availability or distribution of water beyond their farm boundaries, the crucial question to be asked is "What are the options to cope with the decreasing water supply (or the increasing costs of it) at the farm or field inlets?" To answer this question, we have to look at the flows of water in rice fields and understand where reductions in water use can be achieved without impairing yield.

The water balance of a rice field

Irrigated lowland rice in Asia is transplanted or direct (wet) seeded into puddled paddy fields. Land preparation of a paddy consists of soaking, plowing, and puddling (i.e., harrowing under shallow submerged conditions). Puddling is mainly done for weed control, but also increases water retention, reduces soil permeability, and eases field leveling and transplanting (De Datta 1981). Soaking is a one-time operation and requires water to bring the topsoil to saturation and to create a ponded water layer. The amount of water required for soaking can be as low as 100–150 mm in heavy clay soils (De Datta 1981), but can be much higher in lighter-textured soils. The crop growth period runs from establishment (transplanting, or emergence in the case of direct seeding) to maturity, during which fields are typically flooded with 5–10 cm of water. Under flooded conditions, water is required to match several outflow processes. Because of the standing water, there is hydrostatic pressure that continuously "pushes" water downward through the puddled layer. When this water flows vertically downward below the root zone, it is called percolation (P), and, when it flows laterally underneath bunds, it is called seepage (S) (Fig. 1). Both flow rates are governed by the water head (depth of ponded water) on the field and the resistance to water movement in the soil. Because they are difficult to separate in the field, S and P are often taken together as one term, SP. Typical SP values for paddy fields vary from 1 to 5 mm d^{-1} in heavy clay soils to 25–30 mm d^{-1} in sandy and sandy loam soils (Wickham and Singh 1978, Jha et al 1981). Water is released into the air by evaporation (E) from the ponded water layer and transpiration (T) by the crop. Again, E and T are difficult to separate in the field and they are mostly considered together as evapotranspiration (ET). Typical ET values of rice in the tropics are 4–5 mm d^{-1} in the wet season and 6–7mm d^{-1} in the dry season (De Datta 1981). Finally, overbund flow (or surface runoff) is the spillover when water depths rise above the paddy bunds.

For a crop growth duration of 100 days (typical for modern high-yielding varieties), total water requirements vary from 675 to 4,450 mm, depending on the season and soil characteristics (Table 1), with 1,500–2,000 mm as a typical value in

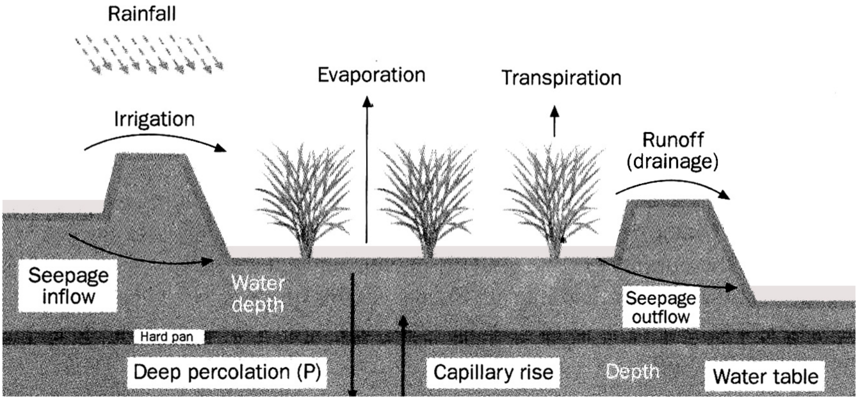


Fig. 1. Components of the water balance of a flooded puddled rice field.

Table 1. Typical daily and seasonal rates of water use in paddy rice production in the tropics. [a]

	Daily rate ($mm\,d^{-1}$)	Seasonal rate (mm)
Land preparation	–	175-750
Evapotranspiration		
Wet season	4-5	400-500
Dry season	6-7	600-700
Seepage and percolation		
Heavy clays	1-5	100-500
Loamy/sandy soils	25-30	2,500-3,000

[a] Total season = 675-4,450 mm, common value = 1,500-2,000 mm.

many lowland areas. Of all outflows of water from a paddy field, only transpiration is "productive" water use because it leads directly to crop growth and yield formation. Transpiration is essential to crop growth since it provides cooling and is the driving process for water flow in the plants that carries nutrients from the roots to the shoot. Most of the water requirements in paddy rice, however, are caused by the large losses from seepage, percolation, and evaporation from the ponded water layer. These flows are unproductive as they do not contribute to crop growth and yield formation.

Water management strategies to reduce water input

Large reductions in water input can potentially be realized by reducing the unproductive seepage and percolation and evaporation flows (Tuong 1999, Bouman and Tuong 2001). There are basically two ways to do so: (1) increasing the resistance to water flow in the soil and (2) decreasing the hydrostatic water pressure and the duration of flooded water. The resistance to water flow can be increased by changing the soil physical properties. Cabangong and Tuong (2000) have shown the beneficial effects of an additional shallow soil tillage before land preparation to close cracks that cause rapid bypass flow at land soaking. Thorough puddling results in a good compacted plow soil that impedes vertical water flow (De Datta 1981). Soil compaction using heavy machinery has been shown to decrease soil permeability in northeast Thailand in sandy/loamy soils with at least 5% clay (Sharma et al 1995). Finally, researchers have even experimented with introducing physical barriers underneath paddy soils such as bitumen layers and plastic sheets (Garrity et al 1992). However effective, though, most of these soil improvements are expensive and beyond the financial scope of farmers.

Reducing SP flows through reduced hydrostatic pressure can be achieved by changed water management. Instead of keeping the rice field continuously flooded with 5-10 cm of water, the floodwater depth can be decreased, the soil can be kept around saturation (SSC—saturated soil culture), or alternate wetting and drying (AWD) regimes can be imposed. In SSC and AWD, the duration of standing water in the field also decreases, which leads to reduced losses of water by evaporation. Under these management schemes, the hydrology of the soil changes from anaerobic under flooded and SSC regimes to alternately anaerobic and aerobic under AWD. Ultimately, rice may be grown under completely aerobic conditions and continuous SP and evaporation from standing water may be eliminated completely. Below, these water management technologies are reviewed in more detail.

Saturated soil culture (SSC)

In SSC, the soil is kept as close to saturation as possible. This mostly means that a shallow irrigation is given to obtain about 1-cm floodwater depth a day or so after the disappearance of standing water. From 1988 to 1997, Tabbal et al (2002) experimented with the implementation of SSC in farmers' fields in Central Luzon, Philippines. They compared the yield and water use of the farmers' conventional practice of keeping the field continuously flooded with that of SSC (Table 2). The water inputs under the conventional practice ranged from 577 to 3,500 mm, depending on soil type and groundwater depth. With SSC, the water inputs decreased by 30–60% and the yield dropped by 4-9%, with one exceptional value of 30% in the very permeable soil of Guimba-2 in 1991. Because the water inputs decreased more than the yields, the water productivity (calculated as the ratio of yield over total water input) increased by 30-115%.

Bouman and Tuong (2001) compiled a database on SSC and AWD from their own IRRI experiments and experiments reported in the literature. Their database contains information from 31 pot and field experiments carried out in north-central India, the Philippines (Luzon), and Japan. In the 34 data points on SSC, water input decreased by 5% to 50% from the continuously flooded check, with an average of 23%. The yields decreased by only 6% on average, so that water productivity increased.

Table 2. Yield, water inputs, and water productivity under continous standing water (CSW) and under saturated soil culture (SSC), Central Luzon, Philippines, 1988-97 dry seasons.

Location	Year	Crop establishment	Water inputs[a] (mm)		Yield (t ha^{-1})		Water productivity (g grain kg^{-1} water)	
			CSW	CSW	CSW	SSC	CSW	SSC
Guimba-1	1988	Transplanted	2,197	914	5.0	4.6	0.23	0.50
Guimba-1	1989	Transplanted	1,679	1,164	5.8	5.6	0.35	0.48
Guimba-2	1990	Transplanted	2,028	1,227	5.3	4.8	0.26	0.39
Guimba-2	1991	Transplanted	3,504	2,053	4.9	3.6	0.14	0.18
Muñoz	1991	Transplanted	694	373	7.4	6.7	1.06	1.81
Muñoz	1991	Wet-seeded	631	324	7.6	7.3	1.20	2.27
Talavera	1993	Transplanted	728	477	7.0	6.6	0.96	1.39
Talavera	1993	Wet-seeded	577	391	8.2	7.7	1.42	1.90
San Jose	1997	Wet-seeded	2,875	1,516	8.4	7.8	0.29	0.52

[a] Water inputs include rainfall and irrigation water applied during the crop growth period only. They do not include water inputs for land preparation.

Implementing SSC requires good water control at the field level and frequent shallow irrigations that are labor-intensive. Borell et al (1997) experimented with raised beds in Australia to facilitate SSC practices. Water in the furrows (30-cm width and 15-cm depth) kept the beds (120 cm wide) at saturation. Compared to flooded rice, water savings were 34% and yield losses 16–34%. Thompson (1999) found that SSC in southern New South Wales, Australia, reduced both irrigation water input and yield by a bit more than 10%, thus maintaining the irrigation water productivity. A yield decline caused by cold damage is likely for current varieties grown using SSC in that environment. Borrell et al (1997) pointed out the need for further research to determine which components of the water balance were responsible for the differences in total water use.

Alternate wetting and drying (AWD)

In AWD, irrigation water is applied to obtain 2–5-cm floodwater depth after a certain number of days (ranging from 2 to 7) have passed after the disappearance of ponded water. Though some researchers reported a yield increase under AWD (Wei and Song 1989, Mao Zhi 1993), our recent work indicates that this is the exception rather than the rule (Belder et al 2002, Cabangon et al 2001, Tabbal et al 2002). In 92% of the 174 data points collected by Bouman and Tuong (2001), AWD resulted in decreased water input, though at the expense of 0–70% decreased yield compared with that of the flooded checks, depending on the number of days between irrigations and soil conditions (Fig. 2). Mostly, however, yield losses were smaller than the reductions in water inputs and water productivities increased with decreased water inputs (Fig. 3). Thus, there is a trade-off between land productivity (i.e., yield) and water productivity. In the most severe cases of AWD, water inputs decreased to only 300-400 mm and water productivities reached maximum levels of 2 g rice kg^{-1} water.

Figure 4 shows so-called water production functions for two examples of AWD field experiments in India and closed-pot experiments in growth chambers in Japan. The lowest curved line is from Indian experiments in soils with SP rates of 21 mm d^{-1} and low nitrogen inputs of 80 kg N ha^{-1} and zero P and K (Jha et al 1981). Yields were low and water consumption was high. On the right-hand side of the curve are the data of continuously flooded treatments. Going to the left are first AWD treatments that cut back SP while not affecting yield levels. Either the crop was able to satisfy its transpiration requirements or the low level of nutrients was more yield-limiting than water. Further to the left are data of more severe AWD treatments, and yields dropped when crop water consumption was negatively affected. The second, higher curve, is also from Indian experiments, but with lower SP rates (9–14 mm d^{-1}) and higher nutrient inputs (120 kg N ha^{-1}, 60 kg P_2O_5 ha^{-1}, and 40 kg K_2O ha^{-1}) that resulted in higher yields (Tripathi et al 1986). Going from right to left on this curve, yields dropped faster than in the other experiment in India since water quickly became yield-limiting (compared with nutrients). Both Indian production curves illustrate the law of diminishing returns to water inputs. Water productivities are highest at the left side of the curves where water is the most limiting growth factor, but where yield

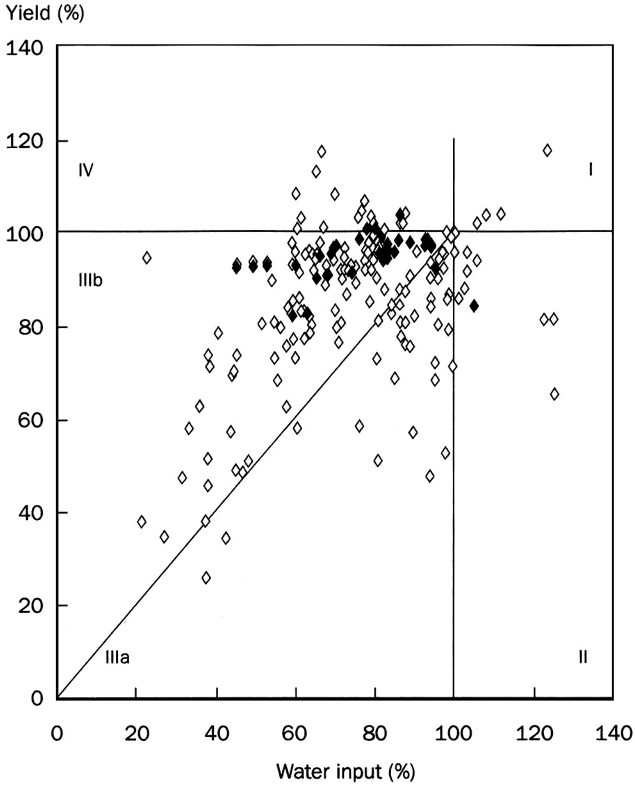


Fig. 2. Relative yield versus relative water input under saturated soil culture (SSC) (♦) and alternate wetting and drying (AWD) (◊) conditions. The relative yield and water inputs are calculated as the yield and water input of the SSC and AWD treatments as percentage of the yield and water input of the checks (continuous flooding), respectively. Data from Indian and Philippine field experiments. (Source: Bouman and Tuong 2001.)

levels are low. The data on the straight line are from closed-pot experiments in Japan (Anbumozhi et al 1998). Since closed pots have no SP losses, reductions in water inputs immediately affected transpiration and, consequently, yields declined steeply with decreased water inputs.

Aerobic rice

A fundamental approach to reduce water inputs in rice is to grow the crop like an irrigated upland crop such as wheat or maize. Instead of trying to reduce water inputs in lowland paddy fields, the concept of having the field flooded or saturated is abandoned altogether. Upland crops are grown in nonpuddled aerobic soil without

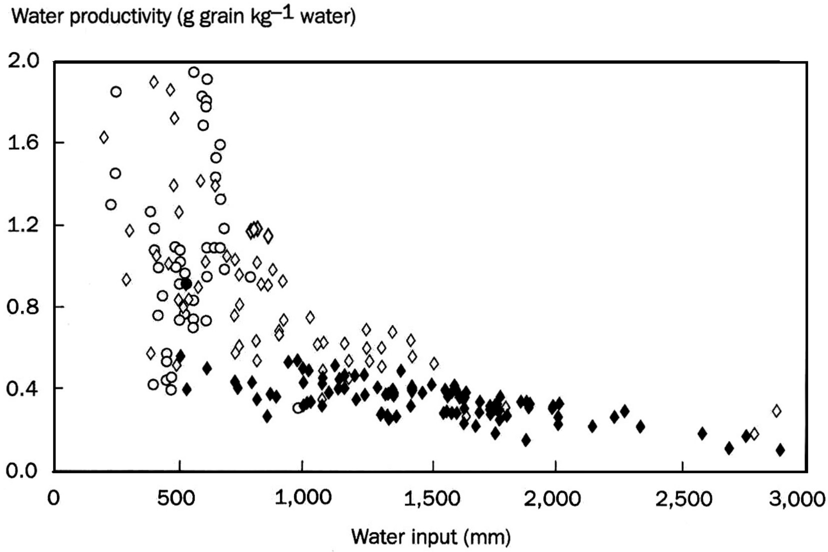


Fig. 3. Water productivity versus water input. ♦ are data from Indian field experiments (N = 99), ◊ are data from Philippine field experiments (N = 61), ○ are data from Japanese and Philippine pot experiments (N = 48). (Source: Bouman and Tuong 2001.)

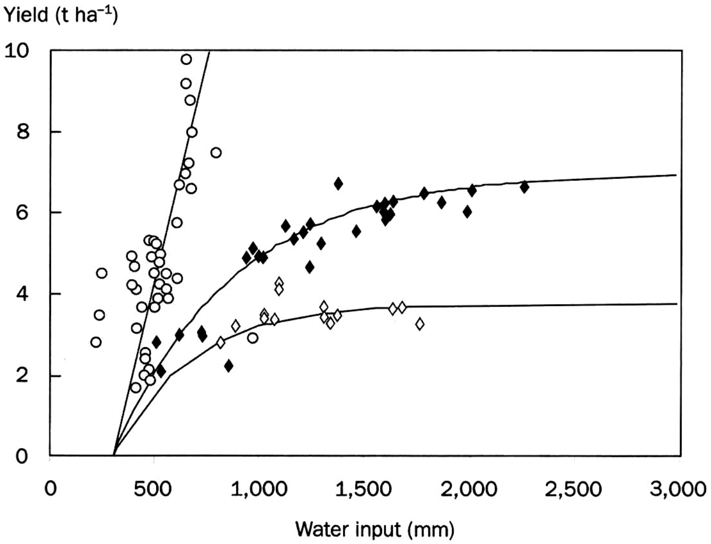


Fig. 4. Yield versus water input. Data from field experiments in India in 1976 and 1978 (◊, Jha et al 1981), in India in 1981-82 (♦, Tripathi et al 1986), and In Japan (○, Anbumozhi et al 1998). The curved lines are fitted production functions of the shape [yield = *a (1- e (b*(water input - c)))]. (Source: Bouman and Tuong 2001.)**

Table 3. Comparison of water use of a hypothetical aerobic rice crop with that of lowland rice on different soils types (characterized by different seepage and percolation rates).

Water flow process	Aerobic rice (mm)		Lowland rice (mm)		
Evaporation	100	100	200	200	200
Transpiration	400	400	400	400	400
Seepage and percolation	–	–	100 (1 mm d^{-1})	500 (5 mm d^{-1})	1,500 (15 mm d^{-1})
Application inefficiency loss	90 (85% eff.)	335 (60% eff.)	–	–	–
Total	590	835	700	1,100	2,100

standing water. Irrigation is applied to bring the soil water content in the root zone up to field capacity after it has reached a certain lower threshold (e.g., halfway between field capacity and wilting point). The amount of irrigation water should match evaporation from the soil and transpiration by the crop. Since it is hardly possible to apply irrigation water to the root zone only, some of it is lost by deep percolation and is unavailable for uptake by the crop. Typical field application efficiencies vary from 60% to 70% using surface irrigation (e.g., flash or furrow irrigation) to more than 90% using sprinkler or drip irrigation. The potential water savings when rice can be grown as an irrigated upland crop are large, especially on soils with high SP rates (Table 3). Besides cutting down on SP losses, evaporation also decreases since there is no continuous standing water layer. Traditional upland rice varieties are grown this way, but they have been selected to give stable yields in adverse environments with minimal external inputs. They are tall and unresponsive to inputs and, under favorable conditions, have a low harvest index (ratio of grain weight to total aboveground plant dry weight) and tend to lodge, or fall over (Lanceras et al 2002). Alternatively, high-yielding lowland rice grown under aerobic conditions shows great potential to save water, but at a severe yield penalty. Achieving high yields under irrigated aerobic conditions requires new varieties of "aerobic rice" with improved lodging resistance and the ability to partition a greater proportion of plant matter into grain.

Temperate aerobic rice. In the temperate zone, studies on lowland rice grown under aerobic conditions with sprinkler irrigation were conducted in the United States by McCauley (1990) and Westcott and Vines (1986). Irrigation water inputs were 20-50% less than under flooded conditions, depending on soil type, rainfall, and water management. The highest-yielding cultivars (7-8 t ha^{-1}) showed yield reductions of 20-30% compared with flooded conditions. The most drought-tolerant cultivars produced the same yields (5-6 t ha^{-1}) under both conditions. Researchers obtained similar results with rice grown under sprinkler irrigation in Australia (Blackwell et al 1985). With high levels of irrigation, yields were 4-6 t ha^{-1} (compared with around 7 t ha^{-1} under flooded conditions) and water inputs were 20-50% of those under flooded conditions. Under the prevailing market structures in the U.S. and Australia, the 20-30% yield loss outweighed the benefits of the water savings, so research was discontinued. In Brazil, a breeding program on upland rice has resulted in improved varieties with a yield potential of up to 6 t ha^{-1} under sprinkler irrigation (da Silveira Pinheiro and da Maia de Castro 2000). These new varieties possess the characteristics of modern plant types: medium stature and tillering, resistance to lodging, and short, erect upper leaves. Farmers grow these varieties commercially on an estimated 250,000 ha (Guimaraes and Stone 2000).

In all of the studies cited above—in the U.S., Australia, and Brazil—high yields are realized only when the soil is kept very wet (soil water tensions below 10-30 kPa) throughout the growing season. In northern China, as in Brazil, breeding efforts have produced temperate aerobic rice varieties (such as "Han Dao 297," "Han Dao 277," "Han Dao 502," "Han 58," "Danjing 5," and "Danjing 8") with a reported yield potential of up to 6 t ha^{-1} under supplementary irrigation (Wang Huaqi et al 2002). These varieties have been released since the 1990s and it is estimated that they are currently grown on 140,000 ha in northern China, replacing traditional lowland rice in water-short irrigated areas and traditional upland crops (such as maize, soybean, and cotton) in low-lying flood-prone areas. The adoption of aerobic rice is facilitated by the availability of efficient herbicides and seed-coating technologies. Recent experiments near Beijing show that water savings of more than 50% can be realized compared with flooded lowland rice (Yang et al 2002). Importantly, yields of 4-5.5 t ha^{-1} are obtained using extremely little water (550-650 mm, versus 1,340 mm under lowland conditions; Table 4), resulting in much drier soil conditions (soil water tensions of 10-300 kPa) than in Brazil and in the studies in the U.S. and Australia. Another study in China comparing aerobic rice under various forms of ground cover with lowland rice confirmed the large potential for water savings (Lin Shan et al 2002).

Bouman et al (2002) and Wang Huaqi et al (2002) evaluated the performance of aerobic rice grown by farmers near Beijing and at a pilot site called Guanzhuang in Anhui Province in 2001 (Table 5). On average, the yield of aerobic rice was 27% to 35% lower than that of lowland rice and water inputs were 55% and 66% lower. Since the reduction in water use was relatively larger than the reduction in yield, the water productivity (g grain per kg of total water used) of aerobic rice was 1.6 to 1.9 times higher than that of lowland rice. On the socioeconomic side, there were considerable differences in net returns and gross margins between aerobic and lowland rice at the two sites. Net returns to aerobic rice cropping (on a per hectare basis) were 26% and 30% lower than those to lowland rice cropping at Guanzhuang and Beijing, respectively. This could be attributed to the lower yields of aerobic rice compared with lowland rice. However, again because of aerobic rice's much lower water use, the net returns per unit of water used were on average twice as high in aerobic rice as in lowland rice. At both sites, the use of family labor was much less in aerobic rice than in lowland rice: 47% less at Guanzhuang and 77% less at Beijing. This is mainly because lowland rice requires much labor for wet-land preparation, transplanting, and irrigation activities. This lower labor requirement of aerobic rice

Table 4. Water inputs from emergence to harvest, yield, and water productivity of aerobic rice varieties HD297 and HD502 and lowland rice variety JD305 grown under flooded and aerobic conditions with different irrigation regimes near Beijing, 2001.

Growth condition	Water inputs (mm)	Yield (t ha^{-1})			Water productivity (g grain kg^{-1} water)		
		JD305	HD297	HD502	JD305	HD297	HD502
Aerobic 1	644	4.2	4.7	5.3	0.65	0.73	0.82
Aerobic 2	577	3.8	4.3	4.6	0.66	0.74	0.80
Aerobic 3	586	2.0	4.2	4.3	0.34	0.72	0.73
Aerobic 4	519	1.5	3.4	3.5	0.29	0.66	0.67
Aerobic 5	469	1.2	2.5	3.0	0.26	0.53	0.64
flooded	1,340	8.8	5.4	6.8	0.66	0.40	0.51

Table 5. Mean biophysical and socioeconomic performance indicators of aerobic rice and lowland rice produced by farmers at Guanzhuang (Anhui Province) and near Beijing, 2001.

Location:	Guanzhuang		Beijing	
Rice type:	Aerobic	Lowland	Aerobic	Lowland
Yield (t ha^{-1})	5.8	7.9	4.6	7.1
Irrigation (mm)	542	1,291	177	1,057
Total water (mm)	6 12	1,361	476	1,394
Total water productivity (g grain kg^{-1} water)	0.95	0.58	0.96	0.51
Production value (\$ ha^{-1})	868	1,016	1,058	1,633
Paid-out costs (\$ ha^{-1})	343	292	322	565
Imputed family labor costs (\$ ha^{-1})	a7	17 1	39	165
Total costs (\$ ha^{-1})	430	463	361	730
Gross margin[a] (\$ ha^{-1})	525	724	736	1,068
Net return[b] (\$ ha^{-1})	438	553	697	903
Family labor use (8-h d ha^{-1})	46	90	12	53
Net returns to water (\$ m^{-3})	0.0715	0.0406	0.1464	0.0648
Price of grain (\$ kg^{-1})	0.15	0.13	0.23	0.23
Price of labor (\$ d^{-1})	1.90	1.90	3.10	3.10

[a] Calculated as production value minus paid-out costs. [b] Calculated as production value minus paid-out costs minus family labor costs.

Source: Wang Huaqi et al 2002.

would then give more time to the family to work outside the farm for additional sources of income. At both sites, farmers were very satisfied with the results from aerobic rice cropping. On their aerobic rice fields, they did not have the option of growing lowland rice because of a water shortage (Guanzhuang) or government restrictions (Beijing).

Tropical aerobic rice. Although no effort has been made yet to breed rice varieties specifically for tropical aerobic rice systems, IRRI has identified several cultivars with high yield potential under aerobic management. Upland rice grown under

Table 6. Total water input (from land preparation to harvest), yield, and water productivity of rice variety Apo under flooded (F) and aerobic (A) soil conditions, IRRI farm, 2001-02.

Item	Dry season 2001		Wet season 2001		Dry season 2002	
	F	A	F	A	F	A
Water (mm)	1,672	744	1,759	959	1,275	852
Yield (t ha^{-1})	5.9	3.56	4.87	4.1	7.33	5.66
Water productivity (g grain kg^{-1} water)	0.35	0.48	0.28	0.43	0.57	0.66

favorable conditions typically reaches maximum yields of more than 4 t ha^{-1}, with yields of 5 t ha^{-1} and more sporadically reported (George et al 2001, 2002). In the early 1970s, De Datta et al (1973) tested lowland variety IR20 in aerobic soil under furrow irrigation at IRRI. Water savings were 55% compared with flooded conditions, but the yield fell from about 8 .t ha^{-1} under flooded conditions to 3.4 t ha^{-1} under aerobic conditions. IRRI started to develop tropical aerobic rice systems in 2001, using existing improved upland and lowland germplasm (Castañeda et al 2002). Using a promising new upland rice variety, Apo, dry-season yields at the IRRI farm in Los Baños, Philippines, reached a maximum of 5.7 t ha^{-1} in 2002 (Table 6). Though yields were on average 26% lower than under flooded conditions, water inputs were 44% lower and water productivities 35% higher. As in China, researchers identified specially bred aerobic rice varieties and proper management of water and nutrients as keys to obtaining high yields.

In India, researchers are currently testing the growing of popular lowland rice varieties under aerobic conditions on raised beds. The first results on yields and water use were comparable with those obtained at IRRI (Singh et al 2002, Sharma et al 2002). Important yield-reducing factors include weeds, micronutrient deficiencies, and nematodes. Keeping the soil flooded for the first few weeks of establishment is a suggested remedy for micronutrient deficiencies and weeds. Research on yield sustainability in aerobic systems has been limited in Asia. In Brazil, it is reported that high yields can be sustained when aerobic rice is grown once in four crops, but not under continuous monocropping (Guimaraes and Stone 2000). A rapid yield decline under continuous upland rice cropping has also been documented in the Philippines (George et al 2002). The decline, which cannot be reversed with inorganic fertilizers, may be related to the buildup of soil pathogens.

Discussion and conclusions

Water in irrigated rice production has been taken for granted for centuries, but the "looming water crisis" may change the way rice is produced in the future. Water-saving irrigation technologies that were investigated in the early 1970s, such as saturated soil culture and alternate wetting and drying, are receiving renewed attention by researchers. These technologies reduce water inputs, though mostly at the expense of some yield loss. Farmers in Asia that are confronted with scarcity or high costs of water have already started to adopt these technologies. In China, various forms of alternate wetting and drying and reduced floodwater depth have been developed and massively adopted by farmers (Li 2001). Surveys in north-central India (A.K. Singh, personal communication) and in Central Luzon (unpublished IRRI data) show that farmers that operate pumps to irrigate their paddy fields consciously apply some form of alternate wetting and drying to save energy costs.

Aerobic rice is a new concept to further decrease water requirements in rice production. It is commercially grown in Brazil and is being pioneered by farmers in northern China. In the heart of the rice-wheat belt in India (Haryana, the Punjab, and Uttar Pradesh), innovative farmers are pioneering growing rice aerobically under furrow irrigation in raised-bed systems (Ladha et al 2000). Changes in the hydrology of rice production will have major consequences for its sustainability and appropriate management practices. Over the centuries, lowland rice has proven to be a remarkably sustainable system, mostly because of its particular anaerobic character. Water-saving irrigation practices shift away from continuous anaerobic conditions to alternate anaerobic-aerobic and continuous aerobic conditions. The shift from anaerobic to aerobic systems will have major consequences for weed, pest, and disease ecology, nutrient and soil organic matter dynamics, and greenhouse gas emissions and carbon sequestration. Weed control is especially a crucial issue in most water-saving irrigation technologies. Water has been the cheapest herbicide ever, but this may not be so anymore in the (near) future. Breeders have to respond to the challenge of breeding varieties that perform well under nonpermanently flooded conditions. The development of aerobic rice varieties is probably the most ambitious challenge of all.

References

Anbumozhi V, Yamaji E, Tabuchi T. 1998. Rice crop growth and yield as influenced by changes in ponding water depth, water regime and fertigation level. Agric. Water Manage. 37:241-253.

Barker R, Dawe D, Tuong TP, Bhuiyan SI, Guerra LC. 1999. The outlook for water resources in the year 2020: challenges for research on water management in rice production. In: Assessment and orientation towards the 21st century. Proceedings of the 19th session of the International Rice Commission, Cairo, Egypt, 7-9 September 1998. Rome (Italy): FAO. p 96-109.

Belder P, Bouman BAM, Spiertz JHJ, Guoan Lu, Quilang EJP. 2002. Water use of alternately submerged/nonsubmerged irrigated lowland rice. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production. Los Baños (Philippines): International Rice Research Institute.

Blackwell J, Meyer WS, Smith RG. 1985. Growth and yield of rice under sprinkler irrigation on a free-draining soil. Aust. J. Exp. Agric. 25:636-641.

Borell A, Garside A, Fukai S. 1997. Improving efficiency of water for irrigated rice in a semi-arid tropical environment. Field Crops Res. 52:231-248.

Bouman BAM, Tuong TP. 2001. Field water management to save water and increase its productivity in irrigated rice. Agric. Water Manage. 49(1):11-30.

Bouman BAM, Wang Huaqi, Yang Xiaoguang, Zhao Junfang, Wang Changgui. 2002. Aerobic rice (Han Dao): a new way of growing rice in water-short areas. In: Proceedings of the 12th International Soil Conservation Organization Conference, 26-31 May 2002, Beijing, China. Tsinghua University Press. p 175-181.

Cabangon RJ, Tuong TP. 2000. Management of cracked soils for water saving during land preparation for rice cultivation. Soil Tillage Res. 56:105-116.

Cabangon RJ, Castillo EG, Bao LX, Lu GA, Wang GH, Cui YL, Tuong TP, Bouman BAM, Li YH, Chen CD, Wang ZJ. 2001. Impact of alternate wetting and drying irrigation on rice growth and resource-use efficiency. In: Barker R, Li YH, Tuong TP, editors. Water-saving irrigation for rice. Proceedings of an International Workshop held in Wuhan, China, 23-25 March 2001. Colombo (Sri Lanka): International Water Management Institute. p 55-80.

Castañeda AR, Bhuiyan SI. 1993. Sediment pollution in a gravity irrigation system and its effects on rice production. Agric. Ecosyst. Environ. 45:195-202.

Castañeda AR, Bouman BAM, Peng S, Visperas RM. 2002. The potential of aerobic rice to reduce water use in water-scarce irrigated lowlands in the tropics. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production. Los Baños (Philippines): International Rice Research Institute.

da Silveira Pinheiro B, da Maia de Castro. 2000. Upland rice in Brazil: impact of altering plant type and grain appearance. Paper presented at the Aerobic Rice Workshop. 7-8 September 2000, International Rice Research Institute, Los Baiios, Philippines.

De Datta SK. 1981. Principles and practices of rice production. Los Baños (Philippines): International Rice Research Institute. 618 p.

De Datta SK, Krupp HK, Alvarez EI, Modgal SC. 1973. Water management in flooded rice. In: Water management in Philippine irrigation systems: research and operations. Los Baños (Philippines): International Rice Research Institute. p 1-18.

Garrity D, Vejpas C, Herrera W. 1992. Percolation barriers increase and stabilize rainfed lowland rice yields on well-drained soils. In: Murty VVN, Koga K, editors. Proceedings of the International Workshop on Soil and Water Engineering for Paddy Field Management, 28-30 Jan. 1992. Rangsit (Thailand): Asian Institute of Technology. p 413-421.

George T, Magbanua R, Roder W, Van Keer K. Trebuil G, Reoma V. 2001. Upland rice response to phosphorus fertilization in Asia. Agron. J. 93:1362-1370.

George T, Magbanua R, Garrity DP, Tubaña BS, Quiton J. 2002. Yield decline of rice associated with successive cropping in aerobic soil. Agron. J. Under review.

Guimaraes EP, Stone LF. 2000. Current status of high-yielding aerobic rice in Brazil. Paper presented at the Aerobic Rice Workshop. 7-8 September 2000, International Rice Research Institute, Los Baños, Philippines.

IWMI (International Water Management Institute). 2000. IWMI global water scarcity study. Colombo (Sri Lanka): IWMI.

Jha KP, Dinesh Chandra, Challaiah. 1981. Irrigation requirement of high-yielding rice varieties grown on soils having shallow water-table. Indian J. Agric. Sci. 51:732-737.

Ladha JK, Fischer KS, Hossain M, Hobbs PR, Hardy B. 2000. Improving the productivity of rice-wheat systems of the Indo-Gangetic Plains: a synthesis of NARS-IRRI partnership research. IRRI Discussion Paper No. 40. Los Baños (Philippines): International Rice Research Institute. 31 p.

Lanceras MR, Laza M, Atlin GN. 2002. Improved upland rice cultivars perform well under low- and high-input management. Poster presented at the 32nd Annual Scientific Conference, Crop Science Society of the Philippines, Bohol, Philippines, 23-26 April 2002.

Li YH. 2001. Research and practice of water-saving irrigation for rice in China. In: Barker R, Li YH, Tuong TP, editors. Water-saving irrigation for rice. Proceedings of an International Workshop held in Wuhan, China, 23-25 March 2001. Colombo (Sri Lanka): International Water Management Institute. p 135-144.

Maclean JL, Dawe DC, Hardy B, Hettel GP, editors. 2002. Rice almanac. Third edition. Los Baños (Philippines): International Rice Research Institute. 253 p.

Mao Zhi. 1993. Study on evaluation of irrigation performance in China. In: Maintenance and operation of irrigation/drainage scheme and improved performance. Proceedings of Asian Regional Symposium, Beijing, China, 1993. p 6-35.

McCauley GN. 1990. Sprinkler vs. flooded irrigation in traditional rice production regions of southeast Texas. Agron. J. 82:677-683.

NIA (National Irrigation Administration). 1996. Annual report 1996. Manila (Philippines): NIA. 46 p.

Pingali PL, Hossain M, Gerpacio RV. 1997. Asian rice bowls: the returning crisis? Oxon (UK): CAB International, in association with IRRI, Los Baños, Philippines. 341 p.

Postel S. 1997. Last oasis: facing water scarcity. New York, N.Y. (USA): Norton and Company. 239 p.

Rosegrant MW. 1997. Water resources in the twenty-first century: challenges and implications for action. Food, Agriculture, and the Environment Discussion Paper 20. Washington, D.C. (USA): International Food Policy Research Institute. 27 p.

Shan Lin, Dittert K, Hongbin Tao, Kreye C, Yangchu Xu, Qirong Shen, Xiaolin Fan, Sattelmacher B. 2002. The ground-cover rice production system (GCRPS)—a successful new approach to save water and increase nitrogen fertilizer efficiency? In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production, Los Baños (Philippines): International Rice Research Institute. p 187-195.

Sharma PK, Ingram KT, Harnpichitvitaya D. 1995. Subsoil compaction to improve water use efficiency and yields of rainfed lowland rice in coarse-textured soils. Soil Tillage Res. 36:33-44.

Sharma PK, Lav Bhushan, Ladha JK, Naresh RK, Gupta RK, Balasubramanian BV, Bouman BAM. 2002. Crop-water relations in rice-wheat cropping under different tillage systems and water-management practices in a marginally sodic, medium-textured soil. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production, Los Baños (Philippines): International Rice Research Institute. p 223-235.

Singh AK, Choudury BU, Bouman BAM. 2002. Effects of rice establishment methods on crop performance, water use, and mineral nitrogen. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production. Los Baños (Philippines): International Rice Research Institute. p 237-246.

Tabbal DF, Bouman BAM, Bhuiyan SI, Sibayan EB, Sattar MA. 2002. On-farm strategies for reducing water input in irrigated rice: case studies in the Philippines. Agric. Water Manage. 56(2):93-112.

Thompson J. 1999. Methods for increasing rice water use efficiency. In: Rice water use efficiency workshop proceedings. Yanco (Australia): CRC for Sustainable Rice Production. p 45-46.

Tripathi RP, Kushawa HS, Mishra RK. 1986. Irrigation requirements of rice under shallow water table conditions. Agric. Water Manage. 12:127-136.

Tuong TP. 1999. Productive water use in rice production: opportunities and limitations. J. Crop Prod. 2(2):241-264.

Tuong TP, Bouman BAM. 2002. Rice production in water-scarce environments. In: Proceedings of the Water Productivity Workshop, 12-14 November 2001. Colombo (Sri Lanka): International Water Management Institute.

Wang Huaqi, Bouman BAM, Dule Zhao, Wang Changgui, Moya PF. 2002. Aerobic rice in northern China: opportunities and challenges. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production. Los Baños (Philippines): International Rice Research Institute. p 143-154.

Wei Zhang, Si-tu Song. 1989. Irrigation model of water-saving high yield at lowland paddy field. Seventh Afro-Asian Regional Conference. International Commission on Irrigation and Drainage, Tokyo, Japan, 15-25 October 1989. Vol. I-C. p 480-496.

Westcott MP, Vines KW. 1986. A comparison of sprinkler and flooded irrigation for rice. Agronomy 78:637-640.

Wickham TH, Singh VP. 1978. Water movement through wet soils. In: Soils and rice. Los Baños (Philippines): International Rice Research Institute. p 337-358.

Yang Xiaoguang, Wang Huaqi, Wang Zhimin, Zhao Junfang, Chen Bin, Bouman BAM. 2002. Yield of aerobic rice (Han Dao) under different water regimes in North China. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK, editors. Water-wise rice production. Los Baños (Philippines): International Rice Research Institute. p 155-163.

Notes

Author's address: International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines.

Acknowledgments: Dr. Shaobing Peng (IRRI), Professor Wang Huaqi (China Agricultural University), and Professor Yang Xiaoguang (China Agricultural University) participated in the field experiments and data collection on aerobic rice reported in this paper.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The IPM approach and lessons in China

Piao Yongfan and Chen Zhiqun

Since the Ministry of Agriculture and Forestry decided to make "integrated pest control with emphasis on prevention" a national principle of plant protection in 1975, remarkable progress in integrated pest management (IPM) has been achieved in China and various IPM technologies for different crops have also been developed. However, many IPM technologies remained mainly in laboratories in institutes and universities in the hands of scientists, researchers, and extension personnel, and only a limited number of IPM packages were translated into practices for pest control. Farmers were still not really involved in IPM, although they had a large potential role to play. With a change in public concern about environmental protection and food safety, people came to understand the importance of IPM. On the other hand, with the development and improvement in the marketing system and significant changes in farming systems, farmers in China nowadays have become independent in agricultural practices. IPM is not only a technical context for researchers and extension personnel, it is also a social issue for farmers regarding poverty alleviation, environmental protection, gender equity, human resource development, and the sustainable development of agriculture. It reminds us to think again critically about the questions, What is IPM? Where should IPM be used? How do we implement IPM? And who uses IPM? Significant achievements in farmer participatory IPM through the field and problem discovery-based agroecological approach provided sound evidence of the successful exploration of IPM based on new concepts and the realization that IPM examined these questions in China in recent years. The main points of view on farmer participatory IPM, lessons learned from the practices, and prospects of IPM are described in this paper.

In the past 30 years, through research and field implementation of integrated pest management, the concept of IPM has been developed along with a deep understanding of its meaning. It has developed from pest control to integrated pest control and from integrated pest management to sustainable management. The control target has shifted from one of the main crop pest species to each pest complex on a given crop, and to the whole agroecosystem. Pest control methods have developed from applying one specific technique to using various techniques in coordination. The control strategy has developed from relying on outside inputs to coordinating and managing complicated internal factors within the agroecosystem. The goal of pest management has also changed from reducing seasonal losses to long-term management, reduction of pesticide use, and sustainable development. Integrated pest management nowadays is not a pure technical context; it involves various aspects, such as critically thinking about what IPM is, who will carry it out, and where IPM should be used.

Technology development of IPM

The most important task for agricultural scientists in China during the 1970s and late '80s was to increase crop yield and reduce yield losses caused by pests to meet the food demand for the increasing national population through intensive pest control. Most Chinese farmers are smallholders having 0.25 hectare. In addition to labor and intensive inputs, crops receive heavy pesticide and fertilizer applications. This leads to negative economic, environmental, and social consequences, such as increased costs, risks of poison, and abundant residues of pesticides in agricultural products, underground water, and soil.

In the 1970s, the problems of environmental pollution, abundant pesticide residues, and pesticide resistance caused by the abuse of chemical pesticides drew much public attention. For instance, the consumption of organophosphates increased several times over that in the late 1950s and residues of organophosphates and organochlorines in water were above the national tolerance level by 425 and 1.5 times, respectively. Dichloro diphenyl trichloroethane (DDT) and benzene hexachloride (BHC) were restricted for use in pest control and integrated pest control became a principle of national plant protection work in 1975. Biological control of pests was regarded as the core of IPM at that time and researchers studied natural enemies, microbial agents, and antibiotic agents as the major components of biocontrol methods. With organization and management by General National Plant Protection, fundamental work and a national survey on the major species of natural enemies of major pests of 10 dominant crops took place from 1970 to 1981. Some 1,303 species of natural enemies of rice pests were identified as well as 850 species of natural enemies of cotton pests. In addition, the IPM research program has been continuously brought into line with the state research plan.

Since 1981, the Chinese government has put the IPM research program into four successive state five-year plans (from the sixth to ninth). This program is presided over by the Ministry of Agriculture, in which about 1,000 scientists from 50 units are engaged in three research areas: crop IPM, biological control, and pesticide resistance management. In the sixth five-year plan, each one of the main pest species (pathogens, insect pests, weeds, and rodents) was regarded as a research target. After exploring and practicing biological pest control, more and more researchers and extension personnel understood that it was very difficult to effectively control pests depending solely on biological control. Biocontrol should be one important component of IPM. Experience with biological control in pest control and ecologically based pest management have been accepted gradually. Cultural control, biological control, and chemical control are understood as the three components of IPM.

The national IPM research program

The concept of IPM for China was also defined at the Second National Scientific Conference on IPM in 1986. IPM is built on the relationship between pests and the environment. IPM relies on natural control factors to keep pests under the economic injury level (ETL) and obtain optimum socioeconomic and ecological benefits. The target of this strategy is not solely to get rid of pests; it uses various natural control techniques and reduces reliance on chemical pesticides. It maintains the ecosystem and ensures high environmental quality that humans depend on; hence, it is a long-term strategy that fits well with the stable development of agricultural production. The intention is to progressively achieve sustainable agriculture in China. In the seventh five-year plan, the target was changed to each pest complex on a given crop (rice, wheat, maize, or cotton). The comprehensiveness, systematics, and practices of research were evidently enhanced and IPM research in the eighth five-year plan was deepening and improving over that of the former five-year plan. Recently, IPM researchers have constructed IPM systems appropriate for each crop in given ecological regions.

IPM demonstrations

Practical IPM technologies include planting trap crops for certain insect pests, drying fields to control disease, controlling irrigation and fertilizer, breeding, and the selection of resistant crop varieties. In addition, the mass production of natural enemies has been emphasized again. Techniques of quality control in the mass production and field release of natural enemies have also greatly improved. Other important components of IPM, such as technology and knowledge of the reasonable use of chemical pesticides, including selecting the environment, natural enemies, and wide-spectrum pesticides, and changing nontarget field-wide sprays into selected spot sprays with an extremely low quantity, were developed and improved as well. Evidence from rice integrated pest control (management) from the 1970s to early ’80s and IPM implementation in rice in South and Southeast China indicated great progress. The implementation of IPM in the main rice area began in the late 1970s, after finding difficulties in pest problem-solving depending solely on biological control. Under the arrangements and management of the general national plant protection station of the Ministry of Agriculture, an integrated rice pest control project was implemented from 1980 to 1982 in the Yangtze River area and South China. Seven rice provinces—Zhejiang, Shanghai, Jiangsu, Anhui, Jiangxi, Hunan, and Guangdong—were involved. Varied pest control methods such as conserving and using natural enemies by restricting and banning the use of wide-spectrum and highly toxic chemical pesticides; selecting resistant varieties to control rice blast, bacterial disease, and other insect pests; and adequately managing irrigation and fertilization for healthy crop growth to increase rice compensation ability were integrated. With the implementation of the IPM project, IPM demonstration area expanded from 1.332 million hectares in 1983 to 5.98 million hectares in 1985. The pesticide cost per 500 kg of grain decreased from 4.39–5.79 yuan in 1980 to 1.79–2.87 yuan in 1984. Pesticide consumption in demonstration areas decreased from 1980 to 1984 by 46.8% in six provinces — Zhejiang, Hunan, Hubei, Jiangsu, Anhui, and Shanghai. In addition, organochlorine pesticide was stopped for use in rice in Zhejiang and Shanghai. The consumption of organochlorine pesticide has decreased dramatically in Hunan Province, but it was replaced by other kinds of pesticide in other main rice provinces.

For IPM in China at this stage, all its activities focus mainly on technical studies aimed at major pest species and crops carried out and applied in laboratory and field experiments in research institutes and universities. The potential role of farmers has not been stressed. The top-down extension system has been expanded to the township level nationwide for pest surveillance, forecasting, and coordinating pest control activities with the planned economy. However, after the economic reform, more and more farmers have been independent in terms of cropping pattern, cultivation, selection of seeds, and other agrochemical inputs. In other words, farmers worked their own land. Thus, the gap between the technology producers (researchers) and the receivers/adopters (farmers), which had existed earlier, has widened. Farmers still commonly spray pesticides. Outbreaks of brown planthopper and cotton bollworm are examples of a resurgence of crop pests induced by pesticides in the country. Outbreaks occurred in central and southern China in 1992 and in the Yellow River cotton zone in 1992-94.

Evolution of the IPM concept and lessons learned from practices

The large improvement in living standard and public concern about environmental protection have made more and more people understand the importance of IPM since the mid-1980s. In addition, with the development and improvement of the marketing system and significant change in farming systems after the late 1980s, farmers in China have become independent in agricultural practices. They decide to choose which crop to plant and mostly depend on market demand and information. They also decide how to manage their own land. Rice-based farmers need not only rice pest control technology but also the associated cultural practices, adequate fertilizer, irrigation technologies, and market information. No researchers or extension personnel could assume the farmers' role of decision-making. This reminds us that it is very important to improve farmers' agroecosystem knowledge, basic skills, and decision-making capability for IPM and sustainable development. In other words, it is very important to understand the different function of different participants in IPM. It is necessary that researchers and extension personnel work with farmers to understand the role of technology. Traditional extension work is not adapted to the real situation and faces new challenges. In addition, farmer empowerment and participatory training with IPM are new approaches to IPM development.

Agricultural extension

Agricultural extension is multidimensional and requires an understanding of science, technology, communication, local culture, and the role of social relationships in agricultural decision-making as well as human resource development. This means that extension agencies will have to strengthen linkages and coordination with research organizations, environmental agencies, educational institutions, NGOs, farmers' groups, and others who recognize that agriculture is sustainable only when it is ecologically sound and economically viable.

Farmer training and education

For farmer training and agricultural technology development, both formal and nonformal training are essential for improving food security and rural development by farmer involvement. Formal agricultural education is needed for the development of skilled manpower to serve the agricultural sector. Nonformal agricultural education is needed for the training of extension personnel and farmers in rural areas. To meet the challenges of agriculture, environmental protection, and human resource development in the 21st century, it is especially important to improve and strengthen communication and human capital in rural areas where the shortage of trained people is a major limiting factor. However, the training methods and curricula are not adapted to the new requirements of farmers. Furthermore, a critical need of farmer training is to examine the problems and issues of rural development and sustainable agricultural development, and to adapt the training system for nonformal education and farmer participatory research.

The FAO rice IPM program

China has carried out field-oriented and farmer-centered IPM training under the support of the FAO IPM program since 1988, which aims at training farmers in the field with IPM, and remarkable achievements have been made. Under the implementation of the FAO IPM program, the concept of IPM has changed from purely technical into an ecological management philosophy and systematic engineering in plant protection. Farmers were understood as having one of the most important roles in IPM, and ways to help farmers improve their agroecosystem knowledge and other skills were also defined. Therefore, the concept of IPM was expanded to cover (1) healthy cropping; (2) conservation of natural enemies; (3) weekly observations of fields for crop growth, pests, natural enemy population dynamics, and other organisms; (4) agroecosystem analysis instead of the traditional economic threshold level; (5) group discussion and farmer decision-making; (6) team-building and systematic planning; (7) IPM follow-up activities in the community; and (8) the effective use of limited natural resources for sustainable development. In addition, farmer empowerment and quality improvement are also important tasks of the program for supporting sustainable community development. From 1989 to 1997, farmer training activities of "training of trainers" (TOT) and "farmer field schools" (FFS) were conducted in 66 counties of 11 provinces, with differences in the reduction in sprays and pesticide quantities and increases in yield and net profit between trained and untrained farmers in results.

Table 1. Number of farmers in IPM training.

Year	FFS	No. of farmers	TOT	No. of trainers	FTOT	No. of farmers
1999	455	13,111	2	62	17	492
2000	469	13,870	3	90	42	1,260
2001	443	14,056	3	90	42	1,260
Total	1,367	41,037	8	242	101	3,012

From 1998 to 2001, during phase IV of the FAO IPM program (community IPM), different participatory IPM training activities of TOT, FFS, FTOT ("farmer training of trainers"), and RTOT ("refresher TOT") were conducted in 47 counties of the six main rice provinces of Guangdong, Sichuan, Hubei, Hunan, Anhui, and Zhejiang. The training scenario is presented in Table 1.

The farmer field school

The farmer field school as the most important nonformal farmer training model in community IPM represents learning by doing as a participatory farmer training process, a farmer-centered approach, agroecosystem-based and community development training, and the exploration of new roles of extension personnel in the country. As a result, it is seen as an effective way to empower farmers and as an effective farmer training approach to help farmers understand their agricultural ecosystem, the principles and concepts of IPM, ecological knowledge, teamwork, systematic planning, and other skills through activities. FFS training focuses on the following:

The field is the primary learning resource. All learning activities take place in the field and are based on observations of what is happening in the field.

Practical experience forms the basis for learning based on one's own decisions. The activities that take place in the field and on farms form the basis for discussions and analysis by farmers who arrive at concepts they test and improve through further field activities.

Decision-making exercises guide the learning process. Training focuses on the analysis of the agroecosystem of the rice crop. The combination of analytical methods, ecological principles, and basic IPM methods helps farmers obtain insights into ecological interactions in the field and provides them with greater confidence in making crop and pest management decisions.

Training lasts the entire cropping season. Farmers understand the IPM relevant to each growth stage of the crop and the natural enemies as well as the factors that influence the decision-making at all stages of plant growth.

The training curriculum is based on real local situations of the FFS. The FFS curriculum and materials are prepared based on their appropriateness, local conditions, problems discovered, and the needs of farmers highlighted in the FFS.

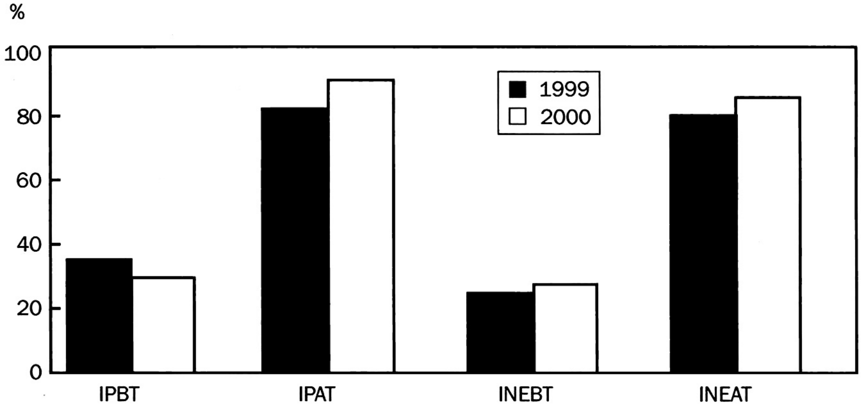


Fig. 1. Recognition of pests and natural enemies. IPBT = identification of pest before training, IPAT = identification of pest after training, INEBT = identification of natural enemy before training, INEAT = identification of natural enemy after training

Benefits from participatory farmer IPM training

With the implementation of the FAO IPM program, great ecological, economic, and social benefits have been achieved and farmers have been trained to understand their agroecosystem much better than before. Some 845 FFS farmers were sampled in 1999 and 838 in 2000. Figure 1 shows the differences in identification of pests and natural enemies before and after IPM training. With the improvement of agroecosystem knowledge, pesticide use and the cost of pest control declined significantly and rice yield and income increased after IPM training. Some 350 and 595 trained farmers and 200 and 210 nontrained farmers were sampled in different provinces in 1999 and 2000, respectively, and Figure 2 shows the differences between IPM and non-IPM farmers.

As was mentioned above, farmers are more independent in China now than in the past. They decide what crop to cultivate on the basis of their own information needs and technologies. To meet the demands of farmers, training activities of the rice-based community IPM program did not focus only on the rice crop; the activities were also extended to other cash crops, such as tea, vegetables, citrus, chrysanthemum, melon, peanut, and others. In total, 168 FFS were carried out on cash crops and 78 women's FFS and 81 trained farmer-led FFS were also conducted in 2000 and 2001. The economic profits and ecological benefits from IPM training on cash crops were significant. Figure 3 (58 trained and 28 nontrained farmers in 1999) shows the dramatic reduction in pesticide sprays on chrysanthemum after IPM training in Shexian County, Anhui Province.

IPM with farmers is not just for training them; it helps them to shift from being recipients of IPM to instigators on the way to sustainable IPM development. IPM follow-up activities such as farmer groups, IPM alumni associations, and IPM production demonstrations proved that the training of trainers and training of farmers

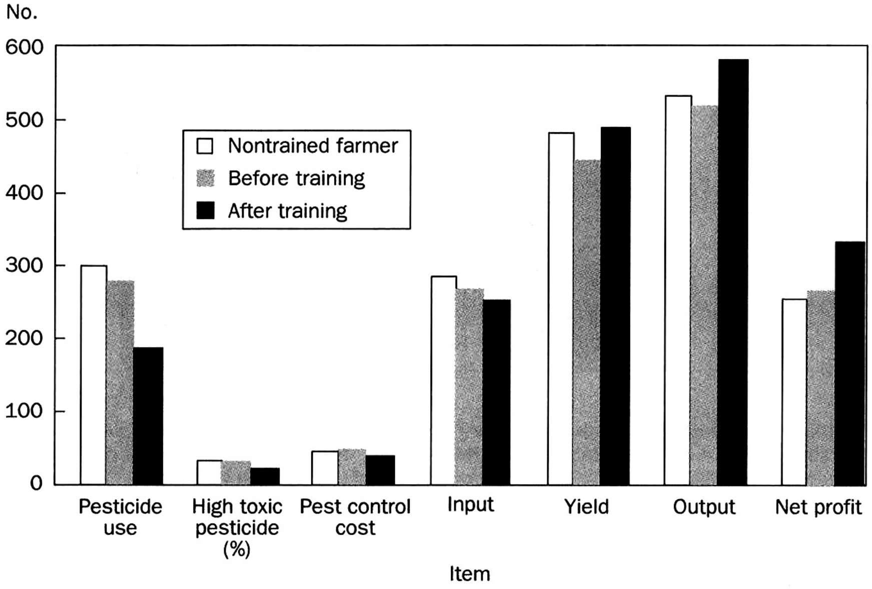


Fig. 2. Pesticide use and economic benefits.

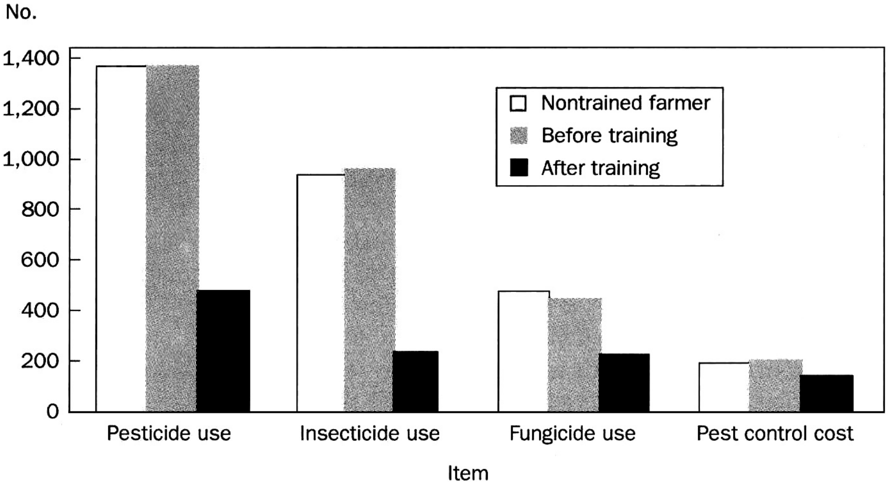


Fig. 3. Change in pesticide use of chrysanthemum farmers.

could be successful in empowering farmers to be confident of IPM and to enrich its context. Through the follow-up activities, the impact of IPM rapidly expanded to other farmers through farmer-to-farmer training, information sharing, exchange of experiences, and group dynamics. Some 624 farmer groups and IPM alumni associations were established with the support of trained facilitators in different townships, counties, and provinces. Members of farmer groups and IPM alumni associations regularly discuss local problems and possible solutions through participatory discussions. One of the critical indicators of successful activities concerning farmers and their interest is the increase in net profits. Focused on increasing farmers' income and market demand with an increase in living standards, a follow-up project on producing IPM agro-products began in 1999 in Sichuan Province. IPM rice, tea, longan, and chrysanthemum, etc., are available in the market and prices are 20-30% higher than for other crops. This attracted more and more farmers to become actively involved in IPM training in FFS. It also gave them access to and nearness to profitable markets with ecologically friendly products as "fruits" of their new efforts. With the demand of the market and the development of IPM products, the first supermarket of IPM products opened in Chengdu City, Sichuan Province, in August 2001.

In addition, with the great change in the labor structure in agriculture, the role of women in agriculture and the community has been widely recognized in the country. Women's power and opportunities for decision-making either in family life or in farming have increased significantly in recent years, while most male labor moves toward seeking jobs in cities and towns. This implies that it is important for the FFS to involve women in IPM. A women's FFS began in Mianzhu City, Sichuan Province, in 1999. Now, more and more women are involved and interested in participatory IPM training. Training has been conducted continuously in Sichuan, Guangdong, Hubei, and Anhui provinces. The number of female participants in IPM training increased rapidly in 2000 and 2001 in China. In Xinshi Town, Mianzhu City, Sichuan Province, seven women's FFS were carried out at the same time in 2001. All the participants were active in the FFS. This caused the local government to assign a special fund to support FFS for women. After most female farmers in Jinlan village, Sichuan Province, were trained, recognition as the "first national IPM village" was given to the village in 2001.

In addition to rice, cotton is another successful crop in the implementation of IPM in China. The FAO/EU cotton IPM program started in 2000 in China and four training of facilitators (TOF) events and 140 FFS were conducted in 11 counties of Shandong, Henan, Hubei, and Anhui provinces. Pesticide sprays declined by about one half in the IPM demonstration area.

What should be involved in IPM?

What is IPM? There could be lots of explanations. But at least one meaningful answer through the abovementioned IPM practices has been realized and accepted by IPM farmers, facilitators, and consumers to some extent. It is related to technology, pesticide, and yield and to methodology, policy, and people. The farmers' roles and contri butions to IPM have been discovered and emphasized through the FFS, and the position of IPM implementation has been shifted from researchers and extension personnel to farmers. FFS have put farmers at the core of IPM. From this point of view, farmer-centered, agroecosystem-based, and participatory research and practices as well as positive and intensive interactions among policymakers, researchers, facilitators, and IPM farmers could be the best answer to the question of where IPM should be located and who should carry it out and how it could be implemented.

Future strategy of IPM development

At first, the traditional methodology of linkages among research, education, and extension agencies resulted in systematic “bottlenecks” in national IPM development and limited its effectiveness in contributing to sustainable development. Linkage issues and encouraging mechanisms should be explored in various ways.

In addition to farmer participatory IPM practices, a reorientation of extension mechanisms, a stronger operational IPM policy, and strict control of agro-chemicals as well as market development of residue-free crop products will mobilize IPM and the sustainable development of agriculture.

Third, to meet the challenges of agriculture, environmental protection and human resource development are especially important for improving and strengthening the human capital of farmers for development in rural areas where the shortage of trained farmer resources is a major factor limiting development. Traditional farmer training methods and curricula are not adaptable to the new requirements and farmer demands, and these problems were found to still be common to all in agriculture.

Fourth, policy support to IPM is important for its implementation and development. IPM should be included in legislation and regulations related to agroecosystems and environmental protection for sustainable development. Prohibiting and restricting the use of certain pesticides are directly related to reducing the risk of pesticides to the environment and human health.

References

Guo Yuyuan. 1999. Research progress in plant protection and plant nutrition. Situations of the research on reducing crop pest disasters in China. China Agriculture Press. 4 p.

Piao Yongfan. 1999. Research progress in plant protection and plant nutrition. Sustainable development of IPM in China. China Agriculture Press. 10 p.

FAO. 2002. Ten years of IPM training in Asia, from farmer field school to community IPM. Bangkok (Thailand): FAO Regional Office for Asia and Pacific.

Notes

Author's addresses: Piao Yongfan, Agriculture Department, Ministry of Agriculture, 11 Nongzhanguannanli, Chaoyang District, Beijing 100026; Chen Zhiqun, National Agro-Technology Extension and Service Center, Ministry of Agriculture, 20 Maizidian Street, Chaoyang District, Beijing 100026, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Ecological benefits of diversification

M.R. Finckh

Within agricultural systems, the ecological benefits of diversification include (1) reductions in diseases, insects, and weeds, (2) greater yield stability, and (3) improved soil fertility and structure and erosion control. In addition, within diversified systems, coevolutionary processes are encouraged, which allow for the development of new combinations of characteristics and specific adaptations to the diversified systems themselves. This results in the conservation and development of genetic resources almost as a side-effect of diversification.

Disease reductions and yield stability are the most important reasons that growers grow cultivar and species mixtures. But also effects on soilborne diseases, weeds, and insects, soil fertility, lodging, and better overwintering survival of plants are commonly reported.

While biodiversity is considered ecologically beneficial in itself, growers have limits to the tolerable diversity that is practical and there is a need to identify and select for *functional diversity.* The best strategy for obtaining good functional diversity may be to produce genetically heterogeneous cultivars. However, this has to be done with great care. For example, diversity to buffer against stresses will be useful, whereas diversity for quality traits within a field or variety is not desirable in agriculture. Concerns also exist, often unfounded, that product quality such as brewing and baking quality may be affected adversely by mixing. However, when breeders, growers, and processors work together, such obstacles can be overcome.

In *The Origin of Species,* Darwin (1872) dedicated the first two chapters to the topics of variation under domestication and variation under nature. He recognized the great potential and value of biological diversity for evolution but also for human use and he also recognized the crucial role of humans in the creation of diversity. It is fascinating to read texts by authors such as Darwin and Humboldt from the 19th century, in which they not only describe the wonders of nature but clearly recognize diversity as one of the important resources of nature and the capability of humans to increase or destroy diversity at will.

One major outcome of human activity in the domestication of plants and animals until the end of the 19th century was a marked increase in the diversity of domesticated species (Darwin 1872). In addition, agricultural activities have led to the creation of many specific habitats influenced by humans such as pasture communities and ruderal plant communities and, within these habitats, noncultivated plants and animals have also diversified (e.g., orchids in nutrient-poor pastures in Europe and many weeds) (Mueller-Dombois and Ellenberg 1974).

Over the past 30 years, the value of biological diversity for the maintenance of our crops and domesticated animals has been widely recognized (e.g., Fowler and Mooney 1990, Harlan 1972, 1975, 1992, Mooney 1997, Vellve 1992), but only a few have dared to give monetary value to diversity (e.g., Pimentel et al 1997). Breeding programs rely on the diversity of genetic resources and much of the diversity found in cultivated plants and animals is the result of continuous selection by humans over long periods of time. While the benefits of diversity to breeders are easily understood, a whole array of ecological benefits to diversity and thus to the diversification of agricultural systems awaits more systematic exploitation.

Historically, agricultural systems were based on crop varieties and landraces that were genetically heterogeneous because of natural selection, random events, and some conscious selection by humans. Diversity probably reached a peak after the 17th century when many crops were distributed and adapted worldwide and the value of leguminous pasture crops was recognized, which added a whole array of them. However, from the middle of the 19th century on, plant breeding, mechanization, and other factors such as inorganic fertilizers, pesticides, and transportation developed. All these factors made it possible to develop cropping systems based on monoculture within fields and sometimes within regions. This development has contributed to weeds, pests, diseases, and some other environmental problems in many ways and it has also resulted in a dramatic loss of agricultural and natural genetic diversity worldwide (e.g., Harlan 1972, Fowler and Mooney 1990).

This paper focuses on the ecological benefits of diversity in agricultural systems, on which much research has been conducted. First, I will outline the possibilities by which diversification can be achieved. Second, I will discuss the mechanisms by which diversification can contribute to the functioning and stabilization of systems, underpinned with a description of the diverse rice agroecosystem in Bhutan. Finally, I will discuss possible constraints to diversification strategies in current agricultural systems and some approaches to solutions.

Diversification strategies

Diversity can be achieved at the level of species or within species and over time (Table 1). Monoculture usually refers to the continuous use of a single crop species over a large area and often over time. When considering pests and pathogens, the definition of monocultures has to be refined to differentiate among species, variety,

Table 1. Possibilities for diversification in space and time (expanded from Finckh et al 2000).

Level of uniformity	Possibilities for diversification
Diversification in space	
Species	Arrangements among and within species, varieties, and resistances using intercropping
Variety	Arrangements among and within varieties and resistances, includes variety mixtures, multilines, and populations
Resistance gene	Arrangements among resistance-multilines and populations
Diversification in time	
Crop rotation	Use of cropping sequences to break disease cycles and improve soil fertility
Relay cropping	Intricate timing of crops within a season, thereby reducing crop-free times (partial intercropping)

and resistance-gene monocultures (Finckh and Wolfe 1998). Within a species, diversity with respect to pests and diseases and ecological requirements can be achieved by using different varieties. However, different varieties often possess the same resistances or susceptibilities to certain pests and diseases. In this case, the use of different varieties may not increase resistance-gene diversity. For example, this was the case in the 1840s, when *Phytophthora infestans,* the causal agent of potato late blight, was introduced to Europe. While many different potato varieties were grown, none possessed resistance to late blight and thus, effectively, there was a monoculture of susceptibility to late blight, leading to devastating epidemics.

The most common means of diversification is diversification over time through crop rotations, that is, the planned change of crops for the management of soil fertility and plant health.

All successful diversification strategies have in common that the aim is functional diversity, that is, diversity that is designed to make use of knowledge about ecological interactions in a system to improve its performance with respect to sustainability and productivity.

Ecological benefits of diversity: mechanisms

Within agricultural systems, the ecological benefits of diversification include (1) reductions in diseases, insects, and weeds, (2) greater yield stability, and (3) improved soil fertility and structure and erosion control. In addition, within diversified systems, coevolutionary processes are encouraged, which allow for the development of new

Table 2. Mechanisms by which diveristy may affect pathogens, insect pests, and weeds of importance (Andow 1991, Liebman and Dyck 1993, Wolfe and Finckh 1997).

Mechanisms reducing disease

- Increased distance between susceptible plants
- Barrier effects of intercrop
- Induced resistance
- Selection for most resistant and/or competitive genotypes
- Interactions among pathogen strains on host plants
- Allelopathic effects of plants on pathogens

Mechanisms reducing insect pests

- Enhancement of natural enemies
- Reduction of host density (reduced resource concentration)
- Reduction of plant apparency (visual or olfactory cues reduced)
- Alteration of host quality (with respect to the insect pest) through plant-plant interactions

Mechanisms reducing weeds

- Reduction of bare soil and layering of crops increase competition
- Variation in tillage needs and operations of intercrops may disturb weeds
- Allelopathic effects

Other beneficial interactions

- Yield enhancement through niche differentiation of hosts
- Compensation for yield losses by less affected hosts
- Better soil cover with intercrop (soil and water conservation)
- Improved soil microbial activity and fertility

Possible unwanted interactions

- Weeds may serve as alternate hosts for pathogens and insects
- Interactions among virus vectors and weeds
- Greater difficulty in specifically reducing weeds with herbicides or mechanically
- Microclimatic effects may enhance certain problems

combinations of characteristics and specific adaptations to the diversified systems themselves.

Effects of diversification on diseases, insects, and weeds

Pathogens, insect pests, and weeds differ fundamentally in their biology and their effects on crops, and different protection mechanisms act with respect to these organisms (Table 2).

Pathogens. Pathogens are mostly dispersed through wind, splashing water, soil, and animals (vectors). In diversified systems, where either plants of different species or plants possessing different resistances are grown in a close neighborhood, the most important mechanisms for disease control are mechanical distance and barrier effects. In addition, resistance reactions induced by avirulent pathogen strains may prevent or delay infection by virulent strains. A large percentage of the reduction in airborne diseases such as the powdery mildews and rusts in cereal cultivar mixtures has been shown to be due to induced resistance (Finckh et al 2000). The protection mechanisms are universal with respect to airborne, splashborne, and some soilborne diseases. Mixtures of plants varying in reaction to a range of diseases will lead to a multitude of additional interactions and the overall response in such populations will tend to correlate with the disease levels of the components that are most resistant to these diseases. In addition, less affected plants may compensate for yield losses because of reduced competition from diseased neighbors (Finckh and Wolfe 1998).

Variety and species mixtures have been shown to reduce diseases in many experimental studies (see Finckh et al 2000 for review). An aspect that cannot be easily explored in field experiments is scale effects on mixture efficacy. By reducing disease, mixtures reduce inoculum within the field and the region. This implies that, with increasing area grown to mixtures, inoculum pressure should be reduced and the effects of mixtures increased. These effects are likely to work only on a large scale. There are two occasions in which these effects are likely to have played a role in enhancing mixture effects. The first was the practice in the former East Germany of producing spring barley as variety mixtures. The percentage of the barley crop sown to variety mixtures in the former East Germany increased from 0 to 92% from 1980 to 1990, while mildew incidence declined by 80% and fungicide use also declined by 80% (Wolfe 1992). Similar reductions in mildew severity were not observed in neighboring countries, where mixtures were not widely used. More recently, rice variety mixtures have been planted in contiguous rice fields containing 812 and 3,342 ha in 1998 and 1999, respectively. Pure-stand controls replicated throughout the region of diversification indicated that variety mixtures decreased blast severity on susceptible varieties by an average of 94% (Youyong et al 2000 and this volume).

The most common diversification strategy in agriculture is not the mixing of species or varieties but the use of diversification over time, that is, crop rotations. While crop rotations are a fundamental tool for soil fertility management (see below), especially in the absence of chemical plant protection, they are essential in crop health management strategies. Crop health can be affected in various ways through rotation. These can be divided into (1) time effects, (2) indirect effects via soil microbial activity, and (3) direct suppressive effects of certain crops on certain pathogens.

(1) Many pathogens overseason in the soil or on crop residues and there is a time limit to how long they can survive in the absence of their hosts. Examples of such pathogens are *Sclerotinia sclerotiorum, Rhizoctonia solani, Fusarium* spp., *Gaeumannomyces graminis, Pseudocercosporella herpotrichoides, Ascochyta* spp., etc. Often, a period of two to four years is sufficient to reduce inoculum to a level to allow for the production of a healthy crop.

(2) Soil microbial activity and diversity contents are enhanced by green manure crops and periods in grass-clover mixtures (Table 3, Vilich and Sikora 1996). While the presence of a pathogen is required to cause disease, the absence of a pathogen is not necessarily required for a healthy crop. In fact, it is the balance between beneficial and detrimental organisms that often determines the outcome. Suppressive soils are a prime example for this. A soil is considered suppressive if, despite the presence of a pathogen, a susceptible crop does not become diseased or becomes less diseased than expected. Suppressive soils have been found in connection to

Table 3. Biomass carbon contents in the top 23 cm of soil in a long-term experiment in Rothamsted (Cook and Baker 1983, p 245).

Management	kg biomass carbon ha^{-1}
Continuous wheat	530
Wheat plus inorganic N	590
Wheat plus manure	1,160
Pasture	2,200
Woodland	1,960

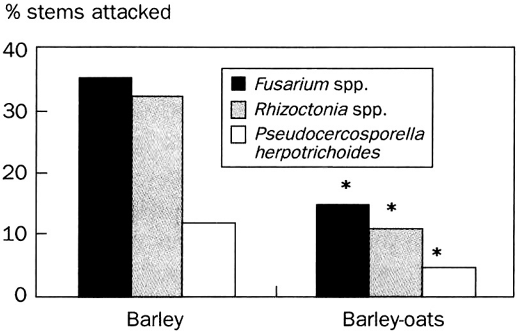


Fig. 1. Effects of oats on foot diseases of barley when grown in species mixtures (adapted from Vilich-Meller 1989).

many diseases of temperate and tropical crops and one of the most prominent examples is described for avocados in Australia by Cook and Baker (1983). Many of the suppressive effects of composts are due to the multitude of beneficial microorganisms that are involved in the decomposition processes. In general, with increasing active microbial biomass in the soil, the sink function of the soil for C, N, and energy increases. Parallel to this, the probability that an essential nutrient that is produced by a host will be present in sufficient amounts for a pathogen will decrease (Cook and Baker 1983).

(3) Certain plants may affect pathogens by secreting compounds that are directly detrimental to pathogens or that stimulate pathogen propagules to germinate in the absence of their host. Catch crops are plants that can be infected by a given pathogen but that do not allow the pathogen to reproduce in them. This can effectively reduce soilborne inoculum. An example is the wild *Solanum* species *Solanum sisymbriifolium* that can serve as a catch crop against potato cyst nematodes (*Globodera* sp.) (Scholte and Vos 2000).

Oats reduce *Fusarium* and other foot diseases of cereals when intercropped or when used as precrops (Vilich-Meller 1992) (Fig. 1) and they are allelopathic to

Table 4. Effects of precrops and fungicides on joint severity Of *Drechsiera tritici repentis, Septoria tritici,* and *S. nodorum* on the wheat variety Apollo in an experiment in southern Germany (data from Odörfer et ai 1994).

Precrop	% Diseased leaf area		Yield (t ha^{-1})	
	No fungicide	Fungicide	No fungicide	Fungicide
Winter wheat	43		4 6.77	7.67
Broad beans	5	0	8.76	10.02
Winter rape	5	0	7.98	8.69
Maize	13	0	7.43	8.26
Red clover	7	1		8.399.38

many weeds. While allelopathic effects and disease suppression are often observed in the genus *Avena,* these effects are species- and even cultivar-specific and interactions with fertility management have been reported (Elmer and LaMondia 1999).

A second genus that has broad beneficial effects on soil health appears to be *Brassica.* Thus, using a precrop of broccoli was as effective in controlling *Verticillium* infections in cauliflower as chloropicrin and only somewhat less effective than metham sodium applications to the soil in an experiment in California (Subbarao et al 1999). Cover crops of mustard (*Sinapis alba*) have also been shown to reduce take-all infections (caused by *Gaeumannomyces graminis*) in subsequent wheat crops (Kirkegaard et al 1998) and 90% to 95% reductions in nematodes (*Meloidogyne* spp.) in vegetable production have been achieved by planting *Tagetes* species (*T. erecta, T. patula*) (Lung et al 2000).

While in organic farming rotations are an absolute must, even in conventional farming they play an important role. For example, it has been found that control of several cereal diseases cannot be achieved by fungicides alone; only in combination with crop rotations could maximum yields and crop health be achieved (Table 4).

One of the most spectacular examples of the effects of neglecting crop rotations is provided by the disastrous epidemics of *Fusarium* in the American Midwest during the 1990s. The typical crops in the region are wheat and maize, which are both susceptible to *Fusarium culmorum* and *F. graminearum.* The pathogen may overwinter on crop residues or be spread via the seed. Although seed is routinely fungicide-treated, the use of minimum tillage practices to reduce soil erosion and conserve energy allowed for residues to stay intact between crops and for a huge amount of soilborne inoculum to build up. During several years in the 1990s, the weather was particularly conducive for development of the pathogen in the Dakotas and other midwestern states and losses from yield reductions and, more importantly, mycotoxin contamination of wheat skyrocketed (McMullen et al 1997). It is interesting to observe that soilborne *Fusarium* is not usually a problem in organic farming because of crop rotations, incorporation of crop residues in the soil, and often higher soil microbial (Vilich and Sikora 1996) earthworm activities (Stephens et al 1994), all leading to a reduction in inoculum. In contrast, however, seedborne infection with *Fusarium* has to be taken much more seriously in organic farming than in conventional farming as no fungicides or effective alternatives for seed treatment against *Fusarium* infection are available.

Insects. In contrast to pathogens for which passive or vectored dispersal is the norm, insects often search actively for their hosts and behavioral, visual, and olfactory cues play an important role. While environmental factors and landing on a nonhost are probably the most important mortality factor for pathogens, natural enemies are at least as important for insect population dynamics (Andow 1991, Letourneau 1997). Host dilution may affect an insect's ability to see and/or smell its hosts. Some hypotheses for the mechanisms of interaction have been proposed (Altieri and Letourneau 1982, Andow 1991) (Table 2).

The natural enemies hypothesis states that predators and parasites are more effective in complex environments because diversity of prey and alternative food sources and microhabitats are greater, allowing for the persistence of generalized natural enemies. Specialized natural enemies, moreover, are less likely to fluctuate because their prey can escape extinction more easily and should therefore provide a more continuous food source even if they are less abundant (Andow 1991). The importance of natural enemies was often recognized only after insecticide applications induced pest resurgence because of the destruction of natural enemy populations. Intercrops and weeds can therefore play can important role in regulating insect pests.

The resource concentration hypothesis (Root 1973) was formulated because insects are more likely to find and remain on their hosts in uniform and concentrated patches than in mixed stands, which was confirmed in experimental studies (Risch et al 1983). Also, interactions among the host components of a species mixture may physiologically affect the suitability of the host plants as a food source (Vandermeer 1989). In general, it appears that a lack of resource concentration is more important than are natural enemies in polycultures. However, the mechanisms work in opposite directions in some cases (Andow 1991).

Associational resistance refers to the reduced herbivore attack that a plant experiences in association with genetically or taxonomically diverse plants and is part of a plant's defensive system (Price et al 1980, Andow 1991). Thus, the concept of diversification for the control of insect pests must go beyond the mixing of resistant cultivars or isogenic lines. Deliberately retaining weeds in fields or planting borders to plant species that support natural enemies, as proposed by Altieri and Letourneau (1982) and others, could thus be understood as the deployment of associational resistance.

Weeds. Weeds usually are early successional plants adapted to colonize open, nutrient-rich spaces. Intercrops, especially cover and mulch crops, compete directly with weeds for these spaces and also for light. Because many weeds are adapted to certain crops and cropping patterns, changing these patterns (e.g., rotations) and management operations connected with different kinds of crops within the same field may make it difficult for weeds to cope (Liebman and Dyck 1993, Liebman and Gallandt 1997). An important consideration is that plants may be weeds during only certain phases of crop development. At other stages, the presence of the same "weeds" may be beneficial because they may provide food and habitat for beneficial insects and erosion control.

However, it is important to keep in mind that weeds may serve as alternative hosts for insect pests and pathogens and that insects often are disease vectors, especially for viruses that may reside symptomless in certain weeds (Table 2).

Competition for nutrients, space, light, and water is an important factor in the control of weeds within a given season and recommended planting densities are often a reflection of the need to suppress weeds. In the context of rotation, such direct competitive effects are only of importance for preventing the buildup of weed seed banks over time and the use of a competitive crop in the rotation may be directly related to weed control considerations. In addition to direct competitive effects, allelopathy and direct pathogen suppressive effects of certain plants may play an important role.

Yield stability

The most important interactions occurring in plant populations are compensation and competition, both of which influence yield and yield stability.

In the absence of disease, cultivar mixtures usually yield similar to or slightly more than the mean of the pure stands (Finckh and Wolfe 1998). Yield increases in genotype mixtures may be explained at least partially by niche differentiation among the components. Allelopathy and synergisms of unknown origin might also play a role. In addition to simple compensation, protection from cold and lodging has been reported (Finckh et al 2000).

In species mixtures, niche differentiation is an even more prominent feature. In almost all cases reported, the overall yield of species in mixtures exceeds the mean of the species grown in monocultures, that is, the *land-use efficiency* is increased (Liebman 1995).

In the presence of disease, mixtures of cultivars frequently yield more than the mean of the components grown as pure stands (see Finckh et al 2000 for review). Although the correlation between disease severity and yield is often clear in pure stands, it is not always so in mixtures. This is because the correlation between disease severity and yield on individual mixture components is often poor (Brophy and Mundt 1991, Finckh and Mundt 1992, Finckh et al 2000). Thus, there may be underlying interactions among component cultivars that can be modified depending on the amount of disease on those components.

Since different cultivars and species tolerate different ranges of environmental variation, it is logical to expect that a mixture of cultivars or species will be more stable in yield than any of the components. Yield stability is considered to be one of the main advantages of cultivar mixtures (Wolfe and Barrett 1980). In practice, the definition of yield stability is high yield over a range of environments (review in Finckh and Wolfe1998). Within large data sets, the variance of the mixture is usually less than that of most, if not all, of the components (Allard 1960, Finckh et al 2000).

Such gains are not, of course, automatic. The environment plays a crucial role together with the appropriate choice of system and variety. The choice of system

Table 5. Problem factors in agriculture and how they can be improved by crop rotation.

Problem factor	Possible ways that rotation can improve the problem
Soil physical properties	Tillage practices, root morphology, soil cover
Soil chemical properties	Plant effects, fertilizer effects
Soil erosion	Improved soil structure, soil cover
Weed problems	Tillage practices, crop morphology, competitive and allelopathic effects
Crop health	Time effects, suppressiveness of crops, enhancement of soil microbial activity

depends on being able to minimize competition and maximize facilitation. An example of facilitation is the benefit often found from intercropping grass species with legume species where the latter frequently supply nitrogen to the former.

Improved soil fertility and structure and erosion control

To properly manage nutrients with crop rotation, many factors have to be considered. For example, when potatoes follow wheat, a relatively long time elapses between the two crops, resulting in potential problems with weeds, nutrient losses, and soil erosion. Therefore, an important component of crop rotation is the use of cover and catch crops and green manure crops that also add to weed and erosion control and prevent nutrient leaching over winter.

If applied properly, crop rotations can reduce problems in agriculture in many ways (Table 5) and many of these effects are achieved simultaneously. Changes in tillage practices according to crop from year to year affect the soil physical structure and nutrient mineralization. Because many weeds are adapted to certain soil conditions and types of disturbances, changes in the disturbance patterns contribute to weed control. For example, the digging and turning of the soil in connection with a root crop such as potato may reduce weeds sensitive to deep soil disturbances. Other weeds, however, may be favored by such activities. One of the most important means of controlling weeds such as thistles and quack grass is the use of two years of grass-clover mixtures with regular mowing. At the same time, pasture and grassland reduce soil disturbance and soil organic matter and earthworm activity increases (Table 3).

Leftover roots from precrops may directly increase soil friability and add organic matter. Organic matter, in turn, provides nutrients for soil microbes that are often involved in the attack and breaking down of pathogen propagules in the soil.

The use of species mixtures often has similar beneficial effects on soil fertility and, in addition, greater effects on erosion and weed suppression. However, if species mixtures are used in rotations, care has to be taken about soilborne diseases. For example, if cereals are mixed with peas or beans, a break of at least four years is required before legumes susceptible to *Ascochyta* spp. can be grown again.

The functioning of a diverse rice agroecosystem in Bhutan

Although the beneficial effects of diversification have been demonstrated on many occasions in experimental studies or in large-scale agriculture (see above), one of the more intriguing questions is how diversity has evolved naturally and possibly contributes without conscious human action to the stability of agricultural systems. To study this, it is necessary to investigate intact indigenous agricultural systems that have not been influenced by modern varieties. The traditional rice agroecosystems in the Himalayan kingdom of Bhutan from 1,200 to 2,600 m altitude are largely free of modem varieties and offer a unique opportunity for such a study. A multitude of rice landraces are grown in Bhutan in many more or less isolated valleys and, depending on the altitude and year, may suffer more or less from rice blast (Thinlay et al 2000a,b). Panicle blast outbreaks, caused by *Pyricularia grisea,* occur occasionally in isolated valleys in the high altitudes above 1,800 m, causing almost complete yield loss. In the lower regions, seedling blast is observed almost year-round, sometimes destroying seedlings. However, damage on adult crops is usually moderate to low (Thinlay et al 2000b). The pathogen was found to be highly variable for molecular and virulence markers with clearly more, and more complex, virulences in the more conducive climate below 1,800 m altitude than in the high altitudes. The wider and more complex spectrum of virulences is mirrored by a wider and more stable spectrum of resistances in the local landraces, indicating that blast represents a selective pressure in the system (Thinlay et al 2000a,b). Not surprisingly, the landraces in Bhutan varied in resistance among and within accessions, indicating genetic heterogeneity within the self-fertile rice crop.

To determine if the heterogeneity for resistance within landraces was due to simple mixing and varietal impurities, 25 single heads each were selected and propagated from two landraces, resulting in two sets of 25 populations (Thinlay 1998). If heterogeneous reactions within a landrace are due to varietal impurities, that is, mixtures of different varieties that are the result of inbreeding themselves, then each single head progeny should react homogeneously to a given isolate. If, however, the reactions to an isolate are variable among the progenies of a single head itself, this suggests that heterozygosity exists and thus outbreeding is ongoing within the landrace.

The landraces themselves and the single-head progenies were tested for their reactions to a set of 14 blast isolates representing the wide virulence spectrum within Bhutan. At least 40 plants per population were inoculated with each isolate. Fully resistant reactions were given a score of 1 and fully susceptible reactions a score of 3. Intermediate reactions were scored 2. Taking the mean of all scores resulted in a reaction index from 1 (all plants resistant) to 3 (all plants susceptible). Intermediate scores indicated variable reactions among the 40 plants tested.

The landrace Tan Tshering reacted almost completely resistant to blast, suggesting at first a homogeneously resistant variety (Fig. 2A). However, within some of the single-head progeny populations, reaction indices were as high as 1.5 because of mixed reactions. This indicates that the single-head progeny segregated for resistance

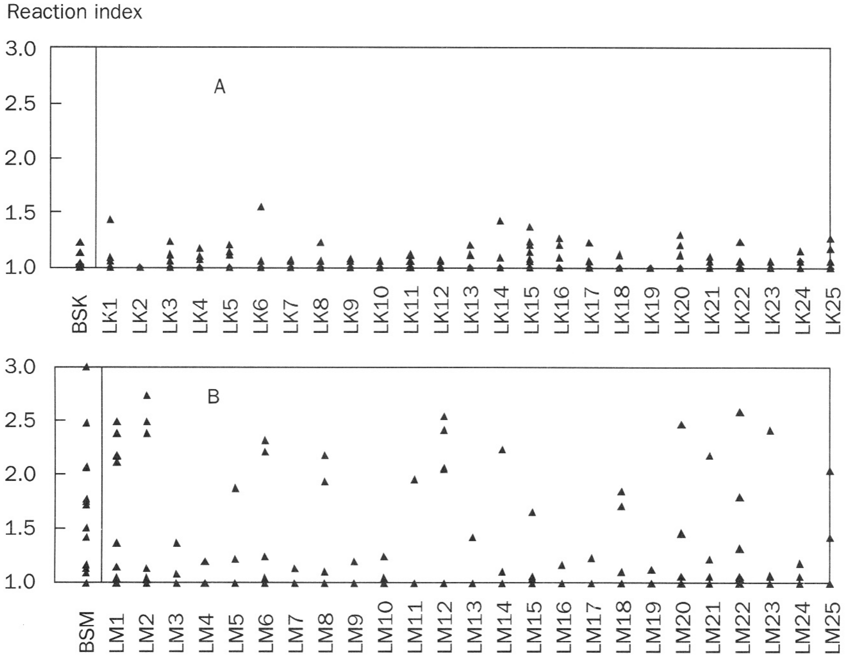


Fig. 2. Reaction indices to 14 Bhutanese blast isolates to a bulk sample and 25 single-head progeny lines derived from the rice variety (A) Tan Tshering and (B) Chumja Maap. At least 40 plants per population were tested with each isolate and scored either fully Susceptible = 3, fully resistant = 1, or intermediate = 2. The mean of all reactions is the reaction index. A reaction index <1.1 indicates a uniformly resistant reaction while higher indices reflect mixed reactions of susceptible and resistant plants within one variety. If the index is >2.4, less than 30% of the plants tested were resistant (data from Thinlay 1998).

and susceptibility. For Chumja Maap, the picture was even more heterogeneous (Fig. 2B). Interestingly, none of the progenies reacted uniformly susceptible to any of the tested isolates, whereas the bulk population was uniformly susceptible to at least one of the isolates (indicated by a reaction index of 3), suggesting that a larger sample size would probably even increase the observed diversity.

These data show that the diversity within landraces with respect to resistance is changing dynamically through outcrossing, thus allowing for ongoing host-pathogen coevolution and continuous adaptation of the landraces to disease pressure. Such diversity allows for much more effective and long-term protection of the system because any synthetic variety mixture is kept from coevolving with its pathogens through continuous human interference through varietal selection and prevention of outcrossing. The results also point to the fact that the conservation and development of genetic resources can be a side effect of diversification. Continuous changes and adaptations have also been found when modern cultivars were subjected to so-called dynamic management, that is, natural selection over time (Paillard et al 2000a,b).

Concluding remarks: constraints to diversification and possible solutions

Although diversification strategies offer great benefits for pest, disease, and weed control and soil fertility management, there are many reasons why growers are hesitant to diversify their systems.

The use of variety mixtures or multilines is popular in some areas of the world where markets are prepared to accept mixtures (e.g., the U.S. and wheat variety mixtures, as long as the right quality classes are mixed) or where breeders and processors work closely hand-in-hand to ensure top quality (e.g., coffee multilines in Colombia) (Finckh et al 2000) or where the benefits are so large that it is worth the extra hand labor, such as in the rice mixed cropping in China (Youyong et al 2000).

The success of the variety mixture approach in spring barley production in the former East Germany in the 1980s was largely driven by the need to reduce pesticide inputs as these had to be purchased with foreign currency. At the same time, barley malt was an important high-quality export commodity. Close collaboration of breeders and maltsters resulted in mixtures that produced high-quality malting barley readily accepted by brewers.

In contrast to the use of variety or species mixtures, crop rotations have fewer practical difficulties. Crop rotations are a must in most low-input systems but they are not usually practiced in many rice-growing areas and they are often neglected in large industrialized settings. Because lowland rice is usually grown under puddled conditions, it depends on the environmental conditions if it is possible to grow any other crop that requires drier conditions. However, in the colder regions, rice is often rotated with other crops such as vegetables, legumes, or wheat. The aerobic management of the soils for part of the year greatly influences the nutrient dynamics of the system and it appears that this could counteract some of the rice yield decline phenomenon observed in the tropical lowlands (Dobermann et al 2000). In large industrialized settings, growers are often reluctant to add new crops to their systems because of necessary investments in machinery, storage, and marketing setup. Also, some of the most beneficial rotation crops are pasture legumes that are only of use in mixed farming systems that include animals. However, the trend in many countries is toward either only animal production on the one hand or stockless farming on the other hand.

Diversification strategies, especially for the management of insects through the introduction of hedge rows, weed strips, or cover crops, are mostly practiced where pesticides are limited, either because of economic reasons or regulations such as in organic farming.

These examples show that, to make better use of diversification strategies, there is a need for close collaboration among growers, breeders, and processors to work out the best possible systems. At the same time, there has to be a clear economic incentive to work out such a system. That will depend on the availability and acceptance of chemical pesticides and thus on the larger political framework.

References

Allard RW. 1960. Relationship between genetic diversity and consistency of performance in different environments. Crop Sci. 1:127-133.

Altieri MA, Letourneau DK. 1982. Vegetation management and biological control in agroecosystems. Crop Prot. 1:405-430.

Andow DA. 1991. Vegetational diversity and arthropod population responses. Annu. Rev. Entomol. 36:561-586.

Brophy LS, Mundt CC. 1991. Influence of plant spatial patterns on disease dynamics, plant competition and grain yield in genetically diverse wheat populations. Agric. Ecosyst. Environ. 35:1-12.

Cook RJ, Baker KF. 1983. The nature and practice of biological control of plant pathogens. St. Paul, Minn. (USA): APS Press.

Darwin C. 1872. The origin of species by means of natural selection or the preservation of favoured races in the struggle for life. Sixth edition. London (UK): Collier Macmillan (ca. 1962).

Dobermann A, Dawe D, Roetter RP, Cassman KG. 2000. Reversal of rice yield decline in a long-term continuous cropping experiment. Agron. J. 92:633-643.

Elmer WH, LaMondia JL. 1999. Influence of ammonium sulfate and rotation crops on strawberry black root rot. Plant Dis. 83:119-123.

Finckh MR, Mundt CC. 1992. Plant competition and disease in genetically diverse wheat populations. Oecologia 91:82-92.

Finckh MR, Wolfe MS. 1998. Diversification strategies. In: Jones DG, editor. The epidemiology of plant diseases. London (UK): Chapman and Hall. p 231-259.

Finckh MR, Gacek ES, Goyeau H, Lannou C, Merz U, Mundt CC, Munk L, Nadziak J, Newton AC, de Vallavieille-Pope C, Wolfe MS. 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. Agronomie 20:813-837.

Fowler C, Mooney PR. 1990. Shattering: food politics, and the loss of genetic diversity. Tucson, Arizona (USA): University of Arizona Press.

Harlan JR. 1972. Genetics of disaster. J. Environ. Qual. 1:212-215.

Harlan JR. 1975. Our vanishing genetic resources. Science 188:618-621.

Harlan JR. 1992. Crops and man. 2nd edition. Madison, Wis. (USA): American Society of Agronomy and Crop Science Society of America.

Kirkegaard JA, Sarwar M, Wong FTW, Mead A. 1998. Biofumigation by brassicas reduces take-all infection. Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga, 1998. p 465-468.

Letourneau DK. 1997. Plant-arthropod interactions in agroecosystems. In: Jackson LE, editor. Ecology in agriculture. London (UK): Academic Press. p 239-290.

Liebman ML, Dyck E. 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3:92-122.

Liebman ML. 1995. Polyculture cropping systems. In: Altieri MA, editor. Acroecology: the science of sustainable agriculture. Second edition. Boulder, Colo. (USA): Westview Press. p 205-218.

Liebman ML, Gallandt ER. 1997. Many little hammers: ecological management of crop-weed interactions. In: Jackson LE, editor. Ecology in agriculture. San Diego, Calif. (USA): Academic Press. p 291-343.

Lung G, El Hamawi M, Gassert W, Walter-Echols G, Weiligmann B. 2000. Alternatives to soil fumigants for the reduction of soilborne pathogens in vegetable, strawberry and ornamental cultures. Mitt. Biol. Bundesanst. Land-Forstwirtsch. 376:510.

McMullen M, Jones R, Gallenberg D. 1997. Scab of wheat and barley: a reemerging disease of devastating impact. Plant Dis. 81:1340-1348.

Mooney PR. 1997. The parts of life: agricultural biodiversity, indigenous knowledge and the role of the third system. Dev. Dialog. Special Issue 1996:1:21-183.

Mueller-Dombois D, Ellenberg H. 1974. Aims and methods of vegetation ecology. New York: Wiley. 547 p.

Odorfer A, Obst A, Pommer G. 1994. The effects of different leaf crops in a long-lasting monoculture with winter wheat. 2. Disease development and effects of phytosanitary measures. Agribiol. Res. 47:56-66.

Paillard S, Goldringer I, Enjalbert J, Doussinault G, de Vallavieille-Pope C, Brabant P. 2000a. Evolution of resistance against powdery mildew in winter wheat populations conducted under dynamic managment. I. Is specific resistance selected? Theor. Appl. Genet. 101:449-456.

Paillard S, Goldringer I, Enjalbert J, Trottet M, David J, de Vallavieille-Pope C, Brabant P. 2000b. Evolution of resistance against powdery mildew in winter wheat populations conducted under dynamic managment. II. Adult plant resistance. Theor. Appl. Genet. 101:457-462.

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B. 1997. Economic and environmental benefits of biodiversity. Bioscience 47:747-757.

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weiss AE. 1980. Interactions among three trophic levels: influence of plants on interactions between herbivores and natural enemies. Annu. Rev. Ecol. Syst. 11:41-65.

Risch SJ, Andow D, Altieri MA. 1983. Agroecosystem diversity and pest control: data, tentative conclusions and new research directions. Environ. Entomol. 12:625-629.

Root RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). Ecol. Monographs 43:95-124.

Scholte K, Vos J. 2000. Effect of potential trap crops and planting date on soil infestation with potato cyst nematodes and root-knot nematodes. Ann. Appl. Biol. 137:153-164.

Stephens PM, Davoren CW, Ryder MH, Doube BM. 1994. Influence of the earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* on *Rhizoctonia solani* disease of wheat seedlings and the interaction with a surface mulch of cereal-pea straw. Soil Biol. Biochem. 26:1285-1287.

Subbarao KV, Hubbard JC, Koike ST. 1999. Evaluation of broccoli residue incorporation into field soil for verticillium wilt control in cauliflower. Plant Dis. 83:124-129.

Thinlay. 1998. Rice blast, caused by *Magnaporthe grisea,* in Bhutan and development of strategies for resistance breeding and management. Dissertation ETH No. 12777. Swiss Federal Institute of Technology, Zurich, Switzerland.

Thinlay, Finckh MR, Bordeos AC, Zeigler RS. 2000a. Effects and possible causes of an unprecedented rice blast epidemic on the traditional farming system of Bhutan. Agric. Ecosyst. Environ. 78:237-248.

Thinlay, Zeigler RS, Finckh MR. 2000b. Pathogenic variability of *Pyricularia grisea* from the high- and mid-elevation zones of Bhutan. Phytopatholgy 90:621-628.

Vandermeer JH. 1989. The ecology of intercropping. Cambridge (UK): Cambridge University Press.

Vellve R. 1992. Saving the seed: genetic diversity and European agriculture. London (UK): Earthscan Publications.

Vilich-Meller V. 1989. Der Einfluss von Mischkulturen auf den Schadernegerbefall am Beispiel der Futtergetreide-Mischung Sommergerste – Hafer. PhD thesis. University of Bonn, Germany.

Vilich-Meller V. 1992. *Pseudocercosporella herpotrichoides, Fusarium* spp. and *Rhizoctonia cerealis* stem rot in pure stands and interspecific mixtures of cereals. Crop Rot. 11:45-50.

Vilich V, Sikora RA. 1996. Diversity in soilborne microbial communities: a tool for biological system management of root health. In: Boland GJ, Kuykendall DL, editors. Plant-microbe interactions and biological control. New York, N.Y. (USA): Marcel Dekker, Inc. p 1-14.

Wolfe MS, Barrett JA. 1980. Can we lead the pathogen astray? Plant Dis. 64:148-155.

Wolfe MS. 1992. Barley diseases: maintaining the value of our varieties. In: Munk L, editor. Barley genetics VI. Copenhagen (Denmark): Munksgaard Int. Publishers, Ltd. p 1055-1067.

Wolfe MS, Finckh MR. 1997. Diversity of host resistance within the crop: effects on host, pathogen and disease. In: Hartleb H, Heitefuss R, Hoppe HH, editors. Plant resistance to fungal diseases. Jena (Germany): G. Fischer Verlag. p 378-400.

Youyong Z, Hairu CJF, Yunyue W, Yan L, Jianbing C, JinYiang F, Shisheng Y, Lingping H, Leung H, Mew TW, Teng PS, Wang Z, Mundt CC. 2000. Exploiting crop genetic diversity for disease control: a large-scale field test. Nature 406:718-722.

Notes

Author's address: Department of Ecological Plant Protection, University of Kassel, Nordbahnhofstr. la, 37213 Witzenhausen, Germany, email: mfinckh@wiz.uni-kassel.de.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Rice cultivar mixtures for blast management and improvement of farmers' income: the Yunnan experience

I.M. Revilla, H. Leung, Y.Y. Zhu, H.R. Chen, Y.Y. Wang, T.W. Mew, and M. Hossain

We reported previously the results of large-scale varietal diversification experiments in rice that provide effective control of a serious disease known as blast. In this system, traditional blast-susceptible glutinous varieties are interplanted with resistant modern hybrid rice, which has resulted in a 94% disease reduction. Glutinous rice yield on mixture farms is higher than that on monoculture farms, and hence provides higher income to farmers. The simplicity and effectiveness of this approach have attracted active participation by farmers. Here we report the economic impact and the rapid expansion of this crop diversification strategy that is changing the rural landscape, as the alternating rows of short and tall rice varieties become a prominent feature of many rice fields in Yunnan and other provinces in China.

Increasing the availability of staple food for home consumption and augmenting household income from rice cultivation are major concerns for farmers in land-scarce Asian countries with rice as the principal crop. As a result, the introduction of modern rice varieties has led to a gradual decline in rice varietal diversity, with many low-yielding traditional varieties going out of circulation in farmers' fields (World Bank 1992, Tuyen 2002). Maintaining adequate diversity and resilience in the agricultural production system is particularly important in the humid tropics of Asia, where disease and pest pressure is unusually high.

The purposeful introduction of biodiversity in cropping systems has been proposed as a means of preventing pest outbreaks, which are prevalent in monoculture crops. Studies on stripe rust of wheat (Mundt et al 1996) and powdery mildew of barley (Wolfe 1992) indicated that genetic diversification is highly effective in controlling epidemic diseases. This conclusion is further supported by the results of large-scale farmer-participatory field experiments in Yunnan Province in China. These experiments demonstrated that interplanting susceptible glutinous rice with resistant hybrid indica rice consistently reduced disease (rice blast) severity and increased the yield of the susceptible variety while maintaining the yield of the resistant variety (Zhu et al 2000).

Here we report the economic impact and the rapid expansion of such a crop diversification strategy that is changing the rural landscape, as the alternating rows of short and tall rice varieties become a prominent feature of many rice fields of Yunnan and other provinces in China.

Methods

One hundred farmer-adopters and 30 nonadopters from 23 villages in Shiping, Jianshui, Mile, and Kaiyuan counties of Hong He Prefecture, Yunnan Province, were personally interviewed from September to October 2000. From the complete list of rice farmers obtained from the local technicians, 10 households per village were randomly selected using the table of random numbers.

A pretested questionnaire was used to produce information on farmers' crop and pest management practices, input use, and income. Adopters were asked detailed questions about their farming situation before and after the adoption of rice interplanting. The "before" situation refers to 1998 or 1999 before the technology of rice interplanting was adopted by farmers. The "after" situation refers to the 2000 rice-cropping season. For comparison, data from the 2000 cropping season were likewise obtained from nonadopters.

Data were analyzed using the program SPSS for Windows® 10.0, in which means were compared using *t*-tests. To assess the impact of the technology of rice interplanting on farmers' income, the costs and returns of production were estimated and compared between adopters before and after technology adoption, and between adopters and nonadopters.

Results and discussion

Economic impact of the project

As previously reported (Revilla et al 2001), adopting rice interplanting had the following effects: (1) reduced pesticide use, (2) increased yield from elimination of crop losses from pests and lodging, and (3) increased production costs on account of higher labor use in planting and harvesting.

Cost savings from the reduction in pest pressure

The most direct benefit from rice interplanting is the reduction in pest pressure, that is, blast disease, which implies some savings in the use of pesticides and labor for spraying pesticides. The average number of sprays was three for the nonadopters compared with one for the adopters, which would have a positive effect on health. Rola and Pingali (1 993) have documented that several diseases are caused by exposure to harmful chemicals during spraying.

Because of the reduced incidence and severity of blast disease, adopters spent only \$1.50 ha^{-1} for pesticides compared with nonadopters' expenditures of \$4.42

Table 1. Cost savings per hectare from reduction in pest pressure, Yunnan Province, China, crop year 2000.

Item	Adopters	Nonadopters
Number of sprays	1	3
Cost of pesticides (US$)	1.50	4.42
Labor for pesticide application (d)	0.63	0.76
Imputed cost of labor (US$)	1.98	2.86
Total cost (US$)	3.48	7.28
Financial benefit (US$)	3.80	

Table 2. Mean yield of glutinous and hybrid rice by type of farmer, Yunnan Province, China, crop year 2000.

Rice yield (t ha^{-1})	Adopters		Nonadopters		
	199899	2000	Difference	2000	Difference
Glutinous rice	2.13	2.14	0.01[a]	0.42	1.72[b]
Hybrid rice	8.87	8.94	0.07 ns	9.15	-0.21 ns
Total	11.00	11.08	0.08[c]	9.57	1.51[d]

[a] t = 0.032, P<0.10. [b] t = 5.083, P< 0.001. [c] t = –1.483, P< 0.05. [d] t = 3.365, P< 0.10.

ha^{-1}. There is also a substantial savings in the amount of labor used for spraying pesticides. Comparing the costs incurred by both adopters and nonadopters for pesticides and labor, we estimate that the gains from adopting this technology are about $3.80 ha^{-1} (Table 1).

Yield gains from the reduction in losses

Nearly 25-40% of the yield of monocropped glutinous rice is usually lost because of blast disease (Zhu et al 2000, Zhu 2001). The crop also suffers from lodging when there is a strong wind because of weak stems and taller plants. The method of interplanting one row of glutinous rice with four to six rows of hybrid rice as a form of genetic diversification helps control blast disease and lodging of the glutinous rice plants.

On mixture farms, the yield of glutinous rice has increased by 1.72 t ha^{-1} (Table 2). Nonadopters obtained less than 0.5 t ha^{-1} of glutinous rice because the crop suffered from lodging at the milking stage (Fan Jin Xiang, personal communication, October 2000). When this happens, about 0.5–1.0t of rice could easily be lost (T.W. Mew, personal communication, October 2000). With less than 20–30% of the land allocated to hybrid rice, we noticed that the crop's yield has decreased by 0.21 t ha^{-1}. The combined yield of glutinous and hybrid rice was 11.08 t ha^{-1} for adopters versus 9.57 t ha^{-1} for nonadopters.

The gain in gross revenue is even higher at 26% since glutinous rice fetches a higher price, almost double that of hybrid rice because of higher grain quality and

Table 3. Yield gains from reduction in losses from blast disease and lodging of plants, Yunnan Province, China, 2000.

Item	Adopters	Nonadopters	% difference
Percent of area under glutinous rice	16.88	10.04	68.13
Rice yield (t ha^{-1})			
Glutinous rice	2.14	0.42	409.52
Hybrid rice	8.94	9.15	–2.30
Price (US$ kg^{-1})			
Glutinous rice	2.48	2.90	–14.48
Hybrid rice	1.63	1.67	2.40
Gross revenue ($ ha^{-1})	2,590.13	2,061.46	25.65
Financial gain ($ ha^{-1})	528.67		

Table 4. Mean level of input use per hectare by type of farmer, Yunnan Province, China, crop year 2000.

Inputs	Adopters			Nonadopters	
	1998-99	2000	Difference	2000	Difference
Seeds					
Quantity (kg)					
Glutinous	7.92	5.55	–2.37[a]	25.67	20.12[b]
Hybrid	23.20	23.43	0.23 ns	21.56	–1.87[b]
Cost (US$)					
Glutinous	0.14	0.06	–0.08[b]	0.14	0.08[b]
Hybrid	8.02	7.20	–0.81[b]	7.88	0.68[b]
Pesticides					
Cost (US$)	2.58	1.50	–1.08[b]	4.41	2.91[b]
No. of sprays	2.00	1.00	1.00 ns	3.00	2.00[b]
Labor (person-days)					
Transplanting	4.13	4.70	0.57 ns	3.75	–0.95[b]
Pesticide application	0.70	0.63	–0.07 ns	0.76	0.13 ns
Harvesting	6.14	8.14	2.00[a]	6.93	–1.21[b]

Significant at 5%. significant at 1%.

higher demand for the use of glutinous rice on social occasions (Table 3). The financial benefit in gross revenue from adopting the technology is estimated at $530 ha^{-1}, which is much higher than the cost savings in pesticides.

Additional labor costs

This technology, however, is not costless. Substantial additional costs are incurred, particularly in two farm operations. One is for transplanting labor because adopters have to transplant twice. Another is for harvesting because farmers have to harvest the glutinous and hybrid rice separately. The mixture planting technology requires additional labor of 2 d ha^{-1} (Table 4) and the imputed cost of the additional labor is about $7 ha^{-1}.

Table 5. Costs and returns analysis (in US$) by type of farmer and by year, Yunnan Province, China, crop year 2000.

Item	Adopters		Nonadopters
	199899	2000	2000
Gross value of production	2,485.60	2,590.13	2,061.46
Cost of production			
Seeds			
Glutinous rice	0.14	0.06	0.14
Hybrid rice	8.03	7.20	7.88
Fertilizer	13.74	12.68	7.67
Pesticides	0.09	1.50	4.41
Hired labor	59.81	72.15	27.06
Net returns above cash costs	2,403.79	2,496.54	2,014.30

Costs and returns analysis

To assess the impact of rice interplanting on farmers' income, the costs and returns of production were estimated (Table 5). Because of increased yields from glutinous rice, which commands a higher price in the market, the gross value of production realized by adopters is much higher than that of the nonadopters. Adopters gained an additional \$104.53 ha^{-1} vis-&vis the 1998-99 level.

Contrary to expectations that rice mixture requires more seeds, adopters spent \$0.91 ha^{-1} less for seed in 2000. This may be due to the more efficient use of seeds by farmers when they follow the straight-row planting of both glutinous and hybrid rice. Compared with nonadopters, farmer-adopters saved about \$0.76 ha^{-1} on seed expense.

There was also a reduction of \$1.41 ha^{-1} in pesticide costs among adopters in 2000. Nonadopters spent about \$3.00 ha^{-1} more on pesticides than did the adopters.

Although additional labor costs are incurred for transplanting and harvesting, the savings from pesticides and yield gains from glutinous rice are more than enough to compensate for the increased labor costs. Adopters also used more hired labor than before to enable the male household heads in many instances to engage in higher-income-generating activities such as off-farm employment.

Thus, we see from Table 5 that the net returns above cash costs obtained by adopters are \$92.75 ha^{-1} higher than in 1998-99 and \$482.24 higher than those of the nonadopters in 2000.

Rate of technology expansion

Attracted by the simplicity and effectiveness of the crop-diversification strategy, farmers are adopting it in ever-increasing numbers and changing the rural landscape of China. In the southwestern province of Yunnan in particular, a newly prominent feature of many rice fields is the alternating rows of short and tall rice varieties.

Table 6. Rate of technology adoption and area under rice mixtures, 1997-2002, Yunnan Province,China.

Year	No. of counties of adopters	Area covered (ha)
1997	2	15
1998	2	812
1999	6	3,342
2000	15	43,000
2001	61	107,400
2002	101	230,000

The technology spread so fast that, after the project was launched in 1997, the area under rice mixtures continued to expand. Large-scale training of farmers is one of the technology transfer methods implemented to ensure a faster rate of technology diffusion.

In 1997, the technology of rice cultivar mixture was adopted in only two counties covering an area of 15 ha (Table 6). The technology spread from a mere 812 ha under mixed planting in 1998 to 43,000 ha in 2000. By the end of 2001, about 70% of the rice farm households in the indica rice area of Yunnan Province had adopted mixed planting of rice varieties and the area under mixtures had expanded to 107,400 ha in 61 counties. In 2002, rice interplanting covered an area of 230,000 ha in 101 counties of Yunnan Province. Ten additional provinces in China have evaluated the technology for possible large-scale implementation.

A critical factor that contributed to the fast rate of adoption was the use of local county officials and technicians as trainers. They worked with the farmers closely and actively to demonstrate the technology and this helped encourage more farmers to participate.

Future plans

IRRI is now in the process of further developing the diversification strategy to help resource-poor rice farmers manage pests without pesticides, increase yields, conserve their traditional varieties, and increase their income.

We plan to introduce this system in other ecosystems, especially the upland environment, and extend it to other pests and diseases. To maximize the benefits of this diversification strategy and to extend the impact to a wider area, we must seek a better understanding of the mechanisms behind the yield increase and disease reduction in this system. This will build upon our previous experience and the collective strengths of participating institutions to develop and implement production systems that will “harmonize preservation and productivity.”

References

Mundt CC, Brophy LS, Kolar SC. 1996. Effect of genotype unit number and spatial arrangement on severity of yellow rust in wheat cultivar mixtures. Plant Pathol. 45:215-222.

Revilla IM, Fan JX, Zhu YY, Li SZ, Mew TW, Hossain M. 2001. Adoption of mixture planting for biodiversity in China: its impact on pest management and farmers' income. In: Mew TW, Borromeo E, Hardy B, editors. Exploiting biodiversity for sustainable pest management. Proceedings of the Impact Symposium on Exploiting Biodiversity for Sustainable Pest Management, 21-23 August 2000, Kunming, China. Los Baños (Philippines): International Rice Research Institute. p 217-236

Rola A, Pingali PL. 1993. Pests, pesticides and integrated pest management. In: Pingali PL, Hossain M, editors. Impact of rice research. Proceedings of the International Conference on the Impact of Rice Research, 3-5 June 1996, Bangkok, Thailand. Bangkok (Thailand): Thailand Development Research Institute and Manila (Philippines): International Rice Research Institute. p 135-158.

Tuyen TV. 2002. Community management of rice varieties. Dissertation submitted for PhD degree. University of the Philippines-Los Baños.

Wolfe MS. 1992. Barley diseases: maintaining the value of our varieties. In: Munck L, editor. Barley genetics VI. Copenhagen (Denmark): Munkdgaard International Publishers. p 1055-1067.

World Bank. 1992. World development report 1992: development and environment. New York (USA): Oxford University Press.

Zhu YY, Chen HR, Fan JH, Wang YY, Yan L, Chen JB, Fan JX, Yang SS, Hu LP, Leung H, Mew TW, Teng PS, Wang ZW, Mundt CC. 2000. Genetic diversity and disease control in rice. Nature 406:718-722.

Zhu YY, Chen HR, Fan JH, Wang YY, Yan Li, Chen JB, Li SZ, Zhou JY, Fan JX, Yang SS, Maguang LY, Hu LP, Mundt CC, Borromeo E, Leung H, Mew TW. 2001. Current status and prospects of mixture planting for control of rice blast in Yunnan. In: Mew TW, Borromeo E, Hardy B, editors. Exploiting biodiversity for sustainable pest management. Proceedings of the Impact Symposium on Exploiting Biodiversity for Sustainable Pest Management, 21-23 August 2000, Kunming, China. Los Baños (Philippines): International Rice Research Institute. p 159-167.

Notes

Authors' addresses: I.M. Revilla, M. Hossain, Social Sciences Division, International Rice Research Institute (IRRI), DAPO Box 7777, Metro Manila, Philippines; I.M. Revilla, H. Leung, T.W. Mew, Entomology and Plant Pathology Division, IRRI; YY. Zhu, H.R. Chen, Y.Y. Wang, Key Lab for Phytopathology of Yunnan Province, Yunnan Agricultural University, Kunming City 650201, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Integrating ecological principles for resistance to insect pests of rice

J. Cheng, Y. Lou, Z. Zhu, M. Jiang, and W. Zhao

Plant resistance to insect pests is traditionally defined as the property that enables a plant to avoid, tolerate, or recover from injury by insect populations that would cause greater damage to other plants of the same species under similar environmental conditions. According to modern ecological theory, insect pest control should be the management of the arthropod community in the cropping system. Therefore, the understanding of plant resistance to insect pests has to be expanded and more biotic and abiotic factors in the cropping system, which mediate plant resistance, have to be taken into account. In this paper, some results from field investigations and lab experiments are presented to show the phenomena related to plant resistance and pest control, which were mediated by biological components in the rice ecosystem. For example, secondary insect pests might be caused by a variety resistant to major pests, a herbivore's response to plant resistance would be mediated by mutualism between herbivores, and natural biological control could be enhanced by the plant variety. All these phenomena indicate that the main biological components in a rice cropping system interact through food and information chains and a program of plant resistance to insect pests should be evaluated at the level of the arthropod community. Approaches to integrate ecological principles for insect pest control are discussed.

Plant resistance to insect pests is traditionally defined as the property that enables a plant to avoid, tolerate, or recover from injury by insect populations that would cause greater damage to other plants of the same species under similar environmental conditions. The most dramatic early success in plant resistance was the control of the grape phylloxera, *Phylloxera vitifoliae* (Fitch), in European grapevines (Kogan 1975). Since then, plant resistance has often been used as one of the key tactics in an integrated control program for insect pests because of its unique advantages, including low environmental impact and no cost to farmers. The incorporation of resistance to insect pests into modern cultivars has been a major objective of most rice breeding programs in Asia (Heinrichs 1994).

However, the development of a virulence population of brown planthopper (BPH) after feeding on a resistant variety for several generations provided a typical example, which revealed that plant resistance per se, as one of other control measures, was unable to control the insect pest successfully in the long term (Hare 1994). As a producer in an ecosystem, rice is the most important component and the traits of a rice variety may affect other biological components in the system through the food chain. But the traits of the rice variety might also be affected by environmental factors, including biotic and abiotic components in the system (Kogan 1975). According to modern ecological theory, insect pest control in a cropping system should be the management of the arthropod community in the system (Kogan 1998). Therefore, understanding of plant resistance to insect pests has to be expanded and the biotic and abiotic factors in the cropping system that might mediate plant resistance and affect the efficiency of control of insect pests have to be taken into account. In this paper, some results related to interactions between environmental factors and plant resistance from field investigations and laboratory experiments are presented to elucidate how ecological principles should be integrated for host-plant resistance to insects.

Risk of secondary insect pests caused by varieties resistant to current major pests

Field investigation showed that more than 800 insect species feed on rice and only about 20 species are of major importance and regular occurrence (Cheng 1996). However, the species of major insect pests are changing and the succession of major insect pests in cropping systems indicated that most current major pest species resulted from changes in agricultural techniques, which created favorable ecological conditions for these species. For example, the wide use of organic chloride insecticides (BHC and DDT) in the rice paddy, which destroyed the community of natural enemies in the rice ecosystem, resulted in outbreaks of the small brown planthopper (*Laodelphax striatellus*) and the rice green leafhopper (*Nephotettix cincticeps*) in Japan and China in the 1950s and ’60s (Cheng 1996). The brown planthopper, *Nilaparvata lugens,* the most destructive pest in Asia, also resulted from modern agricultural techniques, including the heavy use of insecticides, high nitrogen inputs, high-yielding varieties, and dense planting (Dyck and Thomas 1979, Kenmore 1980). Outbreaks of the whitebacked planthopper (WBPH) *Sogatella furcifera* in China in the 1980s revealed that the wide use of new varieties might be one of the causes of secondary insect pest problems.

WBPH was a potential pest in the rice ecosystem in China before 1970. Historical data indicated that outbreaks of WBPH occurred only occasionally in some small areas in China during the 1950s to '70s. However, WBPH has become one of the major pests since the late 1970s, when hybrid rice started to be widely planted in southern China (Zhu 1990). In the first years of growing hybrid varieties, the

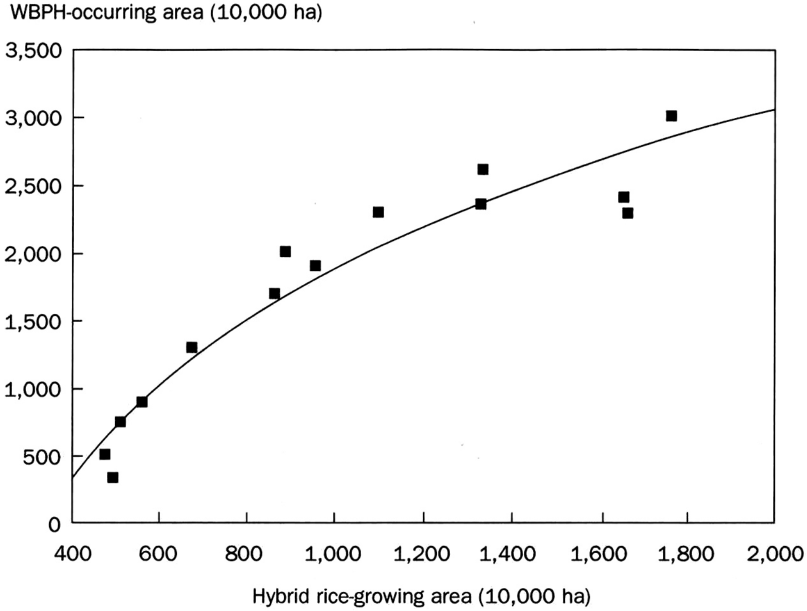


Fig. 1. Relationship of WBPH-occurring area to growing area of hybrid rice in China, 1979-92.

combinations (varieties) of hybrid rice distributed were SY 6 and WY 6, which were resistant to BPH and rice blast, but with unknown susceptibility to WBPH. Figure 1 shows the relationship of hybrid rice-growing area to WBPH-occurring area from the late 1970s to early '90s, which indicated that the increase in WBPH-occurring area was closely related to the increase in hybrid rice-growing area. Results from the laboratory showed that the growth rates of the WBPH on hybrid varieties were much higher than those on conventional indica varieties, which made the WBPH population increase and become a major pest (Huang et al 1994). Statistical analysis using historical data from 443 counties in 14 provinces in southern China also showed that the population sizes of WBPH were closely related to the proportion of area planted to hybrid varieties (Tang et al 1998).

With the development of biotechnology, the breeding of plants with transmitted genes has become a popular technique used in developing plant resistance. This technique has been used in rice variety breeding and some *Bt* rice with high resistance to stem borer (*Chilo suppressalis*) and the leaffolder (*Cnaphalocrocis medinalis*) has been developed. Field investigation showed that the density of rice green leafhopper in a *Bt* rice (KMD1) plot was significantly higher than that in the parental varieties without the *Bt* gene (Hu 2001), which implied that the risk for causing secondary pests also existed in transgenic plants.

“Crossing adaptability” resulted from mutualism between herbivores

One of the results from coevolution in the plant-herbivore system is the development of adaptability to plant resistance through physiological and genetic changes in insects. In the meantime, laboratory experiments showed that mutualism between herbivores also existed in a multispecies system and this kind of mutualism might be termed “crossing adaptability” because this phenomenon indicated that the adaptability to a variety by one herbivore species could be enhanced mutually by another coexisting herbivore species.

BPH and WBPH often co-occur on the same plant and feed on the phloem sap of rice in the field. They share the same habitats throughout most of the rice-growing season and each species has the traits of highly aggregated distribution and rapid population growth (Denno et al 1994). The coevolution of BPH and WBPH in the rice ecosystem caused the two species to develop some strategies to avoid competition, such as differences in time and spatial distribution in the rice ecosystem. At the same time, some mechanisms for mutualism were developed.

Three varieties were selected for the experiment: Zhe 852 (an indica variety moderately resistant, MR, to BPH, but susceptible, S, to WBPH), XS 11 (a japonica variety S to BPH, but MR to WBPH), and XY 9308 (a hybrid variety MR to both BPH and WBPH). Density was set at 24 planthoppers and 4 rice seedlings per pot in total and the ratio of each species was 0:24, 6:18, 12:12, 18:6, and 24:0. The results indicated that the interspecific effects at this density level did not affect the nymphal development duration of BPH, but did affect that of WBPH. The developmental duration of WBPH reared in mixed culture with BPH was significantly shorter than those reared in pure culture with WBPH only, especially for XS 11 and XY 9308, which were MR to WBPH. However, the interspecific effects affected the emergence rates of both species, except for BPH reared on XS 11, which was S to BPH. The emergence rates of planthoppers reared with another species were significantly higher than for those reared with the same species only (Table 1). These results confirmed that both species would get benefits from the direct interspecific effects when the two species co-occurred on the same plants, especially for WBPH and poor food conditions (on MR varieties) (Cheng et al 2001).

The indirect interspecific effects were tested by rearing BPH or WBPH on the seedlings of XY 9308 from the 1st-instar nymph. Three treatments were set: sucked by 18 older instar nymphs of the same species for 5 days prior to the experiment, sucked by 18 older instar nymphs of another species for 5 days prior to the experiment, and healthy rice plants without any feeding by planthoppers. The plants were replaced with plants from the same treatments every 5 days to obtain the consecutive feeding. The planthoppers were allowed to develop into adults, which were transferred to plants treated the same way. The female nymphal development duration, emergence rates, and female longevity and fecundity were measured as shown in Table 2. The results showed that the development durations of female nymphs reared on the rice plants sucked by another species were shorter than those of females reared on healthy plants or rice plants sucked by the same species. The emergence rate and female

Table 1. Impacts of interspecific interaction on nymphal development duration and emergence rate of planthoppers under same total density condition.

Species/ variety	Density [a]	Development duration [b] (d)		Emergence rate (%)
		Female	Male	
BPH				
Zhe 852	6B18W	13.46 ± 0.31 a	13.46 ± 0.20 a	95.83 ± 3.61 a
	18B6W	13.80 ± 0.17 a	13.46 ± 0.07 a	85.55 ± 5.11 a
	24B	14.15 ± 0.22 a	13.61 ± 0.12 a	38.89 ± 6.31 b
XiuShui 11	6B18W	13.98 ± 0.30 a	13.60 ± 0.26 a	89.00 ± 5.58 a
	18B6W	13.71 ± 0.05 a	13.25 ± 0.04 a	88.89 ± 6.93 a
	24B	13.59 ± 0.03 a	13.25 ± 0.00 a	87.50 ± 2.95 a
XY 9308	6B18W	13.48 ± 0.40 a	13.25 ± 0.31 a	100.00 ± 0.00 a
	18B6W	13.56 ± 0.21 a	13.17 ± 0.07 a	65.05 ± 7.47 b
	248	13.63 ± 0.47 a	13.10 ± 0.22 a	68.00 ± 5.73 b
WBPH				
Zhe 852	6W18B	12.10 ± 0.09 b	12.07 ± 0.20 a	96.67 ± 2.98 a
	18W6B	12.67 ± 0.22 a	12.17 ± 0.24 a	83.33 ± 1.96 b
	24W	12.88 ± 0.16 a	12.43 ± 0.13 a	83.59 ± 4.87 b
XiuShui 11	6W18B	13.44 ± 0.28 b	13.16 ± 0.20 b	91.67 ± 4.17 a
	18W6B	13.95 ± 0.20 b	13.19 ± 0.14 b	91.11 ± 3.37 a
	24W	14.83 ± 0.12 a	14.06 ± 0.18 a	60.98 ± 5.38 b
XY 9308	6W18B	12.17 ± 0.14 b	12.00 ± 0.00 b	94.44 ± 4.54 a
	18W6B	13.27 ± 0.24 ab	12.91 ± 0.37 ab	82.68 ± 8.32 a
	24W	13.92 ± 0.59 a	13.64 ± 0.47 a	47.92 ± 13.26 b

[a] B = BPH = brown planthopper, W = WBPH = whitebacked planthopper. [b] Data are means ± standard error. Within a column in each variety, means followed by different letters are significantly different at the 5% level according to Duncan's multiple range test.

longevity and fecundity of planthoppers reared on rice plants sucked by another species were longer or higher than those of planthoppers reared on healthy plants or rice plants sucked by the same species. These results revealed that both BPH and WBPH would also obtain benefits from indirect interspecific effects (Cheng et al 2001).

External resistance among three trophic levels

In the evolutionary process, species developed strategies to defend against their enemies not only at the neighbor trophic level but also among tri-trophic levels. This phenomenon was defined as external resistance (Price 1986). Experiments showed that a rice variety would not only affect the interactions between the rice plant and its pests, but also the interactions between pests and their natural enemies, directly and indirectly.

Emergence rates of *Anagrus nilaparvatae* from parasitic eggs of BPH feeding on various rice varieties were significantly different (Table 3). Comparative studies on the relations between the biological parameter and physical condition of rice varieties

Table 2. Effects of indirect interspecific interaction on biological parameters of brown planthopper and whitebacked planthopper populations:

Species/ treatment	Nymphal development duration (d)		Emergence rate (%)	Female longevity (d)	Fecundity (eggs female^{-1})
	Female	Male			
Brown planthopper (BPH)					
Sucked by WBPH	12.42 ± 0.17 b	11.95 ± 0.23 a	83.33 ± 4.71 a	30.25 ± 1.24 a	958.00 ± 48.89 a
Sucked by BPH	12.68 ± 0.16 ab	12.57 ± 0.45 a	73.33 ± 8.94 a	22.75 ± 0.96 b	587.42 ± 13.84 b
Control	13.08 ± 0.07 a	12.20 ± 0.11 a	70.00 ± 6.56 a	25.33 ± 3.29 ab	772.11 ± 76.11 b
Whitebacked planthopper (WBPH)					
Sucked by WBPH	12.47 ± 0.20 a	11.78 ± 0.46 a	72.22 ± 3.93 ab	21.17 ± 0.95 b	353.00 ± 17.00 b
Sucked by BPH	11.21 ± 0.11 b	10.90 ± 0.26 a	91.67 ± 4.17 a	25.56 ± 0.72 a	550.44 ± 6.40 a
Control	12.22 ± 0.14 a	11.72 ± 0.32 a	58.33 ± 9.43 b	21.50 ± 1.27 b	394.38 ± 36.89 b

[a] Data are means i standard error. Within a column in each variety, means followed by different letters are significantly different at the 5% level according to Duncan's multiple range test.

Table 3. Relationship of rice varieties to densities of siliceous cell in sheath and emergence rate of *Anagrus nilaparvatae*.

Variety	Resistance to BPH [a]	Density of siliceous cells [b] (no. mm^{-2})	Emergence rate (%)
Zhe852	S	20.19 ± 0.90 b	93.09 ± 4.18 (8) a
Xiushui48	S	-	97.22 ± 2.77 (3) a
TN1	S	22.27 ± 1.55 b	86.91 ± 3.45 (9) abc
Guang4	S	21.02 ± 0.94 b	91.94 ± 2.50 (7) a
Shanyou10	MR	22.41 ± 1.41 b	94.19 ± 2.62 (7) a
Xiushui11	S	23.51 ± 1.41 b	87.89 ± 5.05 (5) ab
Nabeshi	MR	19.28 ± 1.24 b	93.05 ± 2.30 (6) a
IR64	R	20.33 ± 0.95 b	89.40 ± 4.13 (5) ab
Xiushui620	MR	21.30 ± 1.51 b	90.41 ± 3.46 (9) a
N22	MR	23.65 ± 1.72 b	75.70 ± 7.89 (5) bc
ZN D40	MR	27.39 ± 1.01 a	73.57 ± 7.11 (5) c

[a] BPH = brown planthopper, S = susceptible, R = resistant, MR = moderately resistant. [b] Data are means ± standard error. Within a column in each variety, means followed by different letters are significantly different at the 5% level according to Duncan's multiple range test.

revealed that emergence rates were significantly related to the density of siliceous cells in the rice sheath: the higher the density of siliceous cells, the lower the emergence rate. Results also showed that the effects of the rice variety related to the effects on natural enemies were not the same as the effects related to planthoppers. For example, XS48, Z852, N22, and G4 were all susceptible to BPH, but their effects on the emergence rate of *A. nilaparvatae* were significantly different. The emergence rate of *A. nilaparvatae* from N22 was only about 75%, which was significantly lower than those from the other three varieties, which were all above 90%. Nabeshi, SY10, and ZND40 were all moderately resistant to BPH, but their effects on the emergence rate were also significantly different. The emergence rates of *A. nilaparvatae* from Nabeshi and SY10 were above 90%, but that from ZND40 was only 74% (Lou and Cheng 1996b). Rice varieties could also affect the survival and fecundity of *Cyrtorhinus lividipennis* (Lou et al 2002).

The olfactory response test revealed that rice volatiles affected the foraging behavior of *A. nilaparvatae* and *C. lividipennis,* and more parasitoids were oriented to the odors from healthy rice plants compared with the ambient air (control). The parasitoid/predator preferred the plant-BPH complex over healthy plants (Lou and Cheng 1994, 2001a,b). Experimental results also indicated that the attractiveness of the healthy plants and plant-BPH gravid female complex was significantly related to rice varieties (genotypes) (Fig. 2) (Lou and Cheng 1996a).

Laboratory experiments demonstrated that the functional responses of *A. nilaparvatae* and *C. lividipennis* were affected by rice varieties. A comparison of results from functional response experiments on various varieties showed that the instantaneous attack rates were not significantly different, but the handling times were significantly different. These results indicated that the maximum number of eggs consumed daily by the parasitoid and predator on various varieties was significantly different. One of the reasons was the difference in egg distribution on

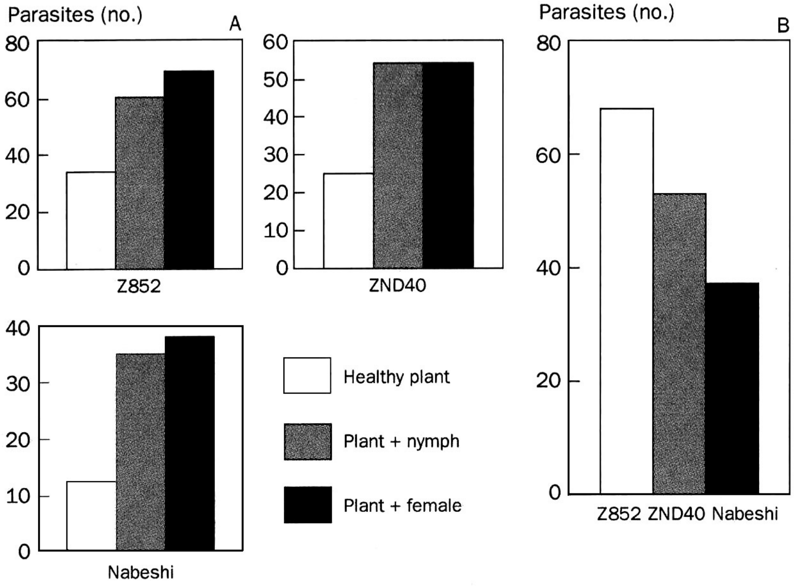


Fig. 2. Behavioral responses of *Anagrus nilaparvatae* to volatiles from various treatments of rice varieties. (A) Comparison among healthy plant, plant + brown planthopper nymphs, and plant + female brown planthopper adults; (B) comparison among three varieties.

the rice plant. More eggs were on the upper part of the rice sheath when the interval between the vascular bundles was narrow (e.g., variety ZND40) and more eggs were laid in the lower part of the rice sheath when the interval was wide (in a variety such as 2852). *A. nilaparvatae* always prefers to parasitize the eggs on the upper part of the rice sheath (Lou and Cheng 1996c).

Discussion

A traditional pest control program is usually designed for a major pest species and the main objective of the program is to reduce yield loss caused by the species under an economically tolerant level. Therefore, a breeding program for varietal resistance to pests is usually based on a one-to-one correspondence between particular resistance genes and particular pest species.

However, the pest problem we are facing in a cropping system is not only a single species based on integrated pest management. In China, there was only the rice stem borer in the 1950s. Rice green leafhopper, small brown planthopper, brown planthopper, and rice leaffolder became major pests in the 1960s, and then the whitebacked planthopper in the ’80s. The number of pest species has been increasing even though great efforts have been put into a cropping system to control pests, which revealed that a successful pest management program could not be based on the species level, but on a community and ecosystem level (Cheng 1996, Kogan 1998).

The experimental results presented in this paper showed that the interactions among the main components in the rice ecosystem were more complex than what we thought. At least three kinds of interactions should be taken into consideration when designing a breeding program.

First, the use of a new variety will affect the performance of other herbivores feeding on rice in the system, not only the target species. As a main producer in the rice ecosystem, the rice plant provides the basic energy and materials for herbivores in the ecosystem. The comparison of WBPH fecundity on hybrid and conventional varieties indicates that one of the main reasons some herbivores are not pests is their reduced fecundity on particular host plants, in other words, the variety is not suitable for these herbivores. A plan to breed new varieties is to improve their quality and yield by modifying old varieties genetically. In the meantime, some traits related to physical and nutritional components for other herbivores also changed. Some of the changes might benefit a particular herbivore and make its growth rate increase dramatically. After a few generations or years, the herbivore could become a major pest, just like what happened for WBPH.

Second, varietal resistance is influenced by environmental factors, including biotic and abiotic ones. The data showed above indicated that the performance of a herbivore on a particular variety varied depending on other coexisting herbivores, which indicated that a field screen should be much more important than a laboratory screen and the mechanisms for pests to adapt to plant resistance could be explored more widely.

Third, the importance of biological agents at the third trophic level should be incorporated into breeding programs. The data in this paper indicate that the foraging behavior of natural enemies can be influenced by the pest resistance traits of rice varieties, and other genes could enhance the effects of natural enemies on the variety. This implied the possibility to incorporate these two kinds of function into the same variety and indicated a new approach for variety breeding programs.

All the data showed that many interactions, among multienvironmental factors, multispecies of herbivores and natural enemies, and multigenes in the rice plant, were involved in pest control, as well as in variety breeding programs. Therefore, ecological principles dealing with interactions among multicomponents have to be integrated into designs of breeding programs for integrated pest management. Information from ecological studies in the rice ecosystem, including community structure, the main components in the food web, and interactive approaches among key components, could provide ideas for designing breeding programs. A breeding program integrating ecological principles should consider more long-term effects, more target species, and more components of resistance, including external resistance, to obtain sustainable control of insect pests.

References

Cheng JA. 1996. Rice insect pests. Beijing (China): Chinese Agricultural Publication.

Cheng JA, Zhao WC, Lou YG et al. 2001. Intra- and inter-specific effects of the brown planthopper and white-backed planthopper on their population performance. J. Asia-Pacific Entomol. 4(1):85-92.

Denno RF, Cheng JA, Roderick GK et al. 1994. Density-related effects on the components of fitness and population dynamics of planthoppers. In: Denno RE Perfect TJ, editors. Planthoppers: their ecology and management. London (UK): Chapman & Hall. p 257-281.

Dyck VA, Thomas B. 1979. The brown planthopper problem. In: Brown planthopper: threat to rice production in Asia. Los Baños (Philippines): International Rice Research Institute. p 3-17.

Grist DH, Lever MAW. 1969. Pests of rice. London (UK): Longmans, Green and Co.

Hare JD. 1994. Status and prospects for an integrated approach to the control of planthoppers. In: Denno RF, Perfect TJ, editors. Planthopper: their ecology and management. London (UK): Chapman & Hall. p 615-632.

Heinrichs EA. 1994. Host plant resistance. In: Heinrichs EA, editor. Biology and management of rice insects. New Delhi (India): Wiley Eastern Limited. p 517-547.

Hu Y. 2001. Influences of *Bt* rice on arthropod community in rice field. M.Sc. thesis submitted to Zhejiang University.

Huang CW, Feng BC, Chen JM. 1994. Effects of rice variety on population development of white-backed planthopper. Insect Knowl. 31(4): 196-198.

Kenmore PE. 1980. Ecology and outbreaks of a typical insect pest of the green revolution, the rice brown planthopper, *Nilaparvata lugens* (Stäl). Ph.D. dissertation. University of California, Berkeley.

Kogan M. 1974. Plant resistance in pest management. In: Metcalf RL, Luckmann WH, editors. Introduction to insect pest management. New York, N.Y. (USA): John Wiley & Sons. p 103-146.

Kogan M. 1998. Integrated pest management: historical perspectives and contemporary development. Annu. Rev. Entomol. 43:243-270.

Lou Yong-gen, Cheng J. 1994. The kairomone from *Nilaparvata lugens* (Stal) and its relation to rice varieties. Acta Phytophyl. Sin. 21:327-332.

Lou Yong-gen, Cheng J. 1996a. Behavioral responses of *Anagrus nilaparvatae* Pang et Wang to the volatile of rice varieties. Entomol. J. East China 5:60-64.

Lou Yong-gen, Cheng J. 1996b. Impacts of rice variety on development, survival and fecundity of *Anagrus nilaparvatae.* Entomol. Sin. 30(1):28-36.

Lou Yong-gen, Cheng J. 1996c. Impacts of morphological characteristics of rice variety on functional response of *Anagrus nilaparvatae.* Acta Ecol. Sin. 8(3):325-331.

Lou Yong-gen, Cheng J. 2001a. Role of rice volatiles in the foraging behavior of *Cyrtorhinus lividipennis* Reuter. Entomol. Sin. 8(3):240-250.

Lou Yong-gen, Cheng J. 2001b. Host-recognition kairomone from *Sogatella furcifera* for the parasitoid *Anagrus nilaparvatae.* Entomol. Exp. Appl. 101:59-67.

Lou Yong-gen, Du M, Guo H, Zhu X, Cheng J. 2002. The indirect effects of rice varieties on growth, development, survival and fecundity of predatory mirid, *Cyrtorhinus lividipennis* Reuter. Acta Phytophyl. Sin. 29(3):205-209.

Price PW. 1986. Ecological aspects of host plant resistance and biological control: interaction among three trophic levels. In: Boethel DJ, Eikenbary RD, editors. Interactions of plant resistance, parasitoids and predators of insects. New York, N.Y. (USA): Wiley. p 11-27.

Tang QY, Hu GW, Tang J, Hu Y, Cheng JA. 1998. Relationship between outbreak frequency of *Sogatella furcifera* (Horvath) and growing area of hybrid rice. J. Southwest Agric. Univ. 20(5):456-459.

Zhu MH. 1990. Study on population dynamics of white-backed planthopper, *Sogatella furcifera* (Horvath). Insect Knowl. 27(5):257-260.

Notes

Author's address: Institute of Applied Entomology, Zhejiang University, Hangzhou 310029, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Climate change and photosynthesis

Rice production, climate change, and methane emissions: adaptation and mitigation options

R. Matthews

Various studies have indicated that, in general, rice yields are likely to increase in the higher latitudes and decrease in the lower latitudes under future climates. Other studies, where crop yield changes are used as the input into economic models, suggest that not only will the poorest countries suffer the most from climate change but also the poorest people within those countries will suffer disproportionately as they are the least likely to be able to adapt.

Various options available to farmers for adaptation to climate change are discussed. At high latitudes, modification of sowing dates should permit a transition from single cropping to double cropping at some locations, while at lower latitudes it should help to avoid severe spikelet sterility caused by high temperatures. Selection for varieties less sensitive to higher temperatures seems capable of restoring yield levels to those predicted for current climates. Options available to reduce methane emissions from rice fields to the atmosphere include midseason drainage, direct wet seeding, the use of inorganic fertilizers, particularly those containing sulfate, and the application of compost and biogas sludge rather than fresh organic material.

Future research should focus on integrated assessment approaches to evaluate adaptation and mitigation options. For developing countries, economic development is still the primary concern, and there is a need to find ways for farmers both to enhance their livelihoods on the one hand and to adapt to climate change and reduce methane emissions, if possible, on the other. Strategies to adapt to climate variability in the short term should assist adaptation to climate change in the longer term.

Because of the large increases in human population predicted for the 21st century and the associated increase in demand for food, the effects of climate change on agriculture are of considerable concern. In particular, the relationship between climatic change and rice production is important, not only because of the significance of rice as a food source throughout the world but also because recent intensification of rice production itself, particularly in the Asian region, contributes to global warming through the release of methane (CH_4) into the atmosphere. Asia currently produces about 94% of the total world production, but, to meet the demands of its rapidly expanding population, an estimated 40-60% increase is required in the next 50 years (Sheehy 2001). However, the IPCC Third Assessment (2001a) identified food insecurity as the primary concern in Asia, with crop production being threatened by thermal and drought stress, sea-level rise, increased flooding, and strong winds from tropical cyclones. There is an urgent need to find ways in which rice agriculture can adapt to these changes and yet still increase production enough to meet demand, and at the same time minimize emissions of greenhouse gases to the atmosphere.

This paper aims to review current thinking on the effects of climate change on rice production, and to discuss farmers' options for adapting to climate change and for reducing methane emissions from rice fields.

Predicted effects of future climates on rice production

In recent years, several modeling studies of the likely effects of climate change on rice production have emerged. Many of these have been limited to single countries or subregions within countries (e.g., Bangladesh-Karim et al 1996; Japan-Seino 1995; China-Zhi Qing et al 1995), while others have attempted to predict the effects of climate change on regional and global rice production. For example, Solomon and Leemans (1990) used a very simple model to predict a yield increase of 0.4% for current rice-growing environments, but little change in the areas sown. In a subsequent study, Leemans and Solomon (1993) used another model based on temperature, solar radiation, and rainfall data to estimate the effects on the production of various crops on a global scale and predicted an 11% increase in global production of rice. Rosenzweig et al (1993), working with collaborators from 18 countries, used several DSSAT (Decision Support System for Agrotechnology Transfer) crop models to simulate likely changes in the production of various crops, including rice, under different General Circulation Model (GCM) scenarios. They predicted that crop yields are likely to decline in the low-latitude regions where crops are currently grown nearer their limits of temperature tolerance, so that any warming subjects them to higher stress, but could increase in the mid and high latitudes where increased warming benefits crops currently limited by cold temperatures and short growing seasons.

Matthews et al (1995a) used the ORYZA1 and SIMRIW rice crop simulation models under scenarios predicted for a doubled-CO_2 ($2 \times CO_2$) atmosphere by the General Fluid Dynamics Laboratory (GFDL), the Goddard Institute of Space Studies (GISS), and the United Kingdom Meteorological Office (UKMO) general circulation models. Overall rice production in the South and Southeast Asian region was predicted by the ORYZA1 model to change by +6.5%, -4.4%, and -5.6% under the GFDL, GISS, and UKMO $2 \times CO_2$ scenarios, respectively, while the corresponding changes predicted by the SIMRIW model were +4.2%, -10.4%, and -12.8%. Declines in yield were predicted under the GISS and UKMO scenarios for Thailand, Bangladesh, southern China, and western India, while increases were predicted for Indonesia, Malaysia, and China (including Taiwan Province) and parts of India. Somewhat surprisingly, marked decreases were also predicted for Japan, largely because of high spikelet sterility and shortened crop durations in the south of the country, which is consistent with the 30% decline predicted by Matsui and Horie (1992). Overall, these changes are likely to have serious repercussions on regional trading patterns, as China is the major importer of rice in the region (43% of total regional imported rice) and Thailand is one of the major rice exporters (87% of total regional exported rice). Similarly, in Bangladesh, the predicted decline in production by both crop models in the GISS and UKMO scenarios is likely to increase the country's need to import even more rice than now.

Most of these studies considered only the effects of climate change on rice production and not the effects on price changes, on national economies, or on the global economy. Rosenzweig and Parry (1994), however, used a world food trade model (the Basic Linked System, Fischer et al 1988) to examine the effects of climate change on world food supply, food prices, and the number of people at risk from hunger, using three levels of adaptation: (1) no adaptation, (2) within-farm adaptation, and (3) adaptation of agricultural infrastructure, such as investment in irrigation systems. They concluded that global cereal production would fall, that cereal prices would rise, and that developing countries would suffer from climate change more than would developed countries. Winters et al (1998) extended this approach by using the predicted yield changes of Rosenzweig and Parry (1994) as inputs into general equilibrium models for Africa, Asia, and Latin America to quantify effects on household income and food consumption levels for different social classes. Results indicated that there would be a global shrinkage of trade because of reduced agricultural production, and that Africa would be affected the most and Asia the least. Poverty was predicted to increase in Africa, but, conversely, to fall in Asia. However, possible increases in global production because of a move from one crop per year to two crops per year at higher latitudes do not seem to have been taken into account in these studies, and may offset to some extent the effects being predicted.

Various other studies indicate that increases greater than +2.5 °C in mean annual temperature will prompt food prices to increase as a result of a slowing in the expansion of global food capacity relative to growth in global food demand (e.g., Reilly 1996, Adams et al 1998, Parry et al 1999). Changes in food supply are also likely to affect the nutrition and health of the poor, particularly as the risk of reduced food yields is greatest in the developing countries, where 790 million people are estimated to be undernourished already (IPCC 2001a).

How can rice agriculture adapt to climate change?

Given the time scale involved, it is highly likely that agricultural systems will adapt in response to a slowly changing climate—historically, crops have been deliberately translocated into different agroclimatic zones, new crops have replaced existing ones, and scarcity of a particular resource (e.g., energy, groundwater) has often led to the development of substitutes (Easterling 1996). In rice production systems, advancement of planting dates to allow an extra rice crop to be grown in the longer growing seasons is a possibility at the higher latitudes, whereas, at lower latitudes, changes in planting dates may help avoid the damaging high temperatures around the time of flowering, which result in spikelet sterility. Similarly, plant breeding programs will also likely develop new varieties more closely adapted to the gradually changing conditions, thereby mitigating the negative, and enhancing the positive, effects of this change. Two possible varietal adaptations that may occur are the use of varieties more tolerant of higher temperatures, particularly in relation to spikelet fertility, and the use of longer-maturing varieties to take advantage of the extended growing season in high-latitude areas (Yoshino et al 1988, Horie 1991, Okada 1991). Other options are for farmers to switch to different crops that are more suited to the new climates of the future, or to develop irrigation systems where none currently exist.

Adjustment of planting dates

Matthews et al (1995b) used the ORYZAl model to investigate how sowing dates could be adjusted to take advantage of longer growing seasons under warmer climates, At Beijing in northern China, the sowing window was predicted to widen considerably from 120 days to about 200 days under the UKMO scenario (+4.2 °C in July temperatures, 8% increase in solar radiation), allowing the possibility of two rice crops per year. If the first crop was sown from the beginning of February to the end of March and the second in June/July, the total annual production was much higher than what could be achieved with a single crop sown in early May as at present. However, yield variability was also higher, suggesting that, although a warmer climate would potentially allow a move from the current single-cropping system to double cropping, the risks associated with this change would also be greater. Similar simulations by Zhi Qing et al (1995) in another study suggested that the double-cropping zone in China might move northward by 5° latitude, although whether this is feasible also depends on the suitability of the land involved for growing rice and possibly the constraints imposed by national boundaries.

This analysis was extended to estimate the potential effect on China's national rice production brought about by a move from single cropping to double cropping in the areas where it becomes possible (Matthews et al 1995b). Taking this transition into account gave predicted changes of +44%, +37%, and +42% in overall national rice production for the GFDL, GISS, and UKMO scenarios, respectively. These were considerably higher than the corresponding values of +12.2%, +2.0%, and +5.6% calculated in the analysis of Defeng and Shaokai (1995) with no adjustment to the cropping system. If this transition occurs and other factors such as water and fertilizer do not become limiting, it would seem that the predicted changes in climate will have a beneficial effect on Chinese rice production.

A similar analysis was carried out to investigate the effect of changing planting dates to avoid high-temperature spikelet sterility in currently warm climates (Matthews et al 1995b). At Madurai in India, for example, all three future scenarios were predicted to reduce rice yields considerably, with the approximately +3.5 °C predicted increase taking temperatures above the critical value beyond which spikelet sterility increases sharply. Delaying planting by one month to avoid these high temperatures in September, when flowering currently occurs, resulted in a restoration of yields, although this delay meant that the following dry-season crop would also be planted later, thereby moving its flowering time into a high-temperature period. Thus, while adjustment of planting dates may be able to maintain yields in the main planting season, often a second crop may not be attainable and total annual production may fall.

Farmers may also change planting dates to take advantage of the wet period and to avoid extreme weather events (e.g., typhoons) during the growing season (IPCC 2001a).

Selection for increased tolerance of spikelet fertility for temperature

In rice, spikelet fertility is very sensitive to temperatures in the region of 33 °C, at which a difference of +1 °C can result in a modest yield increase becoming a large yield decrease. Considerable variation among genotypes in response to high temperatures has been shown to exist (Satake and Yoshida 1978), mainly through avoidance of high midday temperatures by flowering earlier in the morning. To evaluate the effects of selecting for less temperature-sensitive genotypes, Matthews et al (1995b) assumed a +2 °C shift in the response of spikelet fertility to daily maximum temperature, predicting that regional rice production would change by +14.9%, +15.6%, and +12.9% under the GFDL, GISS, and UKMO scenarios, respectively, if this were to occur. Comparing these figures with those of +6.5%, -4.4%, and -5.6% without this adaptation (Matthews et al 1995a), the use of temperature-tolerant genotypes would appear to be able to more than offset the detrimental effect of increased temperatures under future climates.

Other adaptation options

For farmers in a given area, another adaptation option is to switch to crops that are more suited to the new climates they will experience. Often this might mean just adopting crops and cropping practices from neighboring agroecological zones. For example, Zhi Qing et al (1995) suggested that using upland rice cultivars instead of paddy rice cultivars could help to offset the detrimental effects of sharp decreases in rainfall predicted for some areas of China. More expensive, higher-level adaptations, such as changing land-use allocations and developing and using irrigation infrastructure, have been examined in a small but growing number of linked crop-economic models, integrated assessment models, and econometric models (IPCC 2001a).

How can methane emissions from rice agriculture be minimized?

Rice paddy soils, characterized by O_2 depletion, high moisture, and relatively high organic substrate levels, offer an ideal environment for the activity of methanogenic bacteria, and are one of the major anthropogenic CH_4 sources. This is of particular concern, as it has been estimated that the increase in rice production required to meet the demands of an increased population may *increase* CH_4 production by up to 50% (Bouwman 1991). Options to mitigate the rates of emission of CH_4 from rice fields into the atmosphere have been discussed by Neue et al (1995a) and Yagi et al (1997), and generic strategies to reduce emission rates have been devised (e.g., Minami 1997). The most scope for reducing CH_4 emissions from rice agriculture appears to be in irrigated rice ecosystems, whereas rainfed and deepwater rice offer few options (Wassmann et al 2000). In the following, we discuss the main options that have been examined in experiments and modeling.

Water management

As CH_4 is produced only in anaerobic conditions, introducing O_2 into the paddy soil can markedly reduce seasonal emissions (Ratering and Conrad 1998). Draining the field during the growing season, for example, has been shown to reduce seasonal emissions by up to 80% (depending on the baseline used) without reducing rice yields (e.g., Wassmann et al 2000), and is even used extensively in China to increase crop yields by restricting unproductive vegetative growth. Experimental and simulation studies have shown that, in the dry season, drainage periods for less than about a week do not affect yields but can reduce CH_4 emissions significantly (Matthews et al 2000a, Wassmann et al 2000). The disadvantage, however, is that nearly three times as much water may be used over the season (Sass et al 1992) and water for reflooding may not always be available at the right time, particularly in the dry season. In addition, not all rice-growing land is suitable for drainage (Kern et al 1997). In the rainy season, completely controlled flooding is often not possible anyway. Another disadvantage is that periodic draining can increase emissions of the greenhouse gas N_2O (Bronson et al 1997), although calculations by Wassmann et al (2000) suggest that these are not enough to offset the CH_4 mitigation potential.

Increasing rates of percolation of water through the soil may also reduce CH_4 emissions by increasing the rate of O_2 supply to reduce CH_4 production and by carrying dissolved CH_4 into the groundwater, where it is oxidized or emitted elsewhere (e.g., Kimura et al 1992). It has been suggested that this is the cause of the relatively low rates of CH_4 emission from rice paddies in India (Mitra 1992, 1999).

Dry-seeded rice, in which fields are flooded only after crop establishment, can also reduce seasonal CH_4 emissions because of the shorter period in which the field is flooded (Sass et al 1992), but this approach requires mechanization and greater attention to weed control. Direct wet seeding, in which pregerminated seeds are directly seeded on puddled fields without standing water and with the field reflooded 2-3 weeks after crop establishment, has also been shown to reduce CH_4 emissions by 16-22% (Wassmann et al 2000). Although yields are generally lower with this practice, the savings in labor costs make it economically viable.

Inorganic fertilizers

In general, fertilizer increases plant growth and hence CH_4 emissions. However, specific fertilizers can reduce CH_4 production through their effect on soil chemistry. For example, nitrate-containing fertilizers increase soil redox potential (Eh) and reduce the rate and total quantity of CH_4 produced. Similarly, CH_4 production has been reduced by the application of sulfate-containing compounds (e.g., ammonium sulfate [Schutz et al 19891, sodium sulfate [Lindau et al 1993], and phosphogypsum [Corton et al 2000]) because of sulfate-reducing bacteria outcompeting methanogenic bacteria for substrate from organic matter decomposition. The replacement of urea with ammonium sulfate has been found to reduce CH_4 emissions with little or no yield loss, and it is also easy to handle, store, and apply, although its cost may limit its usefulness in this regard (Wassmann et al 2000). In addition, the presence of sulfate in acid rain opens up the intriguing possibility of methane emissions from rice fields being suppressed by the increasing levels of industrial pollution in Asia (e.g., Dise and Veny 2001), although the rates of $SO_4{}^{2-}$ application reported to give a response (approximately 25 kg $SO4^{2-}$ -S had) are considerably less than those used in most field experiments (e.g., 95–1,250kg $SO4^{2-}$ -S ha^{-1} , Corton et al 2000).

Matthews et al (2000a) used the MERES simulation model to investigate the effect of applications of phosphogypsum (PG, mainly calcium sulfate, but so named as it is a by-product during the manufacture of phosphoric acid for fertilizers) on CH_4 emissions and found that there was an initial rapid decline in emissions of about 35% as the application rate increased to about 4,000 kg PG ha^{-1} (approximately 600 kg $SO_4{}^{2-}$-S ha^{-1}), after which the response leveled off. This response was consistent with the field observations in the Philippines of a 27–37%reduction in seasonal emissions with the application of 3,000 kg PG ha^{-1} (Wassmann et al 2000). In practical terms, however, the enhanced levels of radioactivity found in PG (e.g., Luther et al 1993) may be a problem with its use to reduce $CH4$ emissions.

Organic amendments

As the decomposition of organic matter in the soil is the source of substrate for methanogenic bacteria, CH_4 production and emission are usually increased by the addition of organic material (e.g., Schutz et al 1989, Yagi and Minami 1990). For example, Sass et al (1991) found that the incorporation of crop residues doubled CH, emission rates compared with when the residues were removed. Both quantity and quality are important—for example, the incorporation of sludge from biogas generators reduced CH_4 emissions by 60% compared with the incorporation of unfermented manure (Wassmann et al 1994). Biogas production has the dual benefit of reducing net CO_2 emissions through the use of a renewable resource and reducing CH_4 emissions from rice fields by replacing fresh material with prefermented material. Composting and mulching of rice straw can also significantly reduce emissions compared with fresh rice straw, although this involves more labor (Wassmann et al 2000).

Ideally, to reduce CH_4 emissions from rice agriculture, the addition and recycling of organic material should be minimized. However, organic matter is an important source of nutrients, particularly for resource-poor farmers, and is a major contributor to long-term soil fertility. Notwithstanding, in many countries, crop residues are removed from the field and used as fodder or fuel, or alternatively may be burned to save the labor and time involved in recycling. Straw burning, however, releases significant quantities of other greenhouse gases such as CO, $CO2$, and $N2O$ (Miura and Kanno 1997). Overall, as chemical fertilizers become more widely used, the use of organic manures is declining, although CO_2 emissions in the production of chemical fertilizers may more than offset any mitigation effect on CH_4 emissions.

Rice cultivars

Depending on the time of season, up to 90% of the CH_4 emitted from rice fields is through the plants via their aerenchyma (Holzapfel-Pschorn et al 1986). The aerenchyma also act as a conduit for O_2 to reach the roots and the rhizosphere where methanotropic bacteria are able to oxidize CH_4 to CO_2 (Schütz et al 1989). A large root system, therefore, might be expected to result in less CH_4 being emitted, but root senescence and exudation (collectively termed *rhizodeposition*) are also major sources of substrate for methanogenic bacteria. Varietal differences in root oxidation power (Neue and Roger 1993), root exudation rates (Aulakh et al 2001), and CH_4 emission rates (Parashar et al 1990, Mitra 1999, Aulakh et al 2002) have been reported.

Matthews et al (2000a) used the MERES model to investigate the relative importance of rhizodeposition and oxidation rates, and found that across a wide range of root/shoot ratios the CH_4 emission rates remained almost constant, suggesting that each canceled the other out. However, this depended on several assumptions, in particular that the O_2 flux rate through the aerenchyma was proportional to the rhizosphere size. Thus, although some studies have reported a correlation between root system size and CH_4 emission rates (e.g., Wang et al 1997), it is still not really clear which genotype characteristics should be selected for to reduce CH_4 emission potential. Even within a given genotype, there is a large variation in CH_4 emission potential under different environmental conditions and phenological stages (Aulakh et al 2000).

Future research

Most of the studies on the effects of climate change on rice production so far have used equilibrium scenarios following an instantaneous doubling of atmospheric CO_2 concentration from a baseline. In recent years, however, substantial progress has been made in the development of transient scenarios of climate change for use in agricultural impact assessment (IPCC 2001a). The limited number of studies so far that have compared predicted yields under equilibrium and transient scenarios have usually found more benign effects on yield (sometimes even positive) under the latter even though the final climate may be the same (e.g., Semenov et al 1996, Smith et al 1996, Rosenzweig and Iglesias 1998). This has usually been explained by the cumulative “memory” that most crop models have for some variables, such as soil water and nutrient contents. As transient changes are most likely to occur in reality, there is clearly a need for further research in this area, which should also consider transient adaptation of crop management practices.

There is also a need to investigate the effect of sea-level changes on rice production. Several of the rice-growing areas in Asia are coastal or low-lying (e.g., Bangladesh), which may disappear if the sea level were to rise, but which may be extended if it were to fall. Earlier studies ignored this problem as there was considerable uncertainty at the time about whether sea levels would rise or fall under future climates (Schneider 1992). Since then, based upon a "best estimate" of the elements of climate change, the average of several estimates suggests that sea level may rise by almost 50 cm from the present to 2100, although individual estimates have ranged from 9 to 88 cm (IPCC 2001b).

For methane production estimates, there is a need to refine the estimates of the size of the alternative electron acceptor (AEA) pool in different rice-growing soils. Soil iron content seems to be a good proxy parameter (Matthews et al 2000b), but it is not known to what extent the proportion of the active component of the AEA varies between different soils. Related to this, there is a need to clarify more precisely the effect of the individual ions involved in the AEA (i.e., NO_3^-, Fe^{3+}, Mn^{4+}, and SO_4^{2-}), work which is currently under way (van Bodegom et al 2000).

There is a need to integrate the results of a large number of studies of different components of climate change. Rice production is influenced by increasing CO_2 and temperature, but in turn influences CH_4 emissions into the atmosphere. Nitrous oxide, another greenhouse gas, is also emitted from flooded rice fields under certain conditions, but more detailed studies are required to investigate which crop management options result in the least detrimental effect overall on the environment, taking into account all of these factors. Similarly, the interactions of rice/weed populations are of interest, given the stimulatory effects of increasing CO_2 concentrations on photosynthesis and growth. If weeds respond to a greater extent than rice, indirect decreases in rice production could also occur. Given the genetic diversity of native weeds in relation to cultivated rice, this seems a distinct possibility (Neue et al 199b).

To give any credibility to forecasts on changes in regional rice production as a result of climate change, it is probably more important to predict changes in land use, and hence the area of rice cultivation, rather than improving estimates of changes in crop yields. However, predictions so far of these types of changes have been very uncertain, mainly because of the limited capacity of most models to consider the full range of variables that determine potential shifts in cropland. Moreover, the situation is complicated by such factors as the development of new varieties that are able to grow where current varieties are not able to, advances in biotechnology, and also advances in crop protection from pests and diseases.

Most climate-change impact studies to date have investigated particular aspects of climate change (e.g., crop production) in isolation. In reality, however, climate change involves complex interactions among environmental, economic, social, political, institutional, and technological processes. Moreover, adaptation must be addressed in relation to broader societal goals such as sustainable development and equity within and between nations, and also in relation to other existing or possible types of stress. Some attempts at this have been described above (e.g., Rosenzweig and Parry 1994, Reilly 1996, Adams et al 1998, Winters et al 1998, Parry et al 1999). However, first, the adaptation strategies simulated are usually limited compared to the total range of possibilities, which may underestimate the capacity to adapt. Second, it is usually assumed that farmers have perfect knowledge about how the climate is changing, which may overestimate the effectiveness of the adaptations being considered (Schneider et al 2000). The question is how local decisions made at a household level based on imperfect knowledge collectively contribute to changes in land use over time, and how this influences, and is influenced by, global variables such as climate change.

The developing field of complex adaptive systems (CAS), and multi-agent simulation (MAS) in particular, may offer approaches that may help to deal with these issues. Central to this approach is how the aggregated behavior of a large number of components can lead to emergent behavior at a higher level. The global biosphere is an example of a complex adaptive system, as its components can (and do) adapt and reorganize themselves in response to changes from both within and without. A start has already been made using CAS approaches in understanding responses to climate change—Janssen and de Vries (1998), for example, developed a multi-agent model in which the agents had different worldviews (i.e., hierarchists, egalitarians, individualists) influencing the way they responded to climate change. Agents could modify their worldviews if there was a discrepancy between what they expected and what they observed. In the context of rice agriculture, a start could be made by classifying farmers as risk takers, risk avoiders, or midway between these extremes, and seeing which worldview would predominate under different climate-change scenarios.

Conclusions

Considerable progress has been made in understanding how the rice crop responds to the biophysical aspects of climate change such as increased temperatures and CO_2 levels, and also how methane emissions are influenced by soil processes and crop management. Various ways in which crop management can be adjusted to help rice farmers adapt to future climates and minimize CH_4 emissions have also been identified. However, as the emphasis in developing countries shifts more to adaptation to, rather than mitigation of, climate change, future research needs to focus more on adaptive strategies of farming households and of the overall agricultural systems of which rice production is a part. Initial studies have indicated that those who have the least resources and are least able to adapt are the ones likely to be most affected. Efforts need to be made to improve the ability of these people to adapt, but it is important to remember that adaptation is not cost-free. Developing “no-regrets’’ strategies that will be of benefit in both the short term and the long term, such as new crop varieties, seed banks, improved efficiency of water use, and rehabilitation of degraded forests, would appear to be a sensible way forward. In addition, developing ways of identifying both internal and external innovation within farming systems and enhancing the flow of information on these innovations are crucial to improving adaptability.

References

Adams RM, Hurd BH, Lenhart S, Leary N. 1998. Effects of global climate change on agriculture: an interpretive review. Clim. Res. 11:19-30.

Aulakh M, Wassmann R, Bueno C, Kreuzwieser J, Rennenberg H. 2001. Characterization of root exudates at different growth stages of ten rice (*Oryza sativa* L.) cultivars. Plant Biol. 3(2):139-148.

Aulakh MS, Bodenbender J, Wassmann R, Rennenberg H. 2000. Methane transport capacity of rice plants. II. Variations among different rice cultivars and relationship with morphological characteristics. Nutr. Cycl. Agroecosyst. 58:367-375.

Aulakh MS, Wassmann R, Rennenberg H. 2002. Methane transport capacity of twenty-two rice cultivars from five major Asian rice-growing countries. Agric. Ecosyst. Environ. 91:59-71.

Bouwman AF. 1991. Agronomic aspects of wetland rice cultivation and associated methane emissions. Biogeochemistry 15:65-88.

Bronson KF, Neue HU, Singh U, Abao EB. 1997. Automated chamber measurements of methane and nitrous oxide flux in a flooded rice soil. I. Residue, nitrogen, and water management. Soil Sci. Soc. Am. J. 61(3):981-987.

Corton TM, Bajita JB, Grospe FS, Pamplona RR, Asis Jr, CA, Wassmann R, Lantin RS, Buendia LV. 2000. Methane emission from irrigated and intensively managed rice fields in Central Luzon (Philippines). Nutr. Cycl. Agroecosyst. 58:37-53.

Defeng Z, Shaokai M. 1995. Rice production in China under current and future climates. In: Matthews RB, Kropff MJ, Bachelet D, van Laar HH, editors. Modelling the impact of climate change on rice production in Asia. Wallingford (UK): IRRI/CAB International. p 217-235.

Dise NB, Verry ES. 2001. Suppression of peatland methane emission by cumulative sulfate deposition in simulated acid rain. Biogeochemistry 53:143-160.

Easterling WEI. 1996. Adapting North American agriculture to climate change in review. Agric. For. Meteorol. 80:1-53.

Fischer G, Frohberg K, Keyzer MA, Parikh KS. 1988. Linked national models: a tool for international food policy analysis. Dordrecht (Netherlands): Kluwer.

Holzapfel-Pschorn A, Conrad R, Seiler W. 1986. Effects of vegetation on the emission of methane by submerged paddy soil. Plant Soil 92:223-233.

Horie T. 1991. Model analysis of the effect of climatic variation on rice yield in Japan. In: Geng S, Cady CW, editors. Climatic variation and change: implications for agriculture in the Pacific Rim. Davis, Calif. (USA): University of California.

IPCC. 2001a. Climate change 2001: impacts, adaptation & vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge (UK): Cambridge University Press. 1,000 p.

IPCC. 2001b. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge (UK): Cambridge University Press. 944 p.

Janssen M, de Vries B. 1998. The battle of perspectives: a multi-agent model with adaptive responses to climate change. Ecol. Econ. 26:43-65.

Karim Z, Hussain SG, Ahmed M, Erda L. 1996. Assessing effects of climatic variations on foodgrain production in Bangladesh. Water Air Soil Poll. 92(1-2):53-62.

Kern JS, Gong Z, Zhang G, Zhuo H, Luo G. 1997. Spatial analysis of methane emissions from paddy soils in China and the potential for emissions reduction. Nutr. Cycl. Agroecosyst. 49:181-195.

Kimura M, Miura Y, Watenabe A, Murase J, Kuwatsuka S. 1992. Methane production and its fate in paddy soils. I. Effects of rice straw application and percolation rate on the leaching of methane and other soil components into the subsoil. Soil Sci. Plant Nutr. 38:665-672.

Leemans R, Solomon AM. 1993. Modeling the potential change in yield and distribution of the earth's crops under a warmed climate. Clim. Res. 3:79-96.

Lindau CW, Bollich PK, DeLaune RD, Mosier AR, Bronson KF. 1993. Methane mitigation in flooded Louisiana rice fields. Biol. Fertil. Soils 15:174-178.

Luther SM, Dudas MJ, Rutherford PM. 1993. Radioactivity and chemical characteristics of Alberta phosphogypsum. Water Air Soil Poll. 69(3-4):277-290.

Matsui T, Horie T. 1992. Effects of elevated CO_2 and high temperature on growth and yield of rice. Part 2: Sensitive period and pollen germination rate in high temperature sterility of rice spikelets at flowering. Jpn. J. Crop Sci. 61:148-149.

Matthews RB, Kropff MJ, Bachelet D, van Laar HH. 1995a. Modeling the impact of climate change on rice production in Asia. Wallingford (UK): IRRI/CAB International. 289 p.

Matthews RB, Kropff MJ, Horie T, Bachelet D. 1995b. Simulating the impact of climate change on rice production in Asia and evaluating options for adaptation. Agric. Syst. 54:399-425.

Matthews RB, Wassmann R, Buendia L, Knox J. 2000a. Using a crop/soil simulation model and CIS techniques to assess methane emissions from rice fields in Asia. II. Model validation and sensitivity analysis. Nutr. Cycl. Agroecosyst. 58:161-177.

Matthews RB, Wassmann R, Knox JW, Buendia L. 2000b. Using a crop/soil simulation model and GIS techniques to assess methane emissions from rice fields in Asia. IV. Upscaling of crop management scenarios to national levels. Nutr. Cycl. Agroecosys. 58:201-217.

Minami K. 1997. Atmospheric methane and nitrous oxide: sources, sinks and strategies for reducing agricultural emissions. Nutr. Cycl. Agroecosyst. 49:203-211,

Mitra AP. 1992. Greenhouse gas emission in India: 1991 methane campaign. Council of Scientific and Industrial Research and Ministry of Environment and Forests. New Delhi, India.

Mitra S. 1999. Effect of rice cultivars on methane emission. Agric. Ecosyst. Environ. 73(3):177-183.

Miura Y, Kanno T. 1997. Emissions of trace gases (CO_2, CO, CH_4 and N_2O) resulting from rice straw burning. Soil Sci. Plant Nutr. 43:849-854.

Neue H-U, Roger PA. 1993. Rice agriculture: factors controlling emissions. In: Khalil MAK, editor. Atmospheric methane: sources, sinks, and role in global change. Springer-Verlag (Berlin): NATO ASI Series. p 254-298.

Neue H-U, Wassmann R, Lantin RS. 1995a. Mitigation options for methane emissions from rice fields. In: Peng S, Ingram KT, Neue H-U, Ziska LH, editors. Climate change and rice. Berlin (Germany): Springer Verlag. p 136-144.

Neue H-U, Ziska LH, Matthews RB, Qiujie D. 1995b. Reduced global warming: the role of rice. GeoJournal 35:351-362.

Okada M. 1991. Variations of climate and rice production in Northern Japan. In: Geng S, Cady CW, editors. Climate variations and change: implications for agriculture in the Pacific Rim, Davis, Calif. (USA): University of California.

Parashar D, Rai CJ, Gupta PK. Singh N. 1990. Parameters affecting methane emission from rice paddies. Indian J. Radio Space Physics 20:12-17.

Parry M, Fischer C, Livermore M, Rosenzweig C, Iglesias A. 1999. Climate change and world food security: a new assessment. Global Environ. Change 9:S51-S67.

Ratering S, Conrad R. 1998. Effects of short-term drainage and aeration on the production of methane in submerged rice soil. Global Change Biol. 4(4):397-407.

Reilly J. 1996. Agriculture in a changing climate: effects and adaptation. In: Watson RT, Zinyowera MC, Moss RH, editors. Climate change 1995: impacts, adaptations, and mitigation of climate change: scientific-technical analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press. p 429-467.

Rosenzweig C, Iglesias A. 1998. The use of crop models for international climate change impact assessment. In: Tsuji CY, Hoogenboom G, Thornton PK, editors. Understanding options for agricultural production: systems approaches for sustainable agricultural development. Dordrecht (Netherlands): Kluwer Academic Publishers. p 267-292.

Rosenzweig C, Parry M. 1994. Potential impact of climate change on world food supply. Nature 367:133-138.

Rosenzweig C, Parry ML, Fischer G, Frohberg K. 1993. Climate change and world food supply. 3. Environmental change unit, University of Oxford.

Sass RL, Fisher FM, Harcombe PA, Turner FT. 1991. Mitigation of methane emissions from rice fields: possible adverse effects on incorporated rice straw. Global Biogeochem. Cycles 5:275-287.

Sass RL, Fisher FM, Wang YB, Turner FT, Jund MF. 1992. Methane emission from ricefields: the effect of flood water management. Global Biogeochem. Cycles 6:249-262.

Satake T, Yoshida S. 1978. High temperature-induced sterility in indica rice at flowering. Jpn. J. Crop Sci. 47:6-17.

Schneider SH. 1992. Will sea levels rise or fall? Nature 356:11-13.

Schneider SH, Easterling WE, Mearns LO. 2000. Adaptation: sensitivity to natural variability, agent assumptions and dynamic climate changes. Clim. Change 45:203-221.

Schutz H, Holzapfel-Pschorn A, Conrad R, Rennenberg H. 1989. A three-year continuous record on the influences of daytime, season and fertiliser treatment on methane emission rates from an Italian rice paddy. J. Geophys. Res. 94:405-416.

Seino H. 1995. Implications of climate change for crop production in Japan. In: Climate change and agriculture: analysis of potential international effects. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis. Minn., 4-5 Nov. 1992. Madison, Wis. (USA): American Society of Agronomy. p 293-306.

Semenov MA, Wolf J, Evans LC, Eckersten H, Iglesias A. 1996. Comparison of wheat simulation models under climate change. 2. Application of climate change scenarios. Clim. Res. 7:271-281.

Sheehy JE. 2001. Will yield barriers limit future rice production? In: Nosberger J, Geiger HH, Struik PC, editors. Crop science: progress and prospects. Wallingford (UK): CAB International. p 281-305.

Smith JB, Huq S, Lenhart S, Mata LJ, Nemesova I, Toure S. 1996. Vulnerability and adaptation to climate change: interim results from the U.S. Country Studies Program. Dordrecht (Netherlands): Kluwer Academic Publishers. 366 p.

Solomon AM, Leemans R. 1990. Climatic change and landscape-ecological response: issues and analysis. In: Boer MM, de Groot RS. editors. Landscape-ecological impact of climate change. Amsterdam (Netherlands): IOS Press. p 293-316.

van Bodegom PM, Wassmann R, Metra-Corton TM. 2000. A process-based model for methane emission predictions from flooded rice paddies. Global Biogeochem. Cycles 15(1):247-263.

Wang B, Neue HU, Samonte HP. 1997. Effect of cultivar difference ('IR72', 'IR65598', and 'Dular') on methane emission. Agric. Ecosyst. Environ. 62:31-40.

Wassmann R, Lantin RS, Neue HU, Buendia LV, Corton TM, Lu Y. 2000. Characterisation of methane emissions from rice fields in Asia. III. Mitigation options and future research needs. Nutr. Cycl. Agroecosyst. 58:23-36.

Wassmann R, Neue H-U, Lantin RS, Aduna JB, Alberto MCR, Flores MJF, Tan MJP, Denier van der Gon HAC, Hoffmann H, Papen H, Rennenbeg H. Seiler W. 1994. Temporal patterns of methane emissions from wetland rice fields treated by different modes of N-application. J. Geophys. Res. 99:16457-16462.

Winters P, Murgai R, Sadoulet E, Frisvold G, De Janvry A. 1998. Economic and welfare impacts of climate change on developing countries. Environ. Res. Econ. 12(1):1-24.

Yagi K, Minami K. 1990. Effect of organic matter application on methane emission from some Japanese paddy fields. Soil Sci. Plant Nutr. 36599-610,

Yagi K, Tsuruta H, Minami K. 1997. Possible options for mitigating methane emission from rice cultivation. Nutr. Cycl. Agroecosyst. 49(1-3):213-220.

Yoshino MM, Horie T, Seino H, Tsujii H, Uchijima T, Uchijima Z. 1988. The effect of climatic variations on agriculture in Japan. In: Parry ML. Carter TR, Konijn NT, editors. The impact of climate variations on agriculture. Volume 1: Assessments in cool temperate and cold regions. Dordrecht (Netherlands): Kluwer Academic Publishers. p 853-868.

Zhi Qing J, Dao Kuo G, Chen H, Fang J. 1995. Effects of climate change on rice production and strategies for adaptation in southern China. In: Climate change and agriculture: analysis of potential international impacts. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis, Minn., 4-5 Nov. 1992. Madison, Wis. (USA): American Society of Agronomy. p 307-323.

Notes

Author's address: Institute of Water and Environment, Cranfield University, Silsoe, Bedfordshire MK45, 4DT. United Kingdom.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Climate change and its effects on rice in China

Lin Erda, Xiong Wei, and Ma Shiming

Global climate change caused by more greenhouse gas emissions resulting from human activities has been a concern for more than 10 years because it will cause adverse effects on many economic sectors and some regions. The expected range of global warming in 2100 based on 35 emission scenarios is 1.4-5.8 °C. Several impact studies show that agriculture, water resources, coastal zones, and ecosystems are the most affected areas in China because of similar temperature-change trends in most parts of China.

The observed effects of changes in regional climate warming that are relevant to agriculture are related to increasing yield trends in northeast China, longer growing seasons in northern China, improved cotton quality in Xingjiang, and the expansion and advanced phenologies of agricultural pests. But several simulation studies show that rice production would face adverse effects because of a shorter growth period caused by continuous warming climate. Asia has the world's largest area under cereal cultivation and is the largest producer of rice, but by 2010 per capita availability of land in the developing countries of Asia will shrink from the current 0.8 ha to about 0.3 ha. Current rates of land degradation suggest that a further 1.8 million km^2 of farmland could become unproductive by 2050, adding climate stress to a system that must ensure food security in the context of a rapidly growing population.

To further understand the potential effects on rice production in China, two transient general circulation models (GCMs) are being used as the scenarios of climate change, joining the Chinese Weather Generator developed by us and the CERES-rice3.5 model, which were adjusted where necessary to ensure that they could be applied to China to simulate effects on yield. The results show that (1) rice yield will tend to decrease in the main rice areas of China in both 2030 and 2056, (2) CO_2 abatement by 0.5% will not change the trend, and (3) in some regions of high altitude suitable for rice growth in the future, such as in southwestern China, rice yield will tend to increase.

To further reduce uncertainties, a new simulation study is being carried out. A rice model developed by R. Matthews was adopted, in which the spatial simulation was improved. New climate-change scenarios are using baselines of 2025, 2050, and 2080 under two emission scenarios. All scenarios are simulated by the Hadley Centre's RCM-PRECIS (Providing Regional Climates for Impact Studies). The resolution of the regional GCMs is 50 km x 50 km. FAO soil data and rice experimental data of 1978-2001 from all China were used, and long-term land-use changes reflecting socioeconomic development were considered. More exact mapping results are expected soon.

Over the next century, most projections of human-induced climate change fall into ranges of about a 1.4 to 5.8 °C increase in annual global mean surface temperature compared with 2000 (although outlier estimates on both ends of the range can be found in the literature), and a 9 to 88 cm rise in mean sea level (IPCC 2001). Such changes, particularly at the higher ends of the ranges given, represent significant deviations from the climatic conditions of recent centuries. As noted above, warming of the climate and a rise in sea level would continue for centuries beyond 2100.

The projected studies in China show that the area-averaged annual mean warming would be about 2.5–3 °C in China (Zhang and Wang 1993). The maximal value of warming would occur in Northeast China, with 4.33 °C (120°E and 50°N), and the minimum would be in North Tibet, with 2.09 °C (90°E and 35°N). Northeast and Northwest China will be among the most warm-vulnerable regions.

Greenhouse gas-induced changes in climate would have an important effect on agriculture, with the most severe negative effects probably occurring in the regions of high present-day vulnerability that are least able to adjust technologically to such effects. Crop production would be threatened by a combination of thermal and water stresses, sea-level rise, increased flooding, and strong winds associated with intense tropical cyclones. Because of climate change, the main risks of crop productivity would increase. Studies have estimated that the yield potential of the main crops—wheat, rice, and maize—in China will fall by 5-10% under an equilibrium doubled CO_2 climate (Ding 2002). Increased precipitation intensity, particularly during the summer monsoon, could increase flood-prone areas in the temperate and tropical region. There is a potential for drier conditions in arid and semiarid areas during the summer, which could lead to more severe droughts and soil degradation. Food security in the region would be under a tremendous threat. Warmer and wetter conditions should favor pests, diseases, and weeds in South China (Dai 1997). On the other hand, warming would extend the growing period of crops in northern China. In the south part of Northeast China, a cropping system of two crops per year instead of one would be possible, with an increasing yield trend of crops, since the crop growing period would be extended by warming, which leads to a rise in the accumulated temperature (Zhang 2000). There is a similar warming in Xinjiang. Therefore, cotton quality in this region would be improved under an equilibrium doubled CO_2 climate (Lin 1997).

Rice and climate change

Rice is an important food crop for Asia's population. The total area planted to rice is only slightly smaller than the total area planted to either wheat or maize in Asia and more than half of Asia's population depends on rice as its main source of calories and protein. In 1997, rice provided about 700 calories per person per day for about 2.9 billion people, most of whom live in the developing countries of Asia and Africa. During the 1990s, rice production and productivity in Asia grew at a much slower rate than the population. Yield deceleration of rice (the annual growth rate declined from 2.8% in the 1980s to 1.1% in the 1990s) in Asia has been attributed to less land, water scarcity, indiscriminate addition and inefficient use of restorer inputs such as inorganic fertilizers, pesticides, etc., and increased rice imports (Indonesia, the Philippines, etc.). Several other factors have also contributed to the productivity stagnation and the decline of rice (lower output/input ratio) in the intensive cropping system (2–3 rice crops per year). The current yield gap ranges from 10% to 60% between attainable and economically exploitable yields depending on the ecosystem and country. Adverse environments (rainfed and flood-prone) have the highest yield gaps. The yield gaps between rice farmers and research stations in several Asian countries have reached 40–50% because of the environmental effects of the shifting cultivation of upland rice. The key factors currently contributing to the yield gap in different countries of Asia are biophysical, technical/management, socioeconomic, institutional/policy, technology transfer, and adoption/linkage problems.

For rice, the amylose content of the grain, a major determinant of cooking quality, increases under elevated CO_2 (Conroy et al 1994). Cooked rice grain from plants grown in high-CO_2 environments would be firmer than that of today's plants. However, concentrations of iron and zinc, which are important for human nutrition, would be lower. Moreover, the protein content of the grain decreases under combined increases in temperature and CO_2 (Ziska et al 1997).

Several simulation studies (Table 1) show that rice production would face adverse effects because of the shorter growth period caused by continuous warming climate. Higher temperatures reduce productivity because of the combined effects of reduced vegetative growth and spikelet sterility or abortion caused by heat injury during emergence (Matsui and Horie 1992). Although the adverse effects occur to a different extent in the different regions, rice yield in China is expected to decline (Lin 1997). The projected decline in potential yield and total production of rice in China and in some Asian countries because of changes in climate and climatic variability would have a significant effect on trade in agricultural commodities, and hence on economic growth and stability (Matthews et al 1995a). The decline in rice yield is caused by a shortening of the growth period, a decrease in photosynthesis ability, and an increase in respiration; water availability may also become a problem.

Asia has the world's largest area under cereal cultivation and is the largest producer of rice (FAO 1999), but by 2010 per capita availability of land in the developing countries of Asia will shrink from the current 0.8 ha to about 0.3 ha. Current rates of land degradation suggest that a further 1.8 million km^2 of farmland could become

Table 1. Recent studies on the effects of climate change on rice.

Study	Geographic scope	Climate scenario (GCMs are doubled CO_2, unless otherwise noted)	Yield effect without adaptation (range across GCMs unless otherwise noted)	Yield effect with adaptation (range across GCMs unless otherwise noted)	Socioeconomic effect
Parry et al (1997)	Global	Transient scenarios: 4 HadCM2 ensemble scenarios, one HadCM3 scenario (both assume IS92a forcing)		All cereals by 2080s LA: –10% to +10% WE: 0 to +3% NA, EE, AF: –10% to +3% AS: –10% to +5%	By the 2080s: global cereal production: -4% to –2%; cereal prices: +13% to +45%
Yates and Strzepek (1998)	Egypt	GFDL and UKMO doubled CO_2 equilibrium scenarios, GISS-A transient scenario at doubled CO_2	Rice: –27% to –5%	Rice: –13% to –3%	Change in selected economic indicators, consumer-producer surplus: –3% to +6% cal/day: –1% to +5% trade bal.: –15% to +36%
Rosenzweig and Iglesias (1998)	Global	Sensitivity analysis: +2, +4 °C	+4 °C: -8% (rice)	Adaptation more successful at high and mid latitudes than at low latitudes	
Winters et al (1999)	Africa, Asia, Latin America	GISS, GFDL, and UKMO		Africa: 0 Asia: –12% to –3% Latin America: –26% to –9%	Agricultural prices: Africa: –9% to +56% Asia: –17% to +48% L. America: –8% to +46%

continued on next page

Table 1. continued

Study	Geographic scope	Climate scenario (GCMs are doubled CO_2, unless otherwise noted)	Yield effect without adaptation (range across GCMs unless otherwise noted)	Yield effect with adaptation (range across GCMs unless otherwise noted)	Socioeconomic effect
Matthews et al (1995b)	Asia	Sensitivity analysis: +1, +2, +4 °C; GFDL, GISS, and UKMO	+1 °C: -7% to +26% +4 °C: -31% to -7% and -8% to +5%	+14% to +27% (with change in variety)	China: +37% to +44% (with change in cropping system); Region: +13% to +25% (with change in variety)
Wei Xiong et al (2001)	China	HadCM2, ECHAM	-20.1% to -6.8%	-3.47% to +8.23% (with enhanced CO_2)	CO_2 abatement by 0.5% will not change the trends

unproductive by 2050, adding climate stress to a system that must ensure food security in the context of a rapidly growing population. Asian rice monoculture may be reaching productivity limits because of adverse effects on soils (Pingali 1994).

The annual increase in rice paddy production in Asia jumped from 198.7 to 533.5 million t and the harvested area increased from 106.9 million ha in 1961 to 136.5 million ha in 1999. The Asian population increased a little more than twofold from 1.70 billion to 3.58 billion during this time. Yet, per capita consumption of calories in Asia has increased since the 1960s (FAO 1999). This improvement in the food situation has come from an increase in production resulting from the technological advances during this time that have outpaced the growth of the population in Asia. However, because there is a limit to the amount of arable land, while the Asian population continues to grow, the per capita harvested area has consistently decreased. Although cereal production has continued to increase relatively strongly, the per capita harvested area has, in contrast, decreased overall.

The effects of global warming on the international supply and demand of rice and wheat have been evaluated by using a partial equilibrium-type dynamic model for world supply and demand. Based on the world rice and wheat supply and demand model and a unit harvest scenario, the study projected that the serious effects of global warming would be felt as early as 2020. The study suggests that the early effects will not be so severe that humans are unable to control them. However, the gap between supply and demand may grow according to region, so that at times there will be a considerably increased reliance on imports. Furthermore, the problem of short-term fluctuations in the market because of an increased frequency of droughts, floods, and other extreme weather events will be exacerbated, making it necessary to promote measures to combat climate change on a global scale.

Some people have suggested that rice production could decrease to about 70% of that in ordinary years, resulting in a shortage of rice. In China, food shortages a few years ago led to the cultivation of land on steep hillsides, which destroys the natural vegetation cover. As a result, topsoil loss has become a serious problem during the rainy season. The area affected by soil erosion has now increased to 1.16 million km^2, 16.7% of the total territory in China. Each year, 5 billion t of topsoil are washed away, with 2 billion t ending up in the ocean. Desertification in North and Northwest China continues to expand and has now reached about 15.5% of the total land area of China.

China is implementing a household contract system for returning cultivated land to woodland and planting uncultivated areas. An individual contract system will be introduced whereby households are assigned tasks, receive subsidies, and own the trees and other vegetation that they plant. The full program is for about 5 million ha to be planted with trees in 2002. The central government's investment can be used to estimate land-use changes, as the contract requires 4,500 yuan for a 1-ha return of cultivated land to 2 ha of woodland. In 2001, a total of 4.2 billion yuan (US$1 = 8.2 yuan) were used to help plant land with trees, which is equivalent to 1.8-1.9 million ha.

With moderate temperatures, a long-term doubling of current ambient CO_2 under field-like conditions leads to a 30% enhancement in the seed yield of rice, despite a 5-10% decline in the number of days to heading (Horie et al 2000). The grain yield of CO_2-enriched rice showed about a 10% decline for each 1 °C rise above 26 °C. This decline was caused by a shortening of the growth duration and increased spikelet sterility. Similar scenarios have been reported for soybean and wheat (Baker et al 1995, Mitchell et al 1993). Therefore, the effects of elevated CO_2 on rice yield are strongly temperature-dependent and may even become negative at extremely high temperatures (above 36.5 °C) during flowering. This occurs because of an elevated CO_2-induced increase in the degree of spikelet sterility at high temperature (Horie et al 2000). The importance of diurnal climate variability has emerged since the Second Assessment Report (Reilly 1996). Cold temperatures currently limit rice yield in all temperate rice-growing regions.

In general, agronomic adaptation was found to be most effective in mid-latitude developed regions and least effective in low-latitude developing regions (Parry et al 1997, Rosenzweig and Iglesias 1998). However, differences in modeling methodology and aggregation of results often lead to conflicting conclusions in specific regions. For example, in two studies using the same general circulation model (GCM) scenarios, Matthews et al (1995b) simulate large increases while Winters et al (1999) simulate large decreases in rice yield with adaptation across several countries in Asia (Table 1). Hence, confidence in these simulations is low.

An improved study in China

A comparison of rice models showed that their predictions for potential production were quite close to the observed values (Peng et al 1995). To improve the understanding of the effects of climate change on rice production, an improved study was carried out at the Agrometeorological Institute of the Chinese Academy of Agricultural Sciences in China.

Materials and methods

Regions and representative farms. Sixteen regions each have been defined for double and single rice based on agro-climate, and these are the primary rice-growing regions in China: Chongqing (CQ), Chendu (CD), Wuhan (WH), Shaoguan (SG), Shanghai (SH), Nanjin (NJ), Nanchang (NC), Hangzhou (HZ), Guiyang (GY), Changsha (CS), Nanling (NL), Kunming (KM), Shantou (ST), Guangzhou (GZ), Guilin (GL), and Fuzhou (FZ) for double rice; Harbin (HB), Jinnan (JN), Changchun (CC), Zhenzhou (ZZ), Shenyang (SY), Beijing (BJ), Dalian (DL), Chendu (CD), Xian (XA), Shanghai (SH), Taiyuan (TY), Nanjin (NJ), Lanzhou (LZ), Wuhan (WH), Chongqing (CQ), and Yichang (YC) for single rice. One representative farm was selected in every region for single-rice simulation and two for double rice.

Baseline climate data. The general approach for analyzing the possible effects of climate change on crop yield is to determine the yield change under future-scenario and baseline climate. In this study, the daily climatic records from 1961 to 1990 at

Table 2. Design of climate-change scenario applied to the experiments. The scenarios are used on each representative farm to analyze the potential effects of climate change on rice yields in China in 2030 and 2056.

Scenario	General circulation model	Assessment year	CO_2 emission scenario (%)	CO_2 concentration (ppmv)
1 (baseline)	–	–	–	350
2	HadCM2	2030	1.0	521
3	HadCM2	2030	0.5	427
4	ECHAM4	2030	1.0	521
5	HadCM2	2056	1.0	648

long-term climatic stations within the primary growing regions were selected as the baseline climate data. The baseline climate data modified by the climate-change scenario-based anomalies are used further in crop simulations to bring out the effects of climate on crop yield.

Experiments for the effects of climate change on rice: the control experiment. The CERES-Rice model, run with the baseline data of each representative site, is considered as the control experiment for comparing the crop performance of the climate-change scenarios. In addition, field experiments were carried out in Beijing and Nanchang to validate the simulations.

Climate-change scenarios. In our study, the climate-change scenarios used were based on the results of the transient GCMs HadCM2 and ECHAM4 with two CO_2 emission scenarios. The design of climate-change scenario is applied to the experiments as in Table 2.

Results and discussion

Effects of climate change on irrigated rice yield without CO_2 fertilization effects. Without CO_2 fertilization effects, early rice yield, later rice yield, and intermediate rice yield will decrease in all scenarios and locations to a different extent, with the most severe yield decrease located in Chongqing and Fuzhou for early rice and later rice and in Xian and Harbin for intermediate rice (Figs. 1, 2, and 3). With the same CO_2 emission scenario (1.0%), yields in 2056 will decrease more dramatically than those in 2030. However, yields are compared under different CO_2 emission scenarios (0.5% and 1%) and it seems that the mechanism by which the CO_2 emission scenarios affect rice yield without CO_2 fertilization effects is not apparent. In addition, the results derived from HadCM2 and ECMAH4 have no significant difference in general.

Effects of climate change on irrigated rice yield with CO_2 fertilization effects. With CO_2 fertilization effects, irrigated rice yield increases in most scenarios and locations to a different extent (Figs. 4, 5, and 6). For rice, irrigation is beneficial for a yield increase. Compared with the CO_2 emission scenario of 1 %, rice yield under

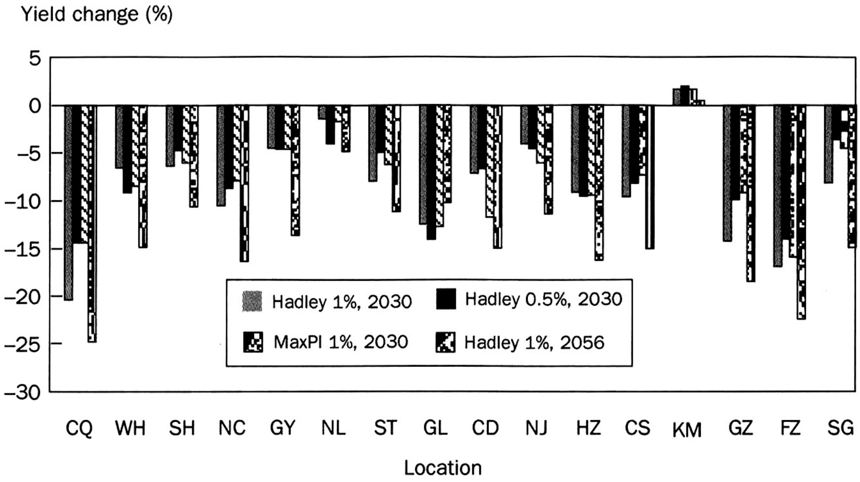


Fig. 1. Comparison between irrigated early rice yields at different locations under four future-climate scenarios and baseline climate without CO_2 fertilization effects (yield change = O). See text for explanation of locations.

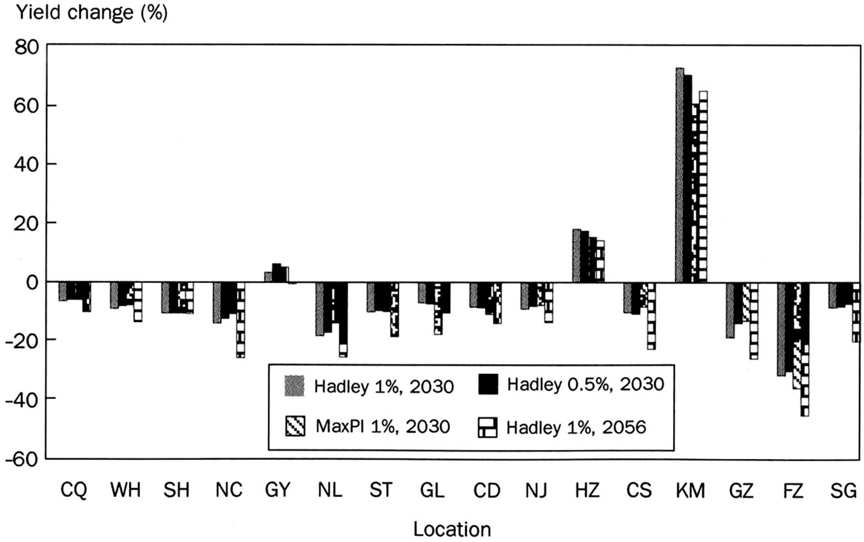


Fig. 2. Comparison between irrigated later rice yields at different locations under four future-climate scenarios and baseline climate without CO_2 fertilization effects (yield change = 0). See text for explanation of locations.

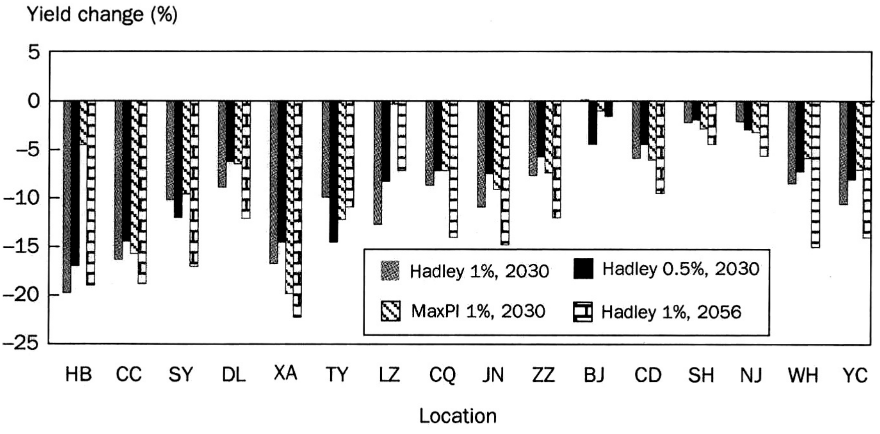


Fig. 3. Comparison between irrigated single rice yields at different locations under four future-climate scenarios and baseline climate without CO_2 fertilization effects (yield change = 0). See text for explanation of locations.

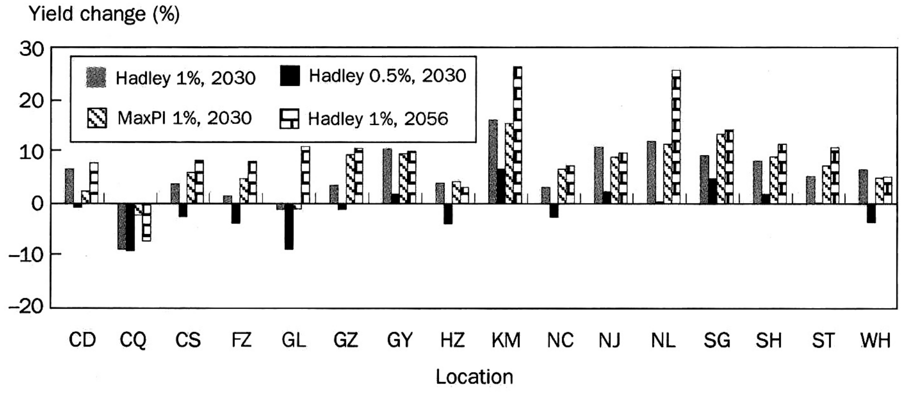


Fig. 4. Comparison between irrigated early rice yields at different locations under four future-climate scenarios and baseline climate with CO_2 fertilization effects (yield change = 0). See text for explanation of locations.

the CO_2 emission scenario of 0.5% increases less. With the same CO_2 scenario (1%), compared with those in 2030, rice yield in 2056 increases at most locations, but decreases at some locations, maybe because the rate of CO_2 fixation in photosynthesis is not limited at the atmospheric CO_2 concentration levels of that time (approximately 648 ppmv) for rice at some locations. In addition, the results derived from HadCM2 and ECMAH4 have no significant difference in general.

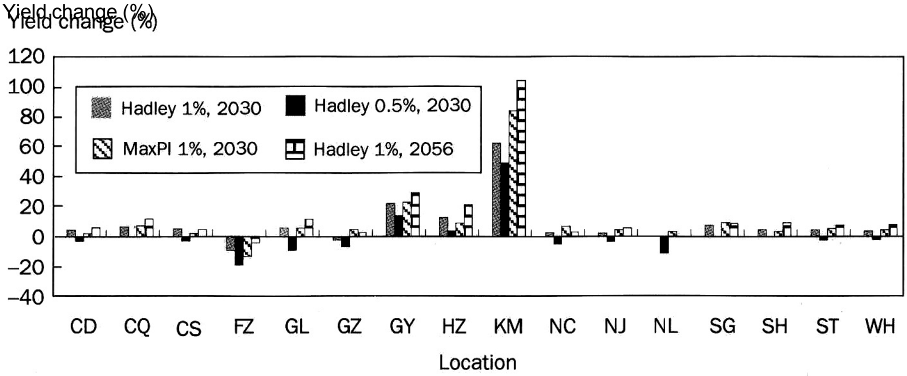


Fig. 5. Comparison between irrigated later rice yields at different locations under four future-climate scenarios and baseline climate with CO_2 fertilization effects (yield change = 0). See text for explanation of locations.

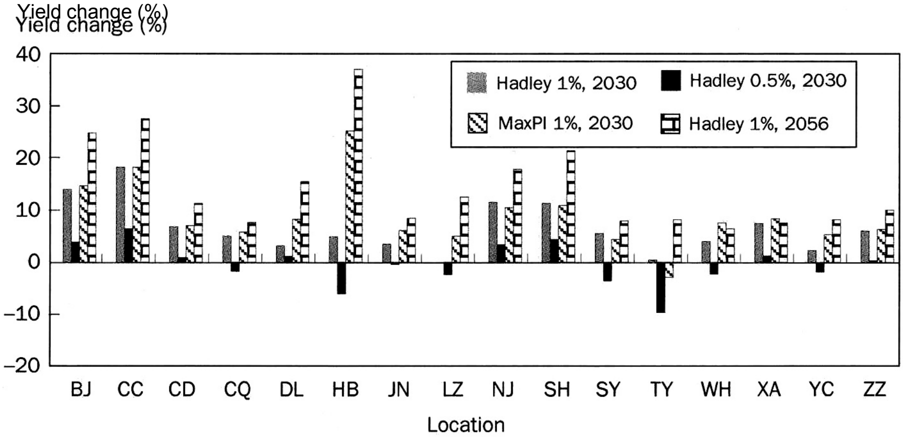


Fig. 6. Comparison between irrigated single-rice yields at different locations under four future-climate scenarios and baseline climate with CO_2 fertilization effects (yield change = 0). See text for explanation of locations.

Limitations of the study

Our study tried to assess the effects of climate change on rice yields in China, analyze crop yield change with a range of greenhouse gas emissions, and study how the extent and timing of the introduction of a range of emission reduction actions determine and affect the rate and magnitude of these effects. Nevertheless, scenario uncertainties exist. The present-day GCMs with coarse resolution are well accepted for global climate-change scenario projections. But they are still inadequate in predicting the regional climate in relation to agriculture (Sinha 1991). The factors currently receiving attention are limited to plant water supply, temperature, and CO_2. Nutrients are assumed to be in abundant supply in the soil so as not to cause any stress to the plant. The crop model embodies several simplifications. Because there are no problem soil conditions (e.g., acidity and soil salinity) and no extreme weather events such as droughts or severe storms, further studies are needed.

Conclusions

The results show that increasing CO_2 concentration leads to an exponential increase in yield because of fertilization effects. But irrigation will be more beneficial than CO_2 under higher temperature. Without CO_2 fertilization effects, rice decreases in yield at all locations except early and later rice in Kunming and later rice in Hangzhou, with the most severe reduction for early rice located in Chongqing. With CO_2 fertilization effects, rice yield increases in most scenarios and locations.

Without CO_2 fertilization effects, under the same CO_2 emission scenario (1 %), rice yields in 2056 decrease more dramatically than those in 2030. However, the yields are compared under different CO_2 emission scenarios (0.5% and 1.0%) and it seems that the mechanism by which the CO_2 emission scenario affects rice yield is not apparent. With CO_2 fertilization effects, compared with the CO_2 emission scenario of 1.0%, rice yield under the CO_2 emission scenario of 0.5% increases less. With the same CO_2 scenario (1.0%), rice yields in 2056 increase more than those in 2030 at some locations. Irrigation will benefit rice production. In addition, the results derived from HadCM2 and ECMAH4 have no significant difference in general.

A current study on China's rice effects

To provide an overview of the overall effects of climate change on agriculture in China, including economic costs of damages and/or adaptation, to provide climate-change scenarios for China based on selected IPCC SRES emission scenarios for the 2020s, 2050s, and 2080s, and to provide socioeconomic scenarios for China relevant to agriculture, for the 2020s and 2050s, an international cooperation project, including regional rice modeling, is being carried out among UK and Chinese scientists. A more advanced methodology is used, as follows.

Materials and methods

To further assess rice yield under climate change, a new climate-change scenario and new methodology were used. The materials in this research include climate-change scenario, a China boundary digital map, a land-use map of the present and future, FAO soil data, and a database on crop variety and planting details.

In total, the effects of seven different climate-change scenarios were evaluated: baseline and 2025, 2050, and 2080 under two emission scenarios (typically A2 and B2 SRES). All the scenarios are predicted by the Hadley Centre's RCM-PRECIS (Providing Regional Climates for Impact Studies). The resolution of the regional GCMs is 50 x 50 km. The simulation period is 1961-90 and 2071-2100. The periods of 2011-2040 and 2041-2071 can be obtained from pattern scaling. For climate scenarios over China, the Hadley Centre RCM system PRECIS is to be set up over China and it has a horizontal resolution of 50 km with 19 levels in the atmosphere (from surface to 30 km in the stratosphere). The climate simulation for baseline and future climate scenarios for different emission scenarios will be performed.

Based on the resolution of climate-change scenarios, all the area of China was divided into almost 2,000 cells, which will be considered as a unit for the simulation. The land-use map will be used in the research and the future land-use map will reflect the development of the socioeconomy. It will act as a mask to delete the cells that cannot be used as rice planting. For every cell, the FAO soil will be used to retrieve the soil attributes and these attributes are the weighted average of the soil units in each cell. To develop agriculture, the crop variety and planting detail database will be analyzed to obtain the trend of the development of agriculture for planting management and crop variety. The selected crop variety and field management will be distributed to each cell.

For its widespread use and validation, CERES-Rice was chosen for the simulation. It has been developed into a regional crop model by R.B. Matthews of Cranfield University (Matthews et al 2000a,b,c,d). As soon as all the input files have been collected, which include soil files for each cell, the crop variety polygon file, and the planting details polygon file, the crop model will be run for every cell. A yield change map covering all of China will be produced.

References

Baker et al. 1995. The potential effects of climate change on ecosystem processes and cattle production on U.S. rangelands. Clim. Change 23:97-117.

Conroy et al. 1994. Influence of rising atmospheric CO_2 concentrations and temperature on growth, yield and grain quality of cereal crops. Aust. J. Plant Physiol. 21(6):741-758.

Dai XS. 1997. Potential effects of climatic variation on geographical distribution of wheat in China. Quart. J. Appl. Meteorol. 8(1): 19-25.

Ding Yihui. 2002. Issue of climate change. Report on the seminar of issue of climate change. Beijing, China.

FAO (Food and Agriculture Organization of the United Nations). 1999. The state of food security in the world. Rome (Italy): FAO. 32 p.

Horiet T et al. 2000. Crop ecosystem responses to climate change: rice. In: Reddy KR, Hodges HF, editors. Climate change and global crop productivity. Wallingford (UK): CAB International. p 81-106.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of WG I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. New York, N.Y. (USA): Cambridge University Press.

Lin E. 1997. Modeling Chinese agriculture impact under global climate change. Beijing (China): Chinese Agricultural Science and Technology Press. p 61-68.

Matsui T, Horie T. 1992. Effects of elevated CO_2 and high temperature on growth and yield of rice. Part 2. Sensitive period and pollen germination rate in high temperature sterility of rice spikelets at flowering. Jpn. J. Crop Sci. 61:148-149.

Matsui T, Horie T. 1997. Effects of high temperature and CO_2 concentration on spikelet sterility in indica rice. Field Crops Res. 5:213-219.

Matthews RB, Kropff MJ, Bachelet D, van Laar HH. 1995a. Modeling the impact of climate change on rice production in Asia. Los Baños (Philippines): International Rice Research Institute, and Wallingford (UK): CAB International. 289 p.

Matthews RB, Kropff MJ, Horie T, Bachelet D. 1995b. Simulating the impact of climate change on rice production in Asia and evaluating options for adaptation. Agric. Syst. 54:399-425.

Matthews RB, Wassmann R, Arah J. 2000a. Using a crop/soil simulation model and GIS technique to assess methane emissions from rice fields in Asia. I. Model development. Nutrient Cycl. Agroecosyst. 58:141-159.

Matthews RB, Wassmann R, Buendia L, Knox J. 2000b. Using a crop/soil simulation model and GIS technique to assess methane emissions from rice fields in Asia. II. Model validation and sensitivity analysis. Nutrient Cycl. Agroecosyst. 58:161-177.

Matthews RB, Wassmann R, Arah J. 2000c. Using a crop/soil simulation model and GIS technique to assess methane emissions from rice fields in Asia. III. Database. Nutrient Cycl. Agroecosyst. 58:179-199.

Matthews RB, Wassmann R, box JW, Buendia L. 2000d. Using a crop/soil simulation model and GIS technique to assess methane emissions from rice fields in Asia. IV. Upscaling of crop management scenarios to national levels. Nutrient Cycl. Agroecosyst. 58:201-217.

Mitchell et al. 1993. Comparison of five models of rice yield showing the effects of change in temperature and in carbon dioxide concentration. In: Ingram JSI, editor. Report of the GCTE rice network experimentation planning workshop. GCTE Working Document. Vol. 19.

Parry M et al., 1997. Climate change and its impacts: global perspective. Some recent results of UK research. Programme, December 1997. Meteorological Office of the Department of Transportation and Regulations S.1. 12 p.

Peng SB, Ingram KT, Neue H-U, Ziska LH, editors. 1995. Climate change and rice. Los Baños (Philipines): International Rice Research Institute. 374 p.

Pingali P. 1994. Technological prospects for reversing the declining trend in Asia's rice productivity. In: Anderson JR, editor. Agricultural technology: policy issues for the international community. Wallingford (UK): CAB International and World Bank. p 384-401.

Reilly J. 1996. Agriculture in a changing climate: effects and adaptation. In: Watson RT, Zinyowera MC, Moss RH, editors. Climate change 1995: impacts, adaptations, and mitigation of climate change: scientific-technical analyses. Contribution of Working Group mitigation of climate change: scientific-technical analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press. p 429-467.

Rosenzweig C, Iglesias A. 1998. The use of crop models for international climate change impact assessment. In: Tsuji GY, Hoogenboom G, Thorton PK, editors. Understanding options for agricultural production. Dordrecht (Netherlands): Kluwer Academic Publishers. p 267-292.

Wei Xiong, Fulu Tao, Yinlong Xu, Erda Lin. 2001. Rice yield change simulation under climate change. Chinese Agrometeorol. 8:1-5.

Winters P et al. 1999. Climate change and agricultural effects on developing countries. In: Frisvold G, Kuhn B, editors. Global environment change and agriculture. Cheltenhamm (UK): Edward Elgar Publishers.

Zhang Houxuan. 2000. The problems concerning the response of China's cropping systems to global climate changes. I. The effect of climate changes on cropping systems in China. Agric. Meteorol. 21(1):9-13.

Zhang Yi, Wang Wei-chyung. 1993. The potential change of gronnel surface air temperature under the condition of global warming induced by CO_2 doubling. In: Xhang Yi et al, editors. Climate change and its impact. Beijing (China): Meteorological Press. p 248-256.

Ziska L et al. 1997. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J. Exp. Bot. 47(302):1353-1359.

Notes

Authors' address: Agrometeorology Institute, Chinese Academy of Agricultural Sciences.

Citation: Mew TW, Bra DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Rising carbon dioxide: implications for weed-crop competition

L.H. Ziska

The ongoing increase in atmospheric carbon dioxide and associated changes in temperature and precipitation will almost certainly alter the growth, reproduction, and location of weedy species, with subsequent effects on weedcrop competition. In the review of data presented here, I examine the role of CO_2 in stimulating photosynthesis and growth, the subsequent consequences for weed biology, and the consequences for chemical weed management. Initial results suggest unfavorable consequences in agronomic systems, including irrigated rice. It is clear that the existing data, although incomplete, suggest that the environmental and economic costs associated with rising CO_2 may be substantial. To that end, I hope that this review will serve as an initial guide for interested parties in assessing the importance of past and current increases in atmospheric CO_2 in relation to weed biology, and will serve to elucidate areas where information is lacking.

Weeds are widely recognized as having negative effects on agricultural crops. Worldwide, crop production losses from weeds are estimated to approximate 12%, with an estimated 25% loss in undeveloped agronomic systems (Parker and Fryer 1975). Climatic outcomes for crops and weed-crop competition have been examined in several critical reviews, including Patterson and Flint (1980), Patterson (1993, 1995a,b), and Bunce and Ziska (2000). The current review acknowledges the importance of such climatic changes, but recognizes that future climatic change is uncertain. A greater consensus now exists on the direct effect of carbon dioxide concentration (CO_2) on plant systems (e.g., Cure and Acock 1986, Kimball 1983, 1993); consequently, the principal focus of this presentation is to integrate what is known about the direct effects of rising CO_2 on weed-crop competition using rice production systems whenever possible as illustrative examples.

What is the current atmospheric CO_2?

Documented and anticipated changes in the concentration of atmospheric carbon dioxide and other trace gases strongly suggest potential changes in climate stability. Such changes could negatively affect agricultural crops and associated weeds. Based on modern records of CO_2 data obtained from the Mauna Loa observatory, atmospheric CO_2 concentration has already risen from 315 μatm in the mid-1950s to approximately 370 μatm today (Keeling and Whorf 2001). The Mauna Loa data represent the longest continuous direct record of measured atmospheric CO_2 for the 20th century. As the global demand for energy and agricultural land increases, deforestation and fossil fuel burning will continue to be anthropogenic sources of atmospheric CO_2. The current rate of increase, approximately 1.5 μatm year^{-1} (e.g., Schimel et al 1996), is expected to continue, with concentrations approaching 600 μatm by the end of the 21st century (IPCC scenarios IS 92e and IS 92 a, respectively, in Schimel et al 1996).

Measurements at Mauna Loa are part of the worldwide Carbon Dioxide Information Analysis Center (cdiac.esd.ornl.gov/home.html), which monitors background atmospheric CO_2. This monitoring network samples air at high elevations away from anthropogenic sources. However, for most areas where people live, or crops grow, there should be macroenvironmental differences in CO_2 related to the amount of industrialization, wind speed, dark respiration, etc., that influence both the average daily CO_2 as well as the diurnal CO_2 pattern. For example, data obtained for the city of Phoenix show the presence of what researchers describe as an "urban CO_2 dome" (Idso et al 1998,2001). CO_2 data on four separate transects from the outskirts of the city to the city center in January 1998 and again in July 1998 show a consistent increase in CO_2 concentration from 370 to 555 μatm. Similarly, recent global data comparing ground-level CO_2 daily averages show much higher values for metropolitan centers near Washington, D.C., and Sydney, Australia (approximately 460 μatm), than for other rural locations (Ziska et al 2001 and Fig. 1). This suggests that atmospheric CO_2 increases anticipated for the globe as a whole may already be occurring in some areas as a result of urbanization.

On a global basis, the increase in atmospheric CO_2 has been accompanied by increases in other radiation-trapping gases such as methane (CH_4) at 0.9% year^{-1}, nitrous oxide (N_2O) at 0.25% year^{-1}, and chlorofluorocarbons (CFCs) at 4% year^{-1} (Ashmore 1990, MacCracken et aL 1990). Recent Intergovernmental Panel on Climate Change (IPCC) reports indicate that the rise in these "greenhouse" gases may lead to a 3-12 °C increase in global surface temperatures, with subsequent effects on climate, although the degree of these temperature/climatic changes remains uncertain (Cushman 1999).

Direct effects of CO_2 on plant function

Although the extent of future temperature increases remains undetermined, there is an acknowledged consensus on the direct effects of increasing CO_2 on plant physiology. CO_2 concentrations above current levels stimulate net photosynthesis in

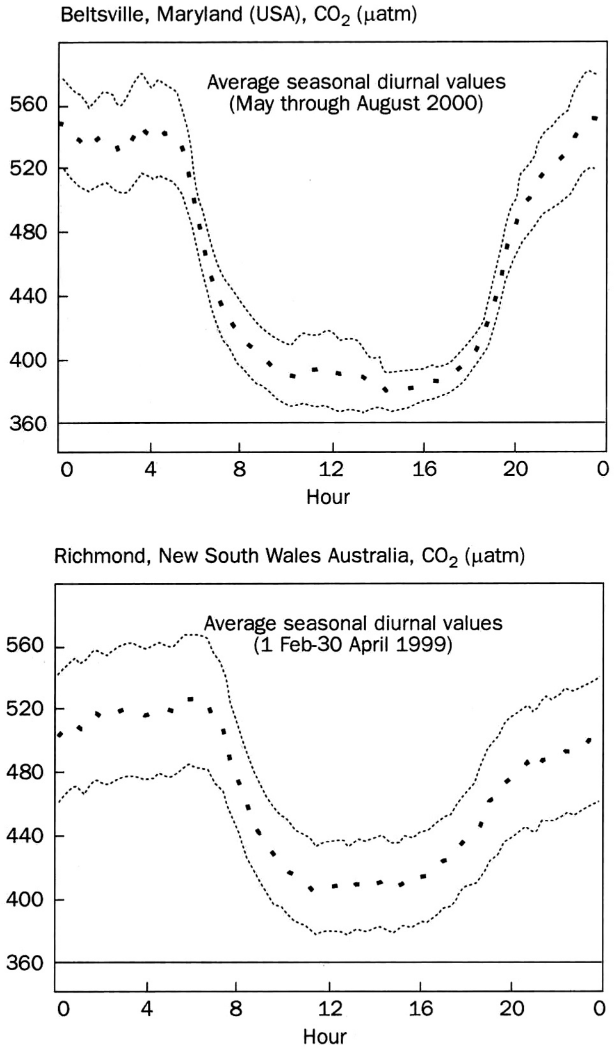


Fig. 1. Average 24-h diurnal CO_2 values for ambient air at two field sites: (A) greenhouses at the University of Western Sydney, New South Wales, Australia, and (B) open-top chambers at the USDA-ARS South Farm, Beltsville, Md., USA. The solid line in each figure represents a constant CO_2 value of 360 µatm. Average 24-h CO_2 values for each site were 468 and 458 µatm, respectively.

C_3 plants by increasing the CO_2 concentration gradient from air to leaf and by reducing the loss of CO_2 through photorespiration. Because oxygen competes with CO_2 for active sites of the enzyme ribulose-bisphosphate carboxylase/oxygenase

(Rubisco), increasing CO_2 (relative to O_2) stimulates photosynthesis and reduces carbon lost via photorespiration. Because the competition between O_2 and CO_2 for active sites is temperature-sensitive, the stimulation of net photosynthesis by elevated CO_2 should increase as the temperature increases. Thus, for plants that rely solely on the C_3 photosynthetic pathway (about 95% of all plant species), increasing CO_2 and temperatures associated with climate change should be favorable for increased growth. Alternatively, plants with the C_4 photosynthetic pathway (about 4% of all known plant species) have an internal mechanism for concentrating CO_2 around Rubisco; theoretically, therefore, increases in external CO_2 concentration should have little effect on net photosynthesis in C_4 plants (for reviews, see Bowes 1996 and Ghannoum et al 2000). However, one of the most consistent responses of both C_3 and C_4 species to elevated CO_2 is a decrease in stomatal conductance (see Morison 1995, Eamus 1991, Bunce 1998). The decrease in stomatal conductance can result in significant increases in leaf transpiration efficiency (CO_2 assimilated/H_2O transpired) or water-use efficiency (WUE, dry matter obtained/H_2O transpired). Hence, under water-limiting conditions, elevated CO_2 should result in significant increases in photosynthesis and biomass for both C_3 and C_4 species.

CO_2 and weed biology

The term "weed" is a descriptive term used to identify a type of plant that is generally recognized as objectionable or undesirable to human activities. Among plants recognized as weeds, some general biological similarities exist, including colonization of disturbed habitats, vigorous growth, prodigious seed production, and seed longevity (see Baker 1974).

One of the most recognized undesirable characteristics of weedy species is interference in crop production. For rice, direct loss in production is estimated at 20%, with losses climbing to 100% if weeds are not controlled (IRRI 2002). Weeding also has a considerable economic cost in rice production systems, with estimates of 50–150 person-days per hectare required for manual weeding. Although flooding has been used as an effective deterrent to weed establishment in past practices, water shortages and competition for existing water supplies suggest a greater reliance on direct seeding and herbicidal control. Overall in rice, as in most agronomic systems, human selection of desirable crop species has led to inadvertent selection of other species that simulate or mimic a particular crop (e.g., commercial and wild (red) rice, both of which are *Oryza sativa*).

Therefore, while crops are likely to benefit from the ongoing increase in atmospheric CO_2, growth of weedy competitors is also likely to be stimulated. Overall, C_3 and C_4 crops show a range of responses from 1.10 to 2.43 times and 0.98 to 1.24 times, respectively, whereas C_3 and C_4 weeds show a range of responses from 0.95 to 2.72 times and 0.6 to 1.6 1 times, respectively, with a projected doubling of ambient atmospheric CO_2 (relative to ambient, see reviews by Patterson and Flint 1990, Patterson 1993, Patterson et al 1999). The range of stimulation for some C_4 weeds, even under optimal water, is somewhat surprising given the expected response of the

C_4 pathway to increasing CO_2. Differences in subtype or degree of CO_2 "leakiness" within the bundle sheath do not provide a general explanation to the relative stimulation among C_4 species to elevated CO_2 and further mechanistic information is needed (Ziska et al 1999a, Ziska and Bunce 1999, Ghannoum et al 1998). For rice specifically, using a range of experimental techniques from temperature gradient tunnels to field open-top chambers to FACE systems, increased CO_2 (200-350 µatm above ambient) has stimulated yields 1.14 to 1.40 times that of current CO_2 (Kim et al 2001, Ziska et al 1997, Horie et al 2000) depending on temperature and fertilizer availability. Although fewer data are available for weeds associated with rice systems, one recognized species, barnyardgrass (*Echinochloa crus-galli*), can show values 1.02 to 1.61 times that of current CO_2 for similar CO_2 increases (Patterson 1993), depending on cultivar and temperature (Potvin and Strain 1985). Overall, the greater range of responses observed for weeds in response to elevated CO_2 is consistent with the suggestion of Treharne (1989) that weeds have a greater physiological plasticity and genetic diversity relative to crop species.

How do environmental limitations (temperature, water, and nutrients) modify the CO_2 enhancement effect in weedy species?

As temperatures increase, larger stimulation of photosynthetic rates by elevated CO_2 should occur at higher temperatures based on photorespiratory carbon loss (see Long 1991 and earlier discussion); however, this is not always observed. For velvetleaf (*Abutilon theophrasti*), increasing day/night temperature with a doubling of CO_2 can either decrease leaf area and biomass (Ackerly et al 1992, Coleman and Bazzaz 1992) or have no effect (Tremmel and Patterson 1993). Similarly, CO_2 enrichment and temperature did not interact for two C_4 weed species associated with rice production (*Echinochloa crus-galli* and *Eleusine indica*) (Potvin and Strain 1985). Alternatively, dry matter in spurred anoda (*Anoda cristata*) increased at 700 µatm when dayhight temperatures increased from 26/17 to 32/23 °C (Patterson et al 1988). Currently, there is little unequivocal evidence for significant differences in response to CO_2 with increasing temperatures. Overall, theoretical limitations based on biochemical models have generally assumed no growth-temperature effects on carboxylation kinetics (V_{Cmax}) and/or no limitation on potential rate of electron transport (J_{max}); however, recent studies with velvetleaf indicate that long-term adaptation to growth temperature may adjust both parameters, thus lowering the temperature sensitivity of CO_2-induced photosynthetic stimulation (see Bunce 2000, Ziska 2001b).

Potential increases in global temperature may be accompanied by changes in both precipitation amounts and frequency. However, because of the indirect effect of CO_2 on stomatal aperture, even under water-limiting conditions, elevated CO_2 can still stimulate plant photosynthesis and growth (e.g., Patterson 1986, Choudhuri et al 1990). For some C_4 weeds, increased photosynthesis and growth at elevated CO_2 may occur only under dry conditions because of increased WUE and reduced water stress.

Suboptimal nutrients are frequently cited as inducing photosynthetic acclimation to elevated CO_2 (see Poorter 1998 and Pettersson and McDonald 1994 for reviews). For Chenopodium album, low N availability did reduce photosynthetic response to CO_2, but only at low temperatures (Sage et al 1990). Similarly, growth response to CO_2 was unaffected by N level in wild radish (*Raphanus raphanistrum*) (Jablonski 1997) and sicklepod (*Cassia obtusifolia*) (Patterson and Flint 1982). However, the growth response to elevated CO_2 was reduced, but not eliminated, in showy crotalaria (*Crotalaria spectabilis*) (Patterson and Flint 1982). Overall, a reduction in the relative photosynthetic and growth response of weeds to elevated CO_2 is likely under extreme nutrient deficiencies. However, such deficiencies may be immaterial to agronomic conditions where nutrients are usually optimal for crop growth.

Weed-crop competition

It has sometimes been assumed that, because different plant species do not compete for CO_2 directly, CO_2 is less important than, say, competition for nutrients or water (e.g., Radosevich et al 1997). However, any resource that affects the growth of an individual alters its ability to compete with individuals of the same or different species (Patterson and Flint 1990). Therefore, competition not only occurs in response to limited resources but also occurs when species respond differently to resource enhancement. For example, in weed-crop interactions, additions of supraoptimal levels of N can increase weedy competition and reduce crop yields because weeds use a given resource (N) more efficiently than crops (e.g., Vengris et al 1955, Appleby et al 1976, Carlson and Hill 1985). Analogous to the N response, species-specific responses to CO_2 have been observed for the increase in atmospheric carbon dioxide that has already occurred during the 20th century (Sage 1995) and that projected for the end of the 21st century (e.g., Poorter 1993). Although, in general, the relative effect of increasing CO_2 is greater for C_3 species than for C_4 species, the observed responses demonstrate a wide range of relative enhancement within and between C_3 and C_4 species (e.g., Patterson and Flint 1990).

It is the difference in relative stimulation between C_3 and C_4 species that is perhaps most relevant to weed-crop competition. It is clear that a disproportionate number of weeds have C_4 metabolism. For example, among the "world's worst weeds," 14 out of 18 are C_4 (Holm et al 1977), whereas, of the 86 plant species that make up 95% of the world food supply, only five are C_4 (Patterson 1995a). Because the C_4 photosynthetic pathway is overly represented in troublesome weedy species, many experiments and most reviews concerned with weed competition and rising CO_2 have reported on C_3 crop-C_4 weed interactions (Alberto et al 1996, Patterson et al 1984, Patterson 1986, 1993, Patterson and Flint 1990). ("Troublesome" refers to weeds that result in a significant reduction in crop yield or quality, Bridges 1992.) Increasing CO_2 increased the crop-weed (i.e., the C_3/C_4) biomass ratio in all of these studies (see Bunce and Ziska 2000 for a review). Based on the relative proportion of C_3 and C_4 photosynthesis between crops and weeds, many global models have

Table 1. Troublesome weeds associated with paddy rice production. "Troublesome" refers to those weeds that are inadequately controlled and interfere with yield, quality, or harvest efficiency. The list is not all-inclusive but includes those weeds most frequently associated with rice as obtained from farmer surveys. Troublesome weeds for the U.S. were tabulated from Bridges (1992). Troublesome weeds on a global basis were obtained from Holm et al (1977). C_3/C_4 indicates photosynthetic pathway.

Troublesome weeds	
U.S.	World
Brachiaria platyphylla (Griseb.) Nash (C_4)	*Cyperus difformis L.* (C_4)
Cyperus esculentus L. (C_4)	*Echinochloa colona* (L.) Link (C_4)
Echinochloa crus-galli (L.) Beauv. (C_4)	*Echinochloa crus-galli* (L.) Beauv. (C_4)
Heteranthera limosa (Sw.) Willd. (C_3)	*Fimbristylis miliacea* (L.) Vahl (?)
Leptochloa fascicularis (Lam.) Gray (?)	*Monochoria vaginalis* (Burm. F.) Presl (C_3)
Oryza sativa (red rice) (C_3)	*Scirpus maritimus* (C_3)

assumed less yield loss because of weedy competition as atmospheric CO_2 increases (see Chapter 4, Rosenzweig and Hillel 1998).

However, the concept that crops are fundamentally C_3 and weeds C_4, and that weed competition will consequently decrease with rising atmospheric CO_2, is overly simplistic. Clearly, there are C_4 crops of economic and nutritional importance (e.g., maize—*Zea mays,* grain sorghum—*Sorghum bicolor,* pearl millet—*Pennisetum americanum,* and *sugarcane—Saccharum officinarum*) and many important C_3 weeds (e.g., lambsquarters—*Chenopodium album,* wild *oat—Avena fatua,* field bindweed—*Convolvulus arvensis,* and Canada thistle—*Cirsium arvense*). Crop-weed interactions vary significantly by region, consequently depending on temperature, precipitation, soil, etc. C_3 and C_4 crops may interact with C_3 and C_4 weeds (Bridges 1992). For example, for rice in the U.S., troublesome weeds include *Heteranthera limosa* and red rice (*O. sativa*), both C_3 species, whereas C_3 weeds in rice on a global basis include *Scirpus maritimus* and *Monochoria vaginalis* (Table 1). Similarly, troublesome C_4 weeds in U.S. rice production include *Brachiaria platyphylla* and *Cyperus esculentus,* whereas, on a global basis, the worst C_4 weeds in rice are *Cyperus difformis* and *Echinochloa colona* (Table 1).

Unfortunately, only a smattering of studies have examined the response of crop and weed species to elevated CO_2 in competition. These investigations fall into two broad categories: those in which the photosynthetic pathway differs and those in which the pathway is the same. With one exception, those studies with differing pathways have contrasted C_3 crops with C_4 weeds (Table 2). Increasing CO_2 increased the crop/weed ratio in all of these studies, which is consistent with the relative stimulation of the C_3 and C_4 photosynthetic pathways by elevated CO_2. The exception was grain sorghum (C_3 crop) with common cocklebur (C_3 weed) (Ziska 2001c). This comparison is significant because cocklebur is listed as a troublesome weed in nine states in the southern or central United States (Bridges 1992). With respect to competitive comparisons for the same photosynthetic pathway, no data are available

Table 2. Competition studies of crop and weed species as a function of CO_2. Although *Echinochloa glabrescens* outcompetes rice at elevated CO_2, if both CO_2 and temperature are considered, *E. glabrescens* is the better competitor (see text).

Weed	Crop	Favored?	Environment	Reference
Different photosynthetic pathway				
Sorghum halapense (C_4)	Meadow fescue	Crop	Glasshouse	Carter and Peterson (1983)
S. halapense (C_4)	Soybean	Crop	Chamber	Patterson et al (1984)
Echinochloa glabrescens (C_4)	Rice	Crop	Glasshouse	Alberto et al (1996)
Paspalum dilatatum (C_4)	Grasses	Crop	Chamber	Newton et al (1996)
Grasses (C_4)	Lucerne	Crop	Field	Bunce (1993)
Amaranthus retroflexus (C_4)	Soybean	Crop	Field	Ziska (2000)
Xanthium strumarium (C_3)	Grain sorghum	Weed	Glasshouse	Ziska (2001c)
Same photosynthetic pathway				
Chenopodium album (C_3)	Soybean	Weed	Field	Ziska (2000)
Taraxacum officinale (C_3)	Lucerne	Weed	Field	Bunce (1995)
Plantago lanceolate (C_3)	Grasses	Weed	Chamber	Newton et al (1996)
Taraxacum and *Plantago* (C_3)	Grasses	Weed	Field	Potvin and Vasseur (1997)

for C_4 crops and weeds, even though individual comparisons of C_4 crops and weeds have indicated a greater relative stimulation to CO_2 concentration for weedy species (Ziska and Bunce 1997). For comparisons of C_3 crops and weeds, the ratio of weed to crop biomass increased in all cases in which weed and crop emerged simultaneously (Table 1). In a study comparing lambsquarters to sugarbeet (*Beta vulgaris*), the competitive advantage of sugarbeet at elevated CO_2 was attributed to the late emergence of the weed species within the experiment (Houghton and Thomas 1996).

Although these studies have compared the relative stimulation of biomass between crops and weeds, only a single investigation has quantified the relative change in yield loss from weedy competition at elevated CO_2 in the field (Ziska 2000). In this instance, soybean (*Glycine max*) was grown at current and current + 250 µatm (elevated) CO_2 with and without the presence of two weeds, lambsquarters (C_3) and red-root pigweed (*Amaranthus retrofexus,* C_4) at a density of two weeds per meter of row. In a weed-free environment, elevated CO_2 resulted in a significant increase in vegetative dry weight and seed yield at maturity for soybean (33% and 24%, respectively). However, for lambsquarters, the reduction in soybean seed yield relative to the weed-free condition increased from 28% to 39% with elevated CO_2, with a 65% increase in the average vegetative dry weight of lambsquarters. For pigweed, soybean seed yield losses diminished with elevated CO_2 from 45% to 30%, with no change in vegetative dry weight of pigweed. Interestingly, the presence of either weed negated the ability of soybean to respond either vegetatively or reproductively to enhanced CO_2 (Ziska 2000). This is of interest since almost all CO_2 enhancement studies involving crops do not consider weed-crop interactions (e.g., Kimball 1983, 1993).

How do environmental limitations (temperature, water, nutrients) alter the CO_2 effect on weedcrop competition?

As with field evaluations of seed loss, only a single experiment has examined the interaction among temperature, CO_2, and crop-weed competition (Alberto et al 1996). In this phytotron study, an assessment of competitive changes based on plant relative yield (PRY) and replacement series diagrams comparing a C_3 crop (rice) and a C_4 weed (*Echinochloa glabrescens*) indicated that rice was favored over the weed with elevated CO_2 (594 µatm) at day/night temperatures of 27/21 °C; however, at day/night temperatures of 37/29 °C, a greater reduction in PRY in rice was observed relative to the C_4 weed (Fig. 2). This suggested that concurrent changes in CO_2 and temperature could still favor a C_4 weed over a C_3 crop in rice production systems.

Whether drought alters the competitive relationships between weeds and crops at elevated CO_2 is unknown. Studies that have examined the interactive effects of increasing CO_2 and water stress on annual weeds and crops in competition are not available. For a given photosynthetic pathway, crops and weeds have similar responses to drought (Patterson 1995b), although the overall effect of weeds may be reduced because of decreased growth of both crops and weeds in response to water availability (Patterson 1995b). Although competition was not determined directly, the proportion

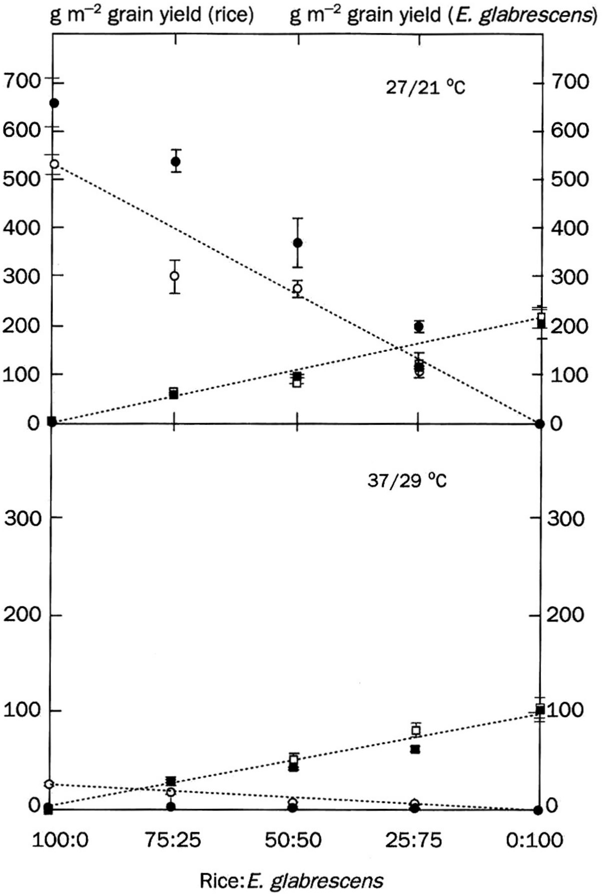


Fig. 2. Replacement series analysis using seed yield of rice (circles) and the weed *Echinochloa glabrescens* (squares) grown at two different CO_2 concentrations (ambient 393 µatm, clear, and 594 µatm, shaded) and two different growth temperatures (27/21 and 37/29 °C, day/night) at planting ratios of 100:0, 7525, 5050, 25:75, and 0100 rice:weed. Lines drawn indicate the anticipated response assuming no competition. Data that fall below the line indicate a reduced response, whereas data above the line indicate a greater than expected increase.

of weed biomass increased with CO_2 to a similar extent in wet and dry treatments in a pasture mixture (Newton et al 1996).

As with the interactive effects of CO_2 and water availability, no studies examine the interaction between increasing CO_2 and nutrient availability for crop-weed competition. Presumably, as with water stress, reductions in growth induced by nutrient availability may lessen the effect of weeds on crop yield (Patterson 1995b).

Although nutrient availability can modify the enhancement response to elevated CO_2 in individual weeds and crops, the relative effect on weed-crop competition will be species-specific and will depend, in part, on soil-plant interactions. Data from a mixed pasture study (Schenk et al 1997) suggested that elevated CO_2 could affect competitive outcomes between ryegrass and white clover depending on the nitrogen supply.

CO_2 and nonagronomic effects of weeds

Aside from the effect on agronomic productivity, weedy species have several other undesirable characteristics. One such aspect that is gaining attention is related to the invasion of natural or managed systems by plant invaders to the point where natural species are displaced or eliminated. Recent work on the response of six invasive species—Canada thistle (*Cirsium arvense*), field bindweed (*Convolvulus arvensis*), leafy spurge (*Euphorbia esula*), perennial sowthistle (*Sonchus amensis*), spotted knapweed (*Centaurea maculosa*), and yellow star thistle (*Centaurea solstitialis*)- to future elevated CO_2 demonstrated a range of responses (overall average of 1.46-fold that of current CO_2), with the largest relative response observed for Canada thistle (1.72 times relative to 380 μatm) (Fig. 3A). Interestingly, the growth response of these same species to the increase in atmospheric CO_2 that occurred during the 20th century (Le., 285 to 380 μatm) was much higher, averaging 2.1 times (Fig. 3B), with Canada thistle again having the strongest response (2.8 times). The relative stimulation of these invasives is approximately 3 times greater than for any other species examined over the same range of CO_2 concentrations (see Sage 1995) and this suggests the possibility that a strong response to recent increases in atmospheric CO_2 may be a common characteristic among invasive species.

Plants may also be deemed weeds based on their negative effect on public health. Such effects may occur through allergenic reactions, skin irritations, mechanical injury, or internal poisoning (Ziska 2001a). To date, little is known regarding the effect of rising atmospheric CO_2 on such species. One exception is that of common ragweed. Ragweed is a ubiquitous weed of agricultural crops and vacant lots. Like most wind-pollinated (anemophilous) plants, ragweed sheds enormous quantities of pollen to achieve reproductive success. Allergies or "hay fevers" are a reaction to inhalation of these airborne pollens. Increasing CO_2 during the 20th century (280 to 370 μatm) resulted in a significant stimulation of leaf photosynthesis (2.7 times), biomass (1.4 times), and pollen production (2.3 times). The response of ragweed to future CO_2 (600-700 μatm) also indicated a significant response to pollen production (1.6-1.9 times) above ambient CO_2 levels (Ziska and Caulfield 2000, Wayne et al 2002). Although additional data, particularly under field conditions, are needed, these preliminary studies indicate a potential direct effect of CO_2 on public health.

Impact of elevated CO_2 on chemical weed management

Even if high CO_2 exists already in urban areas, and even if increased global CO_2 results in greater stimulation of weedy growth at some future date, no detrimental effect of CO_2 on weeds will be observed if weeds can be controlled. At present, the

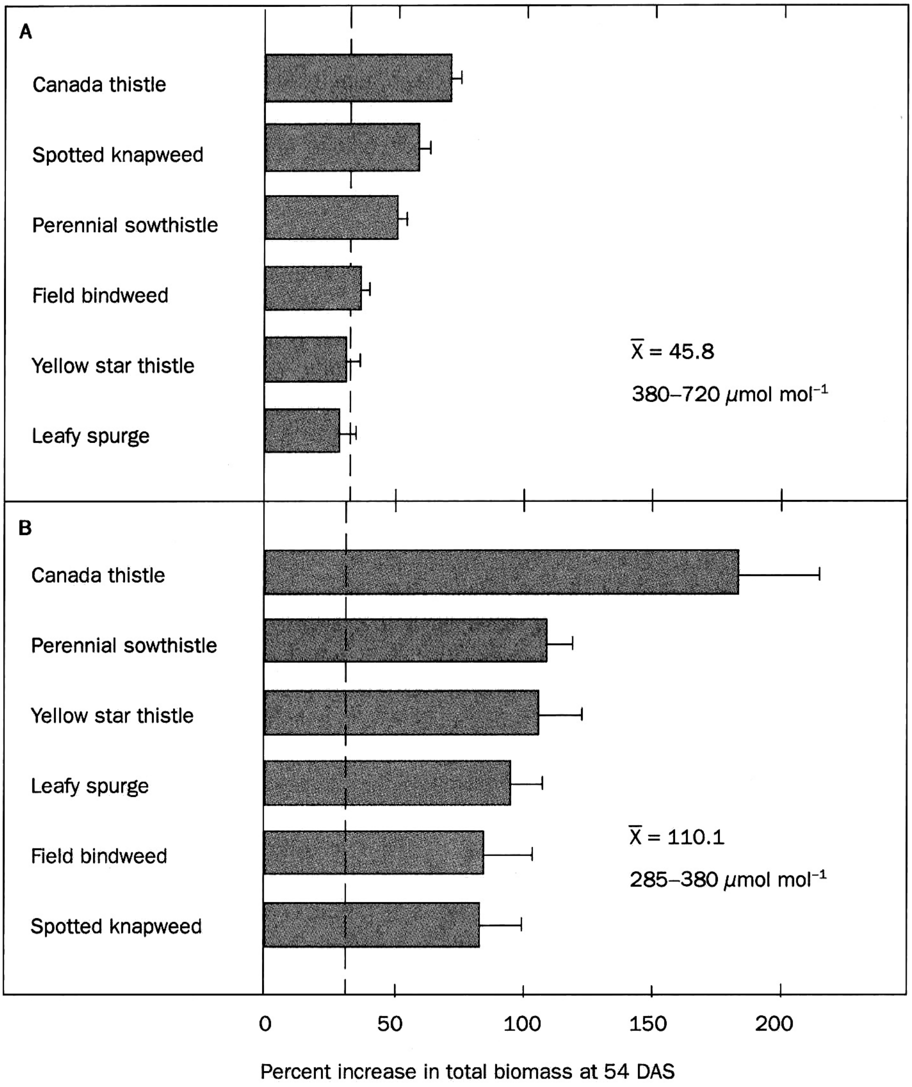


Fig. 3. (A) The average relative increase (%) determined from the ratio of dry weight at elevated (719 µatm) relative to ambient (380 µatm) CO_2 for three experimental runs for each of six invasive weeds at a common harvest date of 54 days after sowing (DAS). Broken line is the average response of plants as reported by Kimball (1983). (6) Same as A, but for CO_2 concentrations of 284 and 380 µatm. Dotted line is the published response of plants from 270 to 380 µatm (Sage 1995). Bars are ± standard error.

principal basis for control in developed countries is chemical weed management through the application of selected herbicides.

But this assumes that CO_2 will not affect herbicide efficacy. Is this a reasonable assumption? Theoretically, efficacy could be reduced by CO_2 by either (1) limiting the amount of herbicide entering the plant or (2) changing the physiological action of the herbicide. Carbon dioxide could reduce foliar absorbtion because of reductions in stomatal conductance and/or changes in leaf cuticular thickness. Decreased stomatal conductance with increasing CO_2 could also reduce transpiration and uptake of foliar-applied herbicides. In addition, for perennial weeds, CO_2-induced stimulation of belowground growth (e.g., rhizomes, tubers, roots) could increase regeneration of weedy species following herbicide application. There are also several CO_2-induced physiological changes, which are herbicide-specific. For example, in glyphosate, CO_2-induced reductions in protein content per gram of tissue could result in less demand for aromatic amino acids. Since glyphosate inhibits aromatic amino acid production through the shikimic acid pathway, this could influence the toxicity of the herbicide. Another example is glufosinate, which inhibits glutamine synthetase with a subsequent decrease in glutamine and serine. Lack of these amino acids inhibits the transanimation of glyoxylate into glycine during photorespiration. In previous studies when photorespiration is suppressed (either by increasing CO_2 or decreasing O_2), the efficacy of glufosinate is reduced (see La Cuesta et al 1992; for a C_3 vs C_4 comparison, see Wendler et al 1993).

Although much remains to be known regarding the effect of rising CO_2 on herbicide efficacy, some initial studies have been conducted. In greenhouse experiments, glyphosate efficacy was reduced with a doubling of CO_2 for both lambsquarters and a perennial weed, quackgrass (*Elytrigia repens*), relative to ambient CO_2 at various stages of growth (Ziska et al 1999b, Ziska and Teasdale 2000). This is significant, in part, because glyphosate is the most widely used herbicide in the world. The basis for the increased tolerance of glyphosate at elevated CO_2 in these experiments is unclear. Short-term switching of the quackgrass to the elevated CO_2 condition prior to spraying did not increase tolerance, suggesting that stomatal closure did not play a role (Ziska and Teasdale 2000). Specific evaluations of uptake, allocation, and physiological interaction are required before a mechanistic basis for increased glyphosate tolerance at elevated CO_2 can be established for these species.

Recent unpublished data for the number-one invasive species in North America, Canada thistle, grown at elevated CO_2 under field conditions for a two-year period indicated a significant increase in belowground biomass (+70–150%) relative to the ambient condition (Fig. 4). The application of recommended rates of two postemergent herbicides, glufosinate (0.376 kg ai ha^{-1}) and glyphosate (2.24 kg ai ha^{-1}), resulted in significant reductions in aboveground (shoot) biomass and belowground (root) biomass relative to unsprayed plots at ambient CO_2 for both herbicides following a 6-week regrowth period. However, in contrast to the ambient CO_2 treatment, glyphosate and glufosinate applications had no effect on shoot and root regrowth, respectively, when Canada thistle was grown at the elevated CO_2 concentration (Fig. 5). For this study, visual shoot symptoms did not differ as a function of CO_2

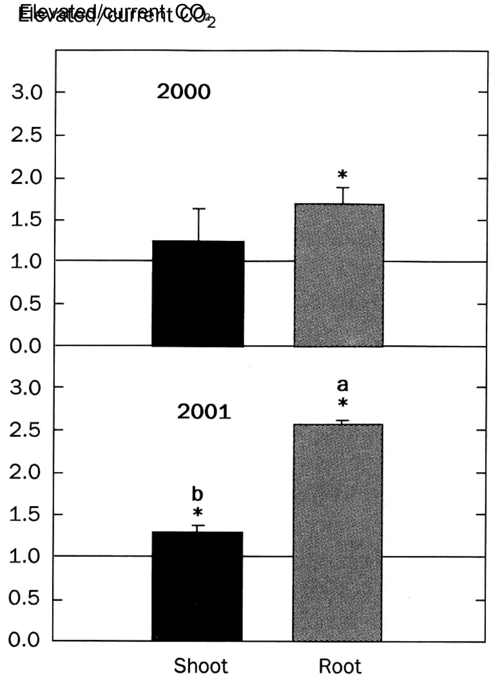


Fig. 4. Shoot and root biomass at elevated (771 µatm) relative to current (421 µatm) CO_2 concentration for field-grown Canada thistle in 2000 and 2001 at the time of herbicide application from the unsprayed plots. Shoot biomass refers to all aboveground herbaceous material. Root biomass was obtained from soil subsamples (2.36 L in volume, to a depth of 30 cm). * indicates a significant difference relative to unity (i.e., no CO_2 treatment effect). Different letters indicate significant differences between the shoot and root elevated:ambient ratio for a given year. Bars are ± standard error.

concentration. Rather, CO_2-induced changes in herbicide tolerance were consistent with the idea that greater CO_2 could stimulate greater belowground growth in perennial weeds. Overall, while control would be possible, reductions in efficacy would add to environmental and/or economic costs.

It can be argued that CO_2-induced changes in efficacy are irrelevant given the rate of atmospheric CO_2 increase (i.e., other herbicides will be developed in the future). However, this ignores current CO_2 gradients between urban and rural areas (eg, Idso 1998). Furthermore, herbicide use can persist over decades (e.g., 2-4D), coinciding with significant increases in atmospheric CO_2 (eg, 310–372 µatm from 1950 to 1999). Given the investment of large companies in genetically modified

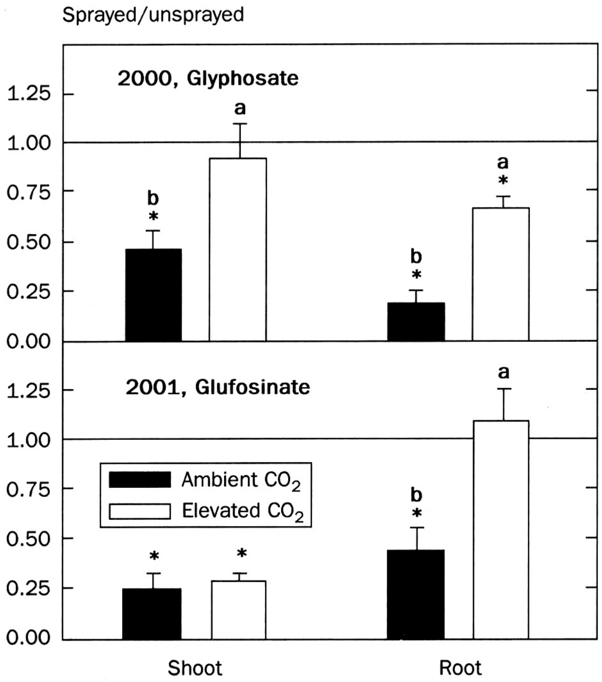


Fig. 5. Ratio of sprayed to unsprayed biomass for shoots and roots grown at the CO_2 concentrations given in Figure 2 six weeks after treatment with recommended rates of either glyphosate (2000) or glufoslnate (2001). * indicates a significant difference relative to unity (i.e., no CO_2 treatment effect). Different letters indicate a CO_2 treatment effect for either shoots or roots. Bars are ± standard error.

crops and their associated herbicides, it seems more likely that the use of current herbicides (e.g., glyphosate) will persist for decades.

Uncertainties and limitations

Given the importance of weed-crop competition, it is striking that so few data are available assessing the impact of rising atmospheric CO_2. Furthermore, almost all available data are based on studies in controlled-environment chambers or glasshouses. This represents a significant limitation since extrapolation of such studies to field environments may differ because of light or edaphic factors. Unfortunately, weeds are usually excluded in field evaluations of CO_2 sensitivity in crop species; therefore, inclusion of weeds would result in a more realistic assessment of crop-weed interactions. Overall, an in-depth analysis of CO_2 and plant biology should include quantification of CO_2-induced changes in secondary compounds and potential allelopathic effects, weed-crop associations that include perennial crops, C_4 weed-crop interactions, integrated evaluations of CO_2 and other environmental changes (e.g., water, temperature, and nutrients) on weedy growth, reproduction and potential crop losses, long-term assessments on weeds that could alter public health (e.g., poison ivy), and experiments that quantify the basis and degree of CO_2-induced changes in chemical, biological, and mechanical weed control.

References

Ackerly DD, Coleman JS, Morse SR, Bazzaz FA. 1992. CO_2 and temperature effects on leaf area production in two annual plant species. Ecology 73:1260-1269.

Alberto AM, Ziska LH, Cervancia CR, Manalo PA. 1996. The influence of increasing carbon dioxide and temperature on competitive interactions between a C_3 crop, rice (*Oryza sativa*), and a C_4 weed (*Echinochloa glabrescens*). Aust. J. Plant Physiol. 23:795-802.

Appleby AP, Olson PD, Colbert DR. 1976. Winter wheat yield reduction from interference by Italian ryegrass. Agron. J. 68:463-466.

Ashmore M. 1990. The greenhouse gases. Trends Ecol. Evol. 5:296-297.

Baker HG. 1974. The evolution of weeds. Annu. Rev. Ecol. Syst. 5:1-24.

Bowes G. 1996. Photosynthetic responses to changing atmospheric carbon dioxide concentration. In: Baker NR, editor. Photosynthesis and the environment. Dordrecht (Netherlands): Kluwer. p 387-407.

Bridges DC. 1992. Crop losses due to weeds in the United States. Champaign, III. (USA): Weed Science Society of America. 401 p.

Bunce JA, Ziska LH. 2000. Crop ecosystem responses to climatic change: crop/weed interactions. In: Reddy KR, Hodges HF, editors. Climate change and global crop productivity. New York, N.Y. (USA): CABI Publishing. p 333-352.

Bunce JA. 1993. Growth, survival, competition and canopy carbon dioxide and water vapor exchange of first year alfalfa at an elevated CO_2 concentration. Photosynthetica 29:557-565.

Bunce JA. 1995 Long-term growth of alfalfa and orchard grass plots at elevated CO_2. J. Biogeochem. 22:341-343.

Bunce JA. 1998. Effects of humidity on short-term responses of stomatal conductance to an increase in carbon dioxide concentration. Plant Cell Environ. 21:115-120.

Bunce JA. 2000. Acclimation to temperature of the response of photosynthesis to increased carbon dioxide concentration in *Taraxacum officinale*. Photo. Res. 64:89-94.

Carlson HL, Hill JE. 1985. Wild oat (*Avena fatua*) competition with spring wheat: effects of nitrogen fertilization. Weed Sci. 34:29-33.

Carter DR, Peterson KM. 1983. Effects of a CO_2 enriched atmosphere on the growth and competitive interaction of a C_3 and C_4 grass. Oecologia 58:188-193.

Choudhuri UN, Kirkham MB, Kanemasu ET. 1990. Carbon dioxide and water level effects on yield and water use of winter wheat. Agron. J. 82:637-641.

Coleman JS, Bazzaz FA. 1992. Effects of CO_2 and temperature on growth and resource use of co-occurring C_3 and C_4 annuals. Ecology 73:1244-1259.

Cure JD, Acock B. 1986. Crop responses to carbon dioxide doubling: a literature survey. Agric. For. Meteorol. 38:127-145.

Cushman RM. 1999. Global climatic-change modeling and monitoring. In: Alexander DE, Fairbridge RW, editors. Encyclopedia of environmental science. Dordrecht (Netherlands): Kluwer Academic Publishers. p 291-298.

Eamus D. 1991. The interaction of rising CO_2 and temperatures with water-use-efficiency. Plant Cell Environ. 14:843-852.

Ghannoum O, Siebke K, von Caemmerer S, Conroy JP. 1998. The photosynthesis of young C_4 *Panicum* leaves is not C_3-like. Plant Cell Environ. 21:1123-1131.

Ghannoum O, Von Caemmerer S, Ziska LH, Conroy JP. 2000. The growth response of C_4 plants to rising atmospheric CO_2 partial pressure: a reassessment. Plant Cell Environ. 23:931-942.

Holm LG, Plucknett DL, Pancho JV, Herberger JP. 1977. The world's worst weeds: distribution and biology. Honolulu, Haw. (USA): University of Hawaii Press. 609 p.

Horie T, Baker JT, Nakagawa H, Matsui T, Kim HY. 2000. Crop ecosystem responses to climate change: rice. In: Reddy KR, Hodges HF, editors. Climate change and global crop productivity. New York, N.Y. (USA): CABI Publishing. p 81-101.

Houghton SK, Thomas TH. 1996. Effects of elevated carbon-dioxide concentration and temperature on the growth and competition between sugar beet (*Beta vulgaris*) and fat-hen (Chenopodium album). Asp. Appl. Biol. 45:197-204.

Idso CD, Idso SB, Balling Jr. RC. 1998. The urban CO_2 dome of Phoenix, Arizona. Phys. Geo. 19:95-108.

Idso CD, Idso SB, Balling Jr. RC. 2001. An intensive two-week study of an urban CO_2 dome in Phoenix, Arizona, USA. Atmos. Environ. 35:995-1000.

IRRI (International Rice Research Institute). 2002. Pests, diseases and weeds of rice. www.riceweb.org/research (3 pages).

Jablonski LM. 1997. Responses of vegetative and reproductive traits to elevated CO_2 and nitrogen in *Raphanus* varieties. Can. J. Bot. 75:533-545.

Keeling CD, Whorf TP. 2001. Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US. Department of Energy, Oak Ridge, Tenn., USA.

Kim HY, Lieffering M, Miura S, Kobayashi K, Okada M. 2001. Growth and nitrogen uptake of CO2-enriched rice under field conditions. New Phytol. 50:223-229.

Kimball BA. 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agron. J. 75:779-788.

Kimball BA. 1993. Effects of increasing atmospheric CO_2 on vegetation. Vegetatio 104/105:65-75.

La Cuesta M, Muñoz-Rueda A, Gonzales-Murua C, Sivak MN. 1992. Effect of phosphinothricin (glufosinate) on photosynthesis and chlorophyll fluorescence emission by barley leaves illuminated under photorespiratory and non-photorespiratory condition. J. Exp. Bot. 43:159-165.

Long SP. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? Plant Cell Environ. 14:729-739.

MacCracken MC, Budyko MI, Hecht AD, Izrael YA. 1990. Prospects for future climate. Chelsea, Mich. (USA): Lewis Publications Inc. 112 p.

Morison JIL. 1985. Sensitivity of stomata and water use efficiency to high CO_2. Plant Cell Environ. 8:467-474.

Newton PCD, Clark H, Bell CC, Glasglow EM. 1996. Interaction of soil moisture and elevated CO_2 on the above-ground growth rate, root length density and gas exchange of turves from temperate pasture. J. Exp. Bot. 47:771-779.

Parker C, Fryer JD. 1975. Weed control problems causing major reductions in world food supplies. FAO Plant Prot. Bull. 23:83-95.

Patterson DT. 1986. Responses of soybean (*Glycine max*) and three C_4 grass weeds to CO_2 enrichment during drought. Weed Sci. 34:203-210.

Patterson DT. 1993. Implications of global climate change for impact of weeds, insects and plant diseases. Int. Crop Sci. 1:273-280.

Patterson DT. 1995a. Weeds in a changing climate. Weed Sci. 43:685-701.

Patterson DT. 1995b. Effects of environmental stress on weed/crop interactions. Weed Sci. 28:71-75.

Patterson DT, Flint EP. 1980. Potential effects of global atmospheric CO_2 enrichment on the growth and competitiveness of C_3 and C_4 weed and crop plants. Weed Sci. 28:71-75.

Patterson DT, Flint EP. 1982. Interacting effects of CO_2 and nutrient concentration. Weed Sci. 30:389-394.

Patterson DT, Flint EP. 1990. Implications of increasing carbon dioxide and climate change for plant communities and competition in natural and managed ecosystems. In: Kimball BA, Rosenburg NJ, Allen LH Jr, editors. Impact of carbon dioxide, trace gases and climate change on global agriculture. ASA Special Publication No. 53. Madison, Wis. (USA): American Society of Agronomy. p 83-110.

Patterson DT, Flint EP, Beyers JL. 1984. Effects of CO_2 enrichment on competition between a C_4 weed and a C_3 crop. Weed Sci. 32:101-105.

Patterson DT, Highsmith MT, Flint EP. 1988. Effects of temperature and CO_2 concentration on the growth of cotton (*Gossypium hirsutum*), spurred anoda (*Anoda cristata*), and velvetleaf (*Abutilon theophrasti*). Weed Sci. 36:751-757.

Patterson DT, Westbrook JK, Joyce RJV, Lingren PD, Rogasik J. 1999. Weeds, insects and diseases. Clim. Change 43:711-727.

Pettersson RP, McDonald JS. 1994. Effects of nitrogen supply on the acclimation of photosynthesis to elevated CO_2. Photosyn. Res. 39:389-400.

Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio 104/105:77-97.

Poorter H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2? Global Change Biol. 4:693-697.

Potvin C, Strain BR. 1985. Effects of CO_2 enrichment and temperature on growth in two C_4 weeds, *Echinochloa crus-galli* and *Eleusine indica.* Can. J. Bot. 63:1495-1499.

Potvin C, Vasseur L. 1997. Long-term CO_2 enrichment of a pasture community. Ecology 78:666-677.

Radosevich S, Holt J, Ghersa C. 1997. Plant responses to CO_2. In: Radosevich S, Holt J, Ghersa C, editors. Weed ecology: implications for management. New York, N.Y. (USA): John Wiley and Sons. p 241-243.

Rosenzweig C, Hillel D. 1998. Effects on weeds, insects and diseases. In: Rosenzweig C, Hillel D, editors. Climate change and the global harvest. Oxford (UK): Oxford University Press. p 101-122.

Sage RF, Sharkey TD, Pearcy RW. 1990. The effect of leaf nitrogen and temperature on the CO_2 response of photosynthesis in the C_3 dicot *Chenopodium album* L. Aust. J. Plant Physiol. 17:135-148.

Sage RF. 1995. Was low atmospheric CO_2 during the Pleistocene a limiting factor for the origin of agriculture? Global Change Biol. 1:93-106.

Schenk U, Jager HJ, Weigel HJ. 1997. The response of perennial ryegrass/white clover swards to elevated atmospheric CO_2 concentrations. I. Effects on competition and species composition and interaction with N supply. New Phytol. 135:67-79.

Schimel D, Alves D, Enting I, Heimann M, Joos F, Raynaud D, Wigley T, Prather M, Der Went R, Ehhalt D, Fraser P, Sanhueze E, Zhou X, Jonas P, Charlson R, Rodhe H, Sadasivan S, Shine KP, Fouquart Y, Ramasawamy V, Solomon S, Srinivasan J, Albritton D, Der Went R, Isaksen I, Lal M, Wuebbles D. 1996. Radiative forcing of climate change. In: Houghton JT, Meira-Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K, editors. Climate change 1995: the science of climate change. Cambridge (UK): Cambridge University Press. p 65-131.

Treharne K. 1989. The implications of the 'greenhouse effect' for fertilizers and agrochemicals. In: Bennet RC, editor. The greenhouse effect and UK agriculture. CAS Paper 19. Ministry of Agriculture, Fisheries and Food, UK. p 67-78.

Vengris J, Colby WG, Drake M. 1955. Plant nutrient competition between weeds and corn. Agron. J. 47:213-216.

Wayne P, Foster S, Connolly J, Bazzaz F, Epstein P. 2002. Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO_2-enriched atmospheres. Ann. Allergy Asthma Immunol. 88:279-282.

Wendler DJ, Haber E, Keddy C. 1993. Effect of phosphinothricin (glufosinate) on photosynthesis and photorespiration of C_3 and C_4 plants. Photo. Res. 243-62.

Ziska LH, Bunce JA. 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C_4 crops and weeds. Photo. Res. 54:199-208.

Ziska LH, Bunce JA. 1999. Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C_4 species. Aust. J. Plant Physiol. 26:71-77.

Ziska LH, Caulfield FA. 2000. Rising CO_2 and pollen production of common ragweed (Ambrosia arternisiifoZia L.), a known allergy-inducing species: implications for public health. Aust. J. Plant Physiol. 27:893-898.

Ziska LH, Teasdale JR. 2000. Sustained growth and increased tolerance to glyphosate observed in a C_3 perennial weed, quackgrass (*Elytrigia repens*), grown at elevated carbon dioxide. Aust. J. Plant Physiol. 27:159-166.

Ziska LH, Namuco O, Moya T, Quilang J. 1997. Growth and yield responses of field-grown tropical rice to increasing carbon dioxide and air temperature. Agron. J. 89:45-53.

Ziska LH, Sicher RC, Bunce JA. 1999a. The impact of elevated carbon dioxide on the growth and gas exchange of three C_4 species differing in CO_2 leak rates. Physiol. Plant. 105:74-80.

Ziska LH, Teasdale JR, Bunce JA. 1999b. Future atmospheric carbon dioxide may increase tolerance to glyphosate. Weed Sci. 47:608-615.

Ziska LH, Ghannoum O, Baker JT, Conroy J, Bunce JA, Kobayashi K, Okada M. 2001. A global perspective of ground level, 'ambient' carbon dioxide for assessing the response of plants to atmospheric CO_2. Global Change Biol. 7:789-796.

Ziska LH. 2000. The impact of elevated CO_2 on yield loss from a C_3 and C_4 weed in field-grown soybean. Global Change Biol. 6:899-905.

Ziska LH. 2001a. My view: weeds and public health. Weed Sci. 49:437-438.

Ziska LH. 2001b. Growth temperature can alter the temperature dependent stimulation of photosynthesis by elevated carbon dioxide in *Abutilon theophrasti*. Physiol. Plant. 111:322-328.

Ziska LH. 2001c. Changes in competitive ability between a C_4 crop and a C_3 weed with elevated carbon dioxide. Weed Sci. 49:622-627.

Notes

Author's address: Plant physiologist, Alternate Crop and Systems Laboratory, USDA-ARS, Bldg 001, Room 323, 10300 Baltimore Avenue, Beltsville, MD 20705; e-mail: lziska@asrr.arsusda.gov.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Effects of climate change on rice production and adaptive technologies

H. Nakagawa, T. Horie, and T. Matsui

Recent research findings on rice responses to CO_2 concentration and air temperature in growth and yield are summarized to parameterize the responses for growth simulation models and to explore adaptive production technologies. Season-long doubling of CO_2 increased rice biomass by about 25% averaged over the reported data obtained under nearly field conditions, while high temperatures may cause decreased rice yield mainly because of high-temperature-induced spikelet sterility, which would be worsened by elevated CO_2. Key traits associated with rice adaptation to climate change and their genetic variations are discussed.

The effects of climate change on rice production in Japan were simulated by the rice growth simulation model SIMRIW. It was predicted that a 1.5 °C increase in T_{50} (the daily maximum temperature at which spikelet fertility becomes 50% because of high-temperature damage) would remarkably mitigate negative effects of climate change in many prefectures in central and southern Japan and increase total rice production in Japan by about 5%. Model simulation under various adaptive technologies indicates that the combination of advanced transplanting and the adoption of later-maturing cultivars may help to exploit the advantage of elevated CO_2 climates for rice production in Japan, although this greatly depends on prefectures.

Anticipated climate change is likely to cause new types of problems in rice production, which would need to be solved to provide opportunities to improve rice productivity. Understanding the responses of yield-determinant processes to climate change and their genetic variations will be essential to develop technologies that mitigate the negative effects of climate change and exploit the potential advantage of elevated CO_2 environments.

A considerable amount of knowledge has been accumulated on rice responses to atmospheric CO_2 concentration and high temperature (Horie et al 2000) and some of these responses were parameterized and incorporated into crop simulation models (Kropff et al 1995, Horie et al 1995b), which were then used to predict the effects of climate change on regional rice yield (Matthews et al 1995, Horie et al 1995b). Horie et al (1996) also assessed the alteration of production technologies under changed climate, including cropping seasons and cultivars. Among them, they showed that a small change in a crop parameter related to high-temperature-induced spikelet sterility had significant effects on predicted yield, indicating that the reliability of that parameter is crucial to the accurate prediction. Detailed information on cultivar differences in japonica rice for high-temperature tolerance (Matsui et al 2001b) and the effects of elevated CO_2 on spikelet sterility at high temperature (Kim et al 1996b, Matsui et al 1997b, Ueda et al 2000) has recently been reported, which was not included in the reported simulation studies.

The objective of the first half of this paper is to summarize recent research findings on rice responses to CO_2 and air temperature, with special attention to genetic variations of key traits, aiming at both suggestions for developing adaptive rice production technologies, including a breeding strategy and the parameterization of the responses for rice growth models. This paper then shows the effects of climate change on rice production in Japan predicted by a rice growth model under the technologies adaptive to future climates, such as advanced transplanting dates and the adoption of late-maturing cultivars and cultivars tolerant of high temperature.

Rice responses to elevated CO_2 and temperature and their varietal differences

Phenological development

Phenological development is one of the important features for adjusting cropping seasons to the environment. Varietal and environmental differences in total growth duration are dominated by the flowering response to daylength and temperature. The critical temperature (base temperature) for phenological development toward heading is about 12 °C for japonica-type rice and 15 °C for indica rice (Nakagawa and Horie 1995) and the optimum temperature ranges from 27 to 32 °C (Horie 1994, Yin et al 1996). Elevated CO_2 shortens the days to heading (Baker et al 1990b, Nakagawa et al 1993, Kim et al 1996a). Doubled CO_2 promoted rice development toward heading by about 5% on average and the promotion rate increases with temperature (Nakagawa and Horie 2000).

A temperature increase of 1 °C shortened days to heading by about 4–5 days for Koshihikari rice at Toyama, Japan, in a simulation study (Nakagawa et al 2001). A combination of elevated CO_2 and about 3 or 4 °C temperature increases is likely to considerably shorten the growth duration of rice. Therefore, the shifts to late-maturing cultivars would be an effective option in many rice cultivation areas under changed climate. Many rice cultivars have diverse flowering responses to daylength and temperature and it is usually easy to find a late-maturing cultivar for the respective regions. However, some exceptions exist. For example, no later-maturing cultivar than the current ones exists in Japanese rice cultivars in the southern part of Japan. Late-maturing gene *ef1* in a japonica rice cultivar of Taiwan Province of China, Taichung65, which extends the basic vegetative period, especially in the presence of complementary gene *se1* (Nishida et al 2001), would be useful for developing later-maturing japonica cultivars for the southern part of Japan.

Photosynthesis and biomass production

An increase in CO_2 generally promotes photosynthesis and biomass production of C_3 plants. Nearly doubled CO_2 increases the leaf-level photosynthetic rate of rice by 30–70% over that at ambient CO_2 (Imai and Murata 1978, Akita 1980, Morison and Gifford 1983, Lin et al 1997). CO_2 enrichment also increases rice biomass production. Nearly doubled CO_2 increased total dry weight at maturity by about 25% ± 12% (mean ± standard deviation, n = 50) on average for reported data obtained from season-long CO_2 enrichment studies under canopy conditions (Fig. 1; Baker et al 1990c, Ziska et al 1997, Nakagawa and Horie 2000, Kim et al 2001). Whether the CO_2 response can be altered by environment and genotype is an important question for developing adaptive technologies as well as predicting the effects of global climate change on rice.

Averaged relative enhancements in total dry weight of japonica (closed symbols in Fig. 1) and indica (open symbols) rice cultivars are 25% and 26%, respectively. No distinct difference in CO_2 response was observed between japonicas and indicas on average at the temperature range of 20 to 32 °C. Relative enhancement is weakly correlated with growth temperature (r = 0.548***), but the modification of biomass responses to CO_2 by temperature is much smaller than that of leaf-level photosynthetic responses (Lin et al 1997, Nakagawa et al 1997) and that predicted by a biochemical photosynthesis model (Long 1991). Above 25 °C, temperature seems to have no effects on relative enhancement. Although low temperature seems to slightly decrease the responsiveness, the biomass response to CO_2 would not be much altered by temperature under tropical and subtropical environments. In fertilizer N by CO_2 experiments conducted on both japonicas (Nakagawa et al 1994) and indicas (Ziska et al 1996b), relative enhancement in biomass production because of CO_2 enrichment increased with the increase in N application and the relative enhancement reached or exceeded 30% with adequate N fertilizer.

Ziska et al (1996a) compared the CO_2 response of 17 rice cultivars grown in pots and showed that the range of biomass responses to increased CO_2 was quite large (10–250%). Moya et al (1998) also showed a cultivar difference in the CO_2 response of biomass production at the field level, although the range of this cultivar difference was much smaller than that of potted plants. Five rice cultivars were grown in minipaddies under TGCs (temperature gradient chambers, Horie et al 1995a), which were regulated to maintain a temperature gradient of about 4 °C within chambers at ambient and doubled CO_2, in 1998 and 1999 (Ueda et al 2000, Fig. 2, see also "Yield" section). Data from temperature plots where no high-temperature-induced spikelet sterility was observed were used for the analysis. Four cultivars showed similar CO_2 responses in total dry weight at maturity (13–17% increase), but japonica upland rice Sensho showed a negligible response to CO_2. The spikelet number of Sensho was suppressed by CO_2 enrichment, while that of other cultivars was increased. At the heading stage, total dry weight of Sensho increased as in other cultivars. In the

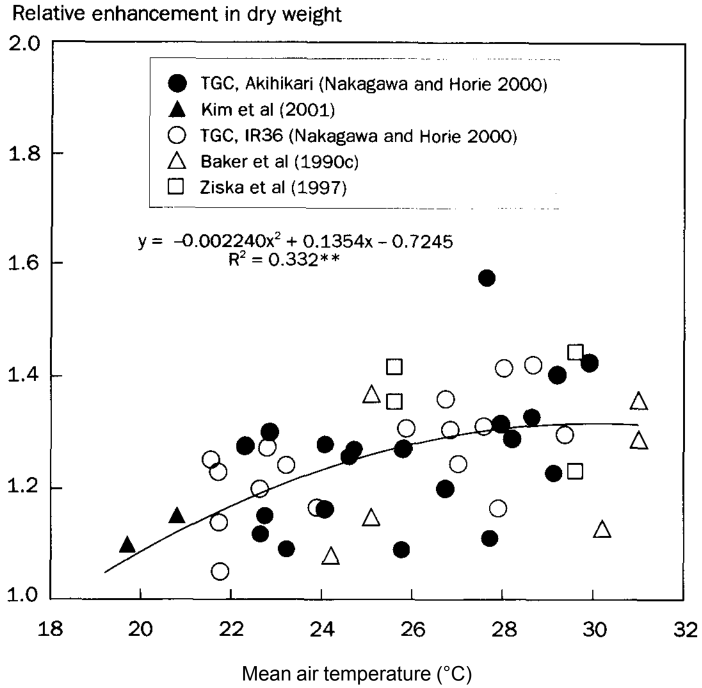


Fig. 1. Effects of mean air temperature on the relative enhancement of rice crop biomass. Plants were grown season-long in ambient and nearly doubled CO_2. The open and closed symbols are for indica and japonica cultivars, respectively. The data are normalized to the values at ambient CO_2 as unity.

case of Sensho, therefore, biomass production during the ripening phase might have been suppressed, presumably by a feedback down-regulation of photosynthesis because of the sink limitation.

Photosynthetic acclimation to elevated CO_2 above 900 μmol mol^{-1} has been reported in several experiments conducted on rice (Imai and Murata 1978, Baker et al 1990a, Rowland-Bamford et al 1991, Nakano et al 1997). Photosynthetic acclimation of rice to CO_2 seemed to be caused mainly by a decrease in leaf nitrogen content expressed on a leaf area basis (N_{leaf}), but not by the feedback of accumulated carbohydrate (Nakano et al 1997), although reduced sink size could induce down-regulation of photosynthesis of rice during the ripening phase (Lin et al 1997) through the feedback of accumulated carbohydrate. In other experiments with ambient and doubled CO_2 levels, no photosynthetic down-regulation was observed during the vegetative phase (Baker et al 1997, Lin et al 1997). In our TGC experiments for 4 years from 1992 onward, N_{leaf} and the SPAD (chlorophyll meter) value (unpublished data) were not much altered by doubled CO_2 treatments, although whole-plant nitrogen concentration (on a dry-weight basis) was always decreased by CO_2 enrichment (Kim et al 1993). As CO_2 enrichment does not change the relation between

N_{leaf} and photosynthesis, the relation among Rubisco (oxygenase) and chlorophyll and N_{leaf}, and the activation state of Rubisco in the case of rice (Nakano et al 1997), photosynthetic down-regulation might not have been the case in the TGC experiments. From that experimental evidence and analysis, we conclude that, across the range from current ambient CO_2 to the doubling of CO_2, photosynthetic acclimation to elevated CO_2 may not be a large factor at the field level during the vegetative phase.

Expecting a beneficial effect on photosynthesis of reallocation of leaf N from extra Rubisco to other components limiting photosynthesis under elevated CO_2 environments, Makino et al (1997) obtained transgenic rice plants with decreased Rubisco by introducing the *rbcS* antisense gene. They selected a transformant with 65% wild-type Rubisco content as a plant set with optimal Rubisco content for CO_2-saturated photosynthesis. The selected transgenic plant had 5–15% higher rates of photosynthesis at elevated CO_2 (1,000 μmol mol $^{-1}$) for a given N_{leaf} However, such an improvement at the level of a single leaf did not necessarily lead to greater biomass production under elevated CO_2 conditions (Makino et al 2000).

Although the intraspecific variation in biomass responses to CO_2 and the progress of genetic engineering hold out the hope that optimum rice cultivars could be bred with future increases in CO_2, our knowledge to specify the traits that enhance responsiveness of biomass production to elevated CO_2 is still lacking at the whole-plant and especially field levels.

Transpiration and water use

An increase in CO_2 increases the stomatal resistance of many plant species. A 56% increase in stomatal resistance (Morison and Gifford 1984a) and 40-49% increase in canopy resistance (Homma et al 1999) were reported for rice subjected to long-term doubled CO_2 treatments. However, doubled CO_2 does not reduce transpiration to a similar extent as the resistance increase because of the increase in leaf temperature and thus the increase in vapor pressure gradient between the leaf and air. Wada et al (1993) reported that season-long transpiration of rice grown under field-like conditions in TGCs was reduced by CO_2 enrichment by 15% at 26 °C but increased by 20% at 29.5 °C. It has been shown from energy budget analysis for rice grown in TGCs that canopy resistance declined at doubled CO_2 with the rise in growing temperature, whereas it was unaffected by temperature at ambient CO_2 (Homma et al 1999). These stomatal responses explain the response of transpiration to temperature and CO_2.

Rice, as with many other C_3 species, displays higher crop water-use efficiencies (WUE) under elevated CO_2. Morison and Gifford (1984b) found that CO_2 enrichment for rice grown in pots increased WUE by 53–63%. For rice grown in a TGC, with CO_2 enrichment at air temperature from 24 to 26 °C, WUE increased by 40–50% (Nakagawa et al 1997). However, with a further increase in air temperature, WUE decreased sharply to about a 20% enhancement at 30 °C.

There are very few reports on cultivar differences in stomatal and transpirational responses of rice to CO_2 and temperature. Understanding the stomatal behavior in elevated CO_2 and high-temperature environments will contribute to selecting adaptive

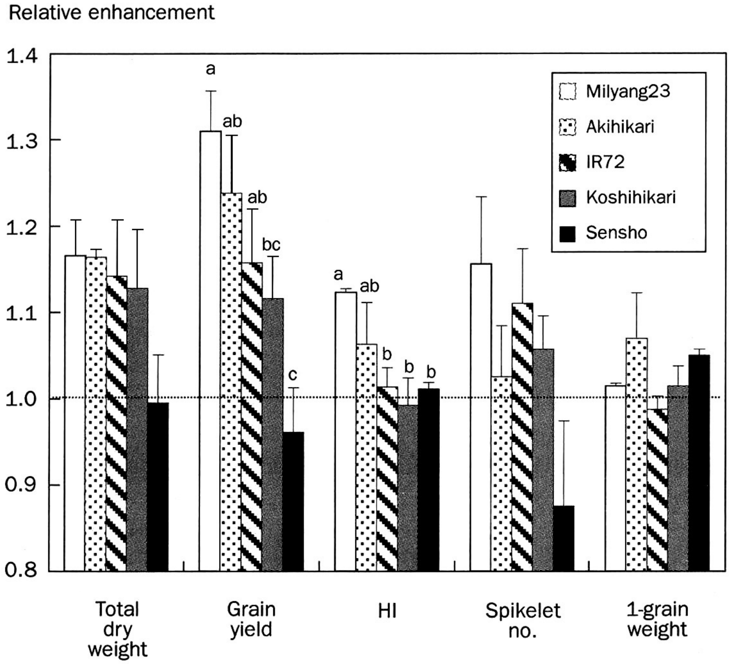


Fig. 2. Relative enhancement by doubled CO_2 of total dry weight at maturity, grain yield, harvest index (HI), spikelet number, and one-grain weight of five rice cultivars (adapted from Ueda et al 2000). Vertical bars indicate the standard errors (n = 3). Columns with the same letters above each item are not significantly different (P<0.05, least significant difference). Cultivar effects are not statistically significant by the F-test for the columns without letters.

rice cultivars because it may have indirect influences on spikelet sterility and respiration rate through transpirational cooling as well as direct effects on the diffusion process.

Yield

Increased biomass production of rice caused by elevated CO_2 has the potential to increase yield, provided flowering and grain filling are not disrupted by some environmental stress such as drought or high temperature (Hone et al 2000).

The five-cultivar trial with TGCs in 1998 and 1999 indicated that there was a larger cultivar difference in the relative yield increase with elevated CO_2 than in the relative biomass increase (Fig. 2). Milyang23 rice showed the highest yield under doubled CO_2 and also the highest relative yield increase (31 %). In contrast, the yield of Sensho was decreased by elevated CO_2 as a result of decreased spikelet number. Harvest index and spikelet number of Milyang23 were increased by CO_2 enrichment more than those of other cultivars, although the relative increase in biomass production was similar to that of the other cultivars except for Sensho, suggesting that higher

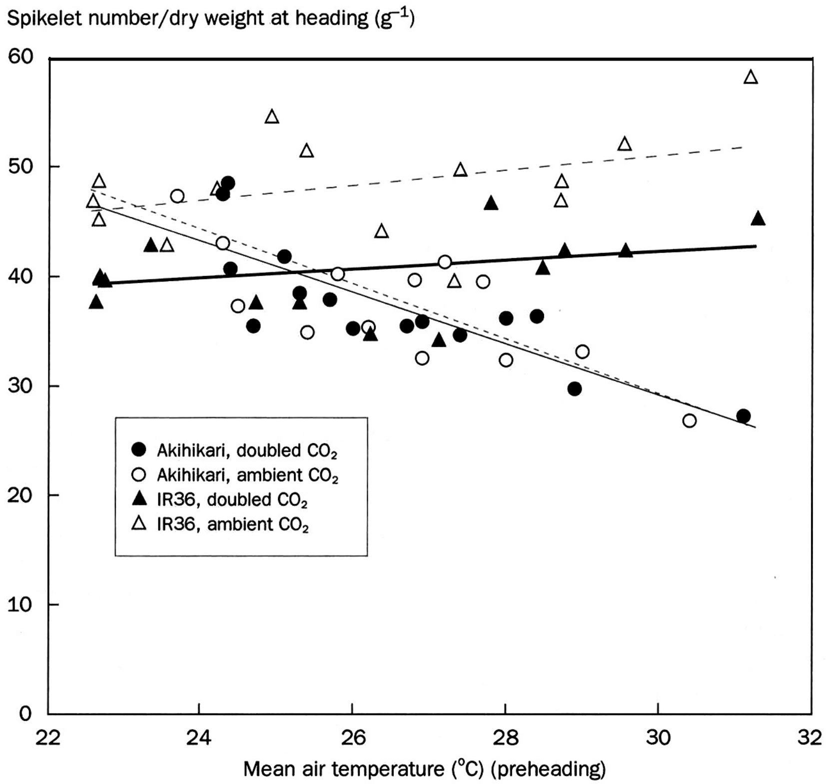


Fig. 3. Spikelet number per unit biomass at the heading stage of Japonica rice Akihikari (Nakagawa and Horie 2000) and indica rice IR36 (unpublished data) grown under ambient and doubled CO_2 as a function of mean air temperature during the preheading phase.

responsiveness of spikelet production to CO_2 may enlarge yield potential under the increased CO_2 environment.

Spikelet number per unit plant biomass at the heading stage decreased with an increase in temperature for japonica cultivar Akihikari grown in TGCs for three growth seasons irrespective of CO_2, while that of indica rice IR36 was not altered by temperature but was decreased by CO_2 enrichment (Fig. 3). Spikelet number of rice is usually highly correlated with accumulated nitrogen at the panicle formation stage (Wada 1969) and is also influenced by biomass production during the spikelet development phase through the regulation of spikelet degeneration (Matsushima 1957). The reduced response of IR36 under elevated CO_2 would imply that nitrogen was a dominant limiting factor for the spikelet production of it in elevated CO_2 plots. Thus, higher temperature environments should give merit to indica rice for the production of spikelets, which would be assured by ample amounts of nitrogen application.

Reproductive growth of the plant is generally more sensitive to extreme temperatures than vegetative growth. Spikelet sterility in rice can be induced by mean daily temperatures below 20 °C at the microspore stage. Temperatures above 35 °C at flowering can also cause spikelet sterility (Satake and Yoshida 1978, Matsui et al 1997a).

Baker et al (1995) and Ziska et al (1997) reported that grain yields of indica cultivars (IR30 and IR72, respectively) declined with increases in temperature. Similar yield reductions at daily mean temperature above 26 °C were reported for cultivar Akihikari, a japonica-type rice, under both doubled and ambient CO_2 (Kim et al 1996b). In that experiment, rice grown at doubled CO_2 suffered more severe yield reductions with increasing temperature than plants in the ambient CO_2. They attributed the greater sensitivity of the CO_2-enriched plant to high temperatures to having a lower spikelet fertility than plants grown in ambient CO_2 (Fig. 4). Figure 4 includes their data (2 years), additional data obtained from similar TGC experiments for the same cultivar in the subsequent 3 years, and also a result of a phytotron experiment (Matsui et al 2001b). In the TGC experiments, fertility was closely related to average daily maximum temperature over the flowering period and this relation is coincident with the response to day temperature in the phytotron experiment with fixed day/night temperature regimes. This is because rice spikelets are most sensitive to high temperatures during flowering and because flowering in rice usually occurs at midday. The daily maximum temperature at which fertility becomes 50% (T_{50}) was 38.5 and 36.6 °C for ambient and doubled CO_2, respectively.

Cultivar differences are considerable in high-temperature tolerance during flowering among both indica and japonica rice genotypes (Satake andYoshida 1978, Matsui et al 2001b). Nine japonica rice cultivars were subjected to constant day (35, 37.5, and 40 °C) and night (26 °C for all) temperatures (Matsui et al 2001b). The day temperature of 35 °C did not cause sterility for all cultivars. The responses of the tolerant (Akitakomachi), medium (Akihikari), and sensitive (Hinohikari) cultivars are shown in Figure 5. There was about a 3 °C difference between the most tolerant and sensitive cultivars. Rice plants usually need 10 or more germinated pollens on the stigmas for normal fertilization. As pollens of rice can germinate below 40 °C (Enomoto et al 1956), pollination is the main determinant process for spikelet sterility in the temperature range from 35 to 40 °C (Matsui et al 2001b). Thus, how high temperature inhibits anther dehiscence is a key question for understanding genotypic difference in spikelet fertility. Rapid swelling of pollen grains in response to floret opening is a driving force for anther dehiscence (Matsui et al 1999). High temperature on the day of flowering decreases the ability of the pollen grains to swell, resulting in poor anther dehiscence. Nipponbare, a high-temperature-tolerant cultivar for spikelet fertility, showed high-temperature tolerance in pollen grain swelling (Matsui et al 2000). Also, cultivar differences were found in anther morphological characteristics between high-temperature-tolerant and sensitive cultivars, that is, the well-developed cavities of the anther and thick locule walls may contribute to the high-temperature tolerance (Matsui et al 2001a). Some rice cultivars have the ability

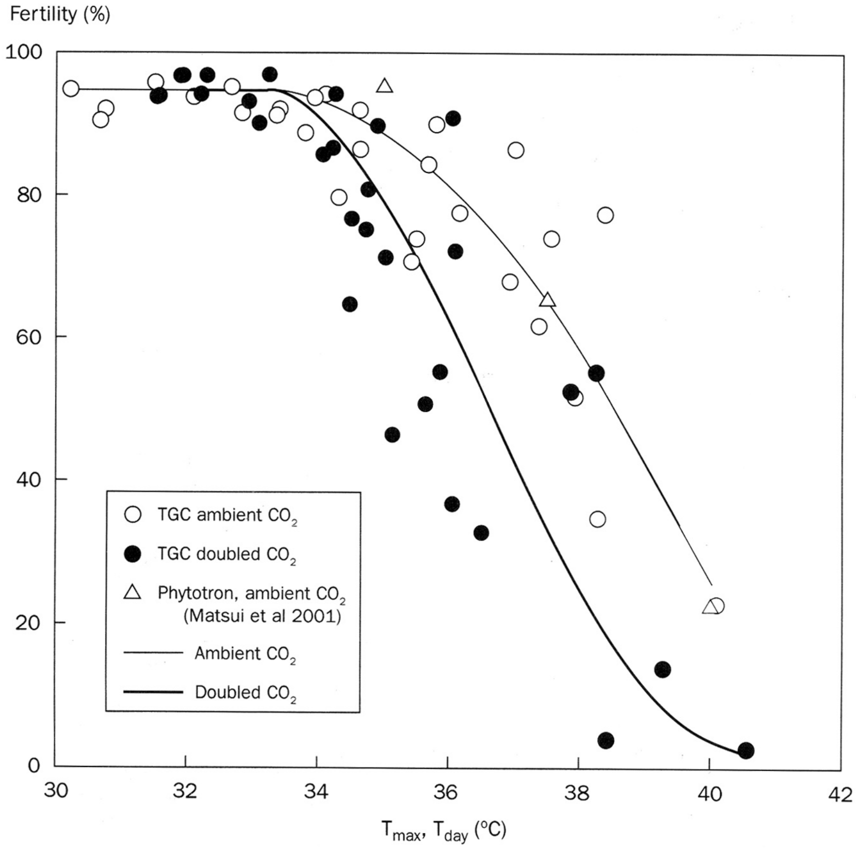


Fig. 4. Relation between average daily maximum temperature during the flowering period T_{max} (for temperature gradient chamber experiments) or daytime temperature T_{day} (for phytotron experiment) and spikelet fertility in rice cultivar Akihikari acclimated to ambient and doubled CO_2 (synthesized with the data from Kim et al 1996b, Ueda et al 2000, and Matsui et al 2001).

to flower early in the morning, thus potentially avoiding the damaging effects of higher temperatures later in the day (Imaki et al 1987, Ueda et al 2000).

Negative CO_2 effects on high-temperature-induced spikelet sterility were also found in IR72, Koshihikari, and Sensho (Matsui et al 1997b, Ueda et al 2000), but not in IR36 and Milyang23 (Kim 1996, Ueda et al 2000). High-temperature-tolerant cultivars in elevated CO_2 were not necessarily the same as those in ambient CO_2 (Ueda et al 2000). The exact mechanism through which the elevated CO_2 increased spikelet susceptibility to high-temperature-induced sterility is unknown, although increased spikelet temperature under CO_2 enrichment is one possibility (Horie et al 2000).

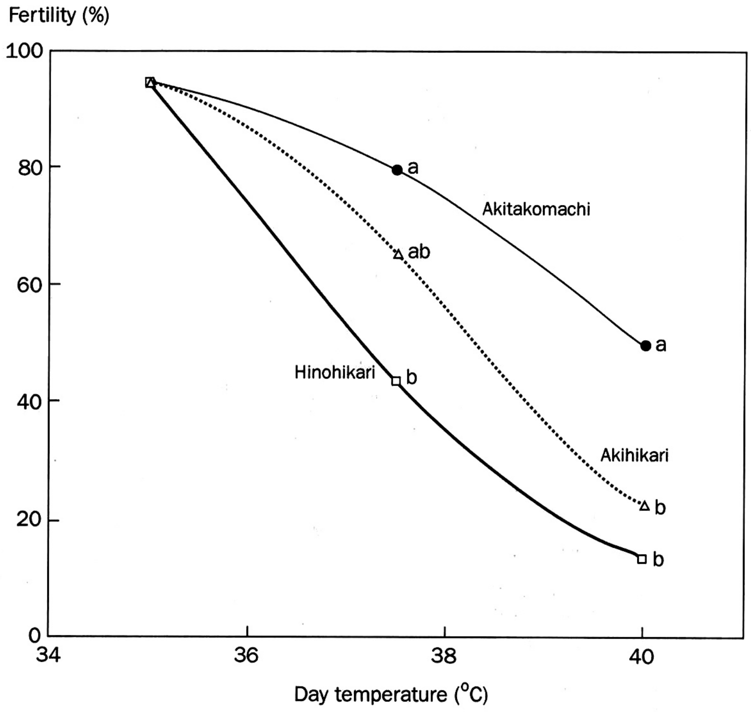


Fig. 5. The percent fertility of the spikelets flowered at various day-temperature conditions (Matsui et al 2001). Day temperature (6 h from 1000 to 1600) was changed, with night temperature being fixed at 26 °C. Symbols with the same letters are not significantly different at the 5% level and at the 1% level for 37.5 and 40.0 °C day-temperature conditions, respectively, by Duncan's multiple range test (n = 3).

Effects of global climate change on irrigated rice production in Japan

Model, input data, and parameters

The effects of global climate change were predicted by using the rice simulation model SIMRIW (Horie et al 1995a) for each prefecture in Japan. SIMRIW is a simplified process model to simulate potential rice growth in diverse climatic conditions. SIMRIW satisfactorily explained differences in irrigated rice yield among locations, cropping seasons, and years (Horie et al 1995a,b).

Daily weather data for the 30 years from 1971 to 2000 at the respective weather stations in all prefectures in Japan were selected. Normal climate for each prefecture was synthesized by averaging daily weather values over the 30 years for each prefecture. This average climate was then used as the baseline to evaluate the effects of climate change on rice yields. Outputs of four general circulation models (GCMs) were used for climate scenarios: the CGCM1 model of the Canadian Center for

Climate Modelling and Analysis (CGCM); CCSR-98 of the Center for Climate Research Studies, Japan (CCSR); CSIRO-Mk2 of the Commonwealth Scientific and Industrial Research Organisation, Australia (CSIRO); and ECHAM4/OPYC3 of the German Climate Research Center (ECHAM). These GCM outputs were obtained from the Web site of the IPCC Data Distribution Centre and processed in a convenient form around Japan (Yokozawa et al 2002). Each GCM run used a gradual increase in CO_2 according to the IS92a CO_2 emission scenario. The future climatic conditions were created by adding the monthly temperature changes from now to 2090-99 in each scenario to the current daily maximum and minimum temperatures of the same month, and by multiplying relative changes in monthly solar radiation by current daily solar radiation values. CO_2 was set at 355 and 710 μmol mol^{-1} for the crop simulation under the current and future climatic conditions, respectively.

As crop parameters for the phenological development of rice, the values derived from cultivars shown in Figure 6 were used for each prefecture. The response of spikelet fertility to daily maximum temperature was parameterized by the following equation (Yin et al 1995):

$$\text{Fertility (\%)} = 95 \left\{ \left(\frac{T_{max} - T_b}{T_o - T_b} \right) \left(\frac{T_c - T_{max}}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right\}^{\alpha}, \text{ for } T_{max} > T_o \qquad (1)$$

where T_{max} is daily maximum temperature averaged over the flowering period and T_b (base temperature), T_o (maximum optimum temperature), T_c (upper critical temperature), and a (curvature factor) are parameters. T_b and T_c were fixed to 10 and 43 °C, respectively, for T_b is not an influential parameter in this case and pollens of the rice plant generally lose their ability to germinate above 43 °C. T_o and a were fitted to the data of Akihikari in Figure 4. As T_o values were not much different between ambient and doubled CO_2, T_o was then fixed at 33 °C and finally only a was estimated. It was estimated for Akihikari that a = 4.77 for ambient CO_2 and a = 12.78 for doubled CO_2. According to the regression curves, T_{50} values corresponding to those a values of Akihikari were 38.5 and 36.6 °C for ambient and doubled CO_2, respectively. Akihikari has medium tolerance for high-temperature-induced spikelet sterility among Japanese rice cultivars (Fig. 5). T_{50} of the most tolerant cultivar, Akitakomachi, in Figure 5 was 40 °C and it was 1.5 °C higher than that of Akihikari. The values of a were similarly determined for the high-temperature-tolerant cultivar under both CO_2, on the assumption that elevated CO_2 decreases T_{50} by the same extent as Akihikari showed. These values of a were used for the simulation for the respective cultivars and CO_2 conditions.

The effects under current technologies and genotypes

The predicted relative changes in rice yield for the respective prefectures under CGCM, CCSR, CSIRO, and ECHAM scenarios were plotted on the map (Fig. 7). In this simulation, T_{50} was set at 38.5 and 36.6 °C for the current and elevated CO_2 climates, respectively. The predicted effects of climate change depend on prefectures

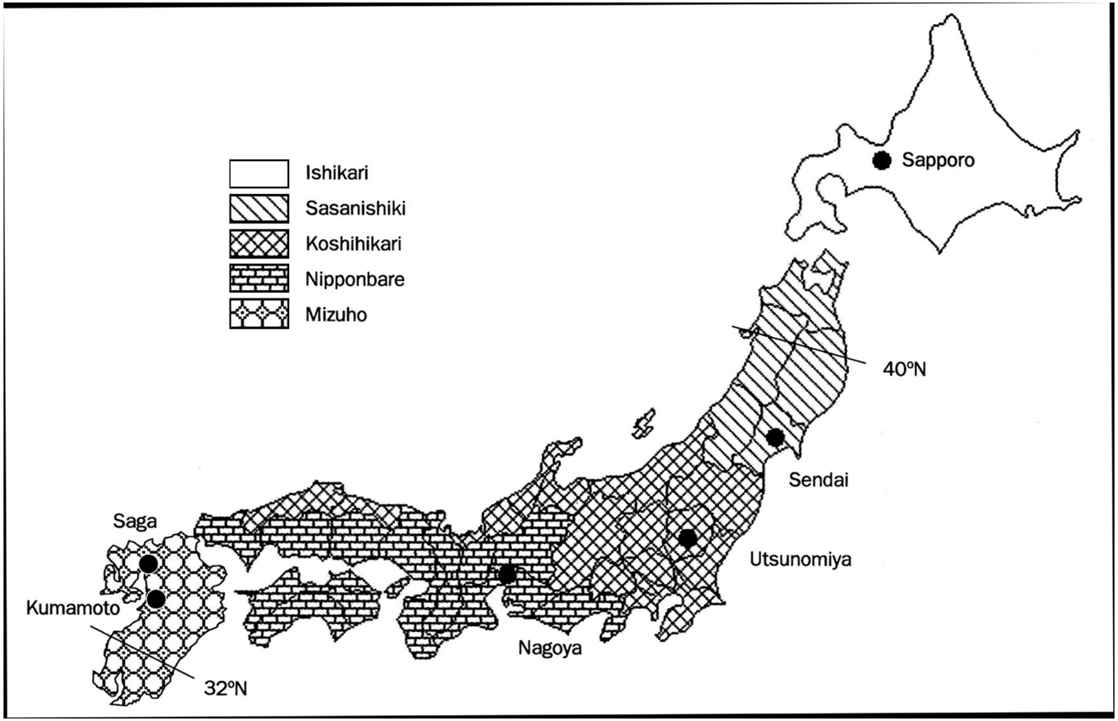


Fig. 6. Cultivars adopted for the prediction of rice yield under climate-change scenarios in each prefecture in Japan (indicated by patterns) and names of several cities that are referred to in the text.

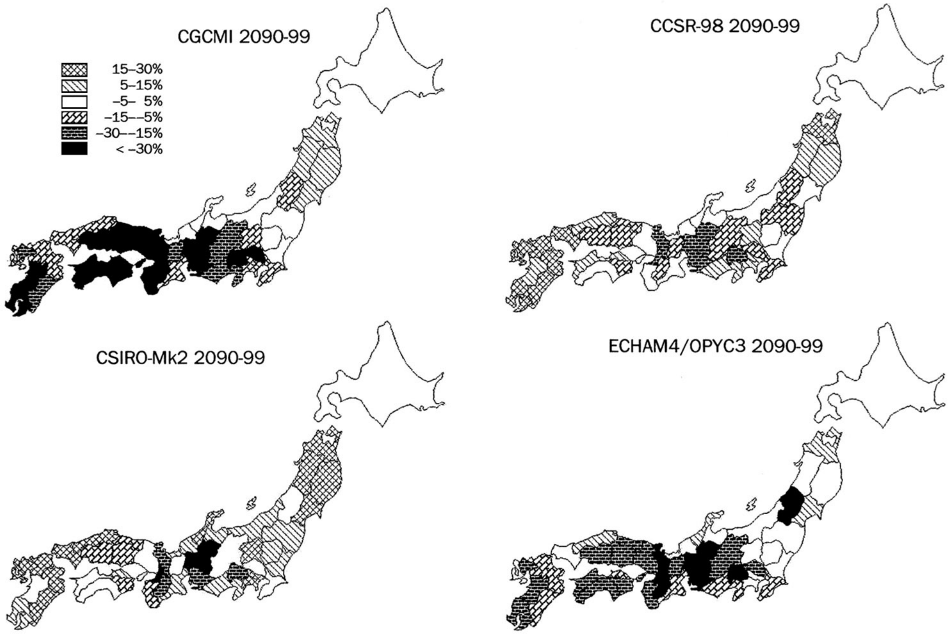


Fig. 7. Effects of doubled CO_2 and associated climate change predicted by four general circulation models on prefectural rice yield in Japan shown by the relative yield increase over the current yield (predicted by SIMRIW with $T_{50} = 36.6$ °C, which means medium high-temperature tolerance under doubled CO_2).

and climate scenarios. Positive effects of climate change, ranging from about 10% (ECHAM) to about 23% (CSIRO), were predicted in several prefectures in northern Japan. In contrast, a severe yield reduction was predicted in many prefectures in central and southern Japan. The relative yield reduction ranged from 27.5% (CCSR) to 63% (CGCM) in the worst prefecture. Four GCMs predicted similar increases in the annual mean temperature averaged over all Japan in 2090-99, ranging from 4.6 °C (CCSR) to 5.1 °C (ECHAM). Predicted increases in daily maximum temperature in August, however, varied among GCMs, from 3.3 °C (CCSR) to 4.8 °C (ECHAM). These differences in maximum temperature in August were the main cause of the large difference in yield reduction among climate scenarios because the maximum temperature in summer is related to spikelet sterility.

Since there are cultivar differences of at least 3 °C in high-temperature tolerance of spikelet sterility in japonica rice (Matsui et al 2001b), it would be relatively easy to adopt high-temperature-tolerant cultivars in southern Japan. Because the T_{50} of a high-temperature-tolerant cultivar is 1.5 °C higher than that of Akihikari (Matsui et al 2001b), T_{50}= 38.1 °C may be an attainable range under doubled CO_2 climates. In the simulation run with T_{50} = 38.1 °C, the predicted yield reduction in the worst prefecture ranged from 3% to 33% under four climate scenarios. When T_{50} of the tolerant cultivar was assumed to be 40 °C, which is the value of the most tolerant cultivar observed under ambient CO_2, yield change ranged from -10% to +16%.

Figure 8 shows the coefficient of variation (CV) of rice yield predicted by SIMRIW for each prefecture in Japan. Future weather for 30 years was created by adding the change in climate to daily data for 30 years from 1971 to 2000, assuming that climate variation itself does not change in the future. Predicted CVs under the current climatic conditions were relatively small and most prefectures with high CV values are concentrated in northern Japan, especially regions facing the Pacific Ocean, which coincided well with actual observations. Under the CCSR climate, CVs were expected to increase in most prefectures in the simulation run with T_{50} = 36.6 °C. Especially in prefectures in central Japan, CVs exceeded 40%. CVs will decrease significantly by improving high-temperature tolerance by 1.5 °C, although still relatively large CVs were predicted in some prefectures.

The effects of climate change on total rice production in Japan were estimated by calculating the mean of predicted relative yield changes of all prefectures weighted with the relative contribution to their total rice production in a recent year (Fig. 9). This figure includes relative yield increase in Japan as a function of high-temperature tolerance expressed by T_{50} for four scenarios and their average, and includes the CV under the CCSR climate. In the worst scenario (CGCM), total rice production of Japan with T_{50} = 36.6 °C was predicted to decrease by about 13%, while it increased by about 8% in the best scenario (CSIRO). The prediction under the CCSR climate was close to the average for four scenarios. The increase in T_{50} was similarly effective for all scenarios. A 1.5 °C increase in T_{50} improved relative yield increase by about 5% on average. When cultivars with $T_{50} > 39$ °C are used, total rice production in Japan would not decrease even under the worst scenario. High-temperature tolerance also considerably decreased the predicted CV value.

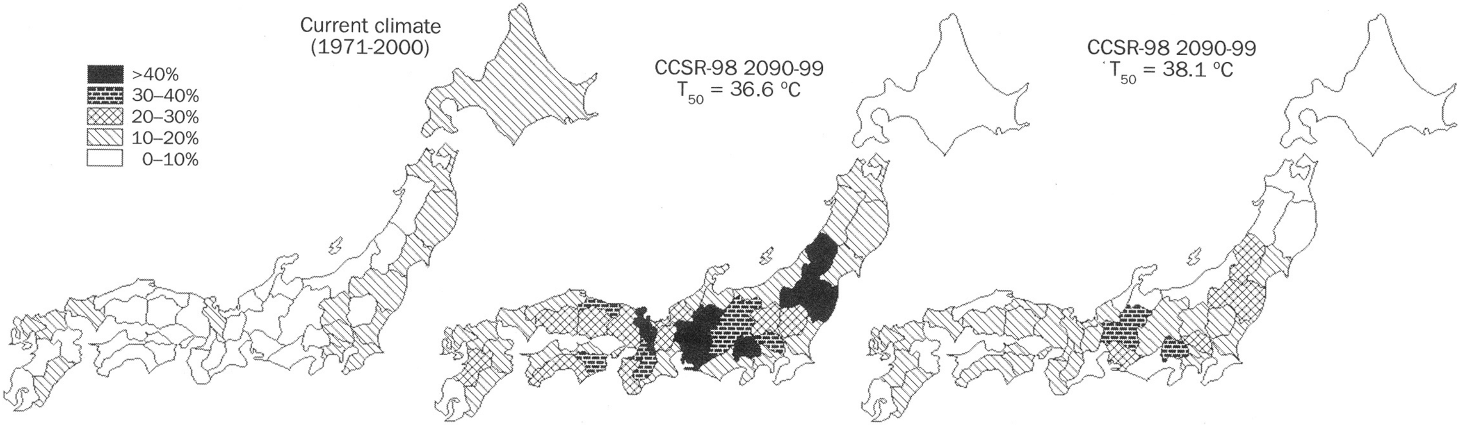


Fig. 8. **Coefficient of variation (CV) in the year-to-year variation of rice yield in each prefecture of Japan predicted by SIMRIW under the current and CCSR climates.**

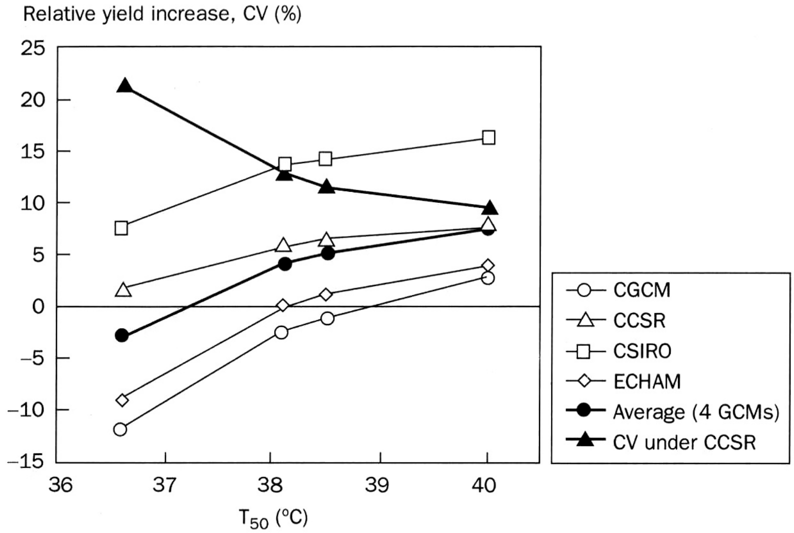


Fig. 9. Predicted increase (for 4 general circulation models and average of results under 4 GCMs) and coefficient of variation, CV (for CCSR climate), in rice yield averaged over all prefectures in Japan as a functlon of T_{50} (the daily maximum temperature at which fertility of spikelets becomes 50%).

Effects of adaptive technologies

It is realistic to assume that, under a climate change, rice production technologies will be adapted to changed climate. For technological adaptation, alterations of cultivars and cropping seasons are most likely to occur under a climate change. Apart from the tolerance for high-temperature damage of spikelets, rice cultivar adaptation will be made mainly through changes in phenological development traits. The effects of alteration of phenology parameters and cropping seasons on the predicted rice yield in Japan were examined under doubled CO_2 climate.

Hone at al (1996) predicted the effects of various transplanting dates and adoption of cultivars with late-maturating traits on several locations in Japan under future climates and showed that the combination of earlier transplanting date and late-maturing cultivars will improve rice yield at a location in northern Japan but not at a location in the south. Similar analysis was applied here to all prefectures in Japan (Fig. 10). The effects of climate change by two climate scenarios (CCSR and CGCM) on rice production in Japan were predicted under the current and changed technologies, that is, one-month-earlier transplanting and/or the adoption of later-maturing cultivars. Later-maturing cultivars currently planted in the south in the respective regions were selected in each prefecture. In the most southern part of Japan, the basic vegetative growth period was assumed to be extended by 5 days, for there were no later-maturing cultivars than Mizuho among Japanese rice cultivars. The adapted technologies here mean the best among four options in each prefecture.

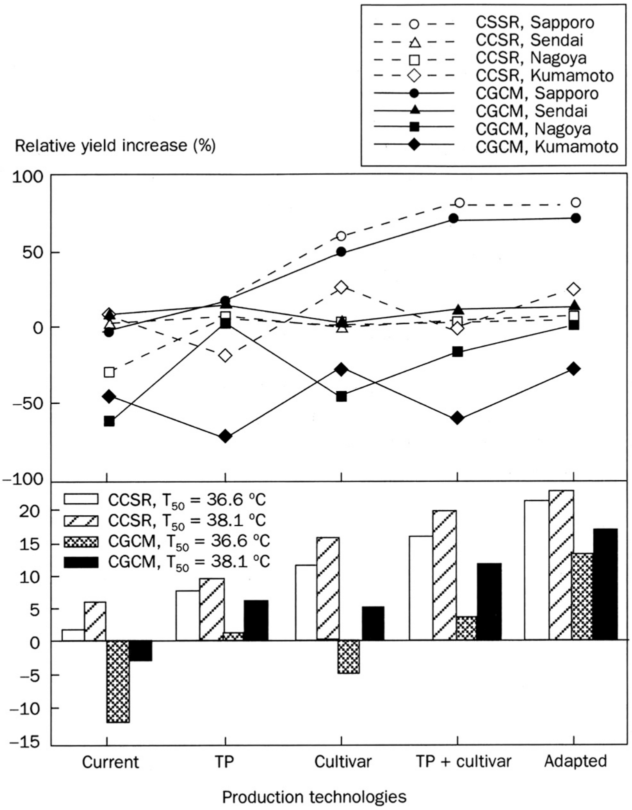


Fig 10. Effects of production technologies on relative change in rice yield by climate change at four locations (upper) and average of the yield changes in all prefectures in Japan (bottom). Current = current transplanting date, current cultivar; TP = one-month advanced transplanting date; Cultivar = adoption of later-maturing cultlvar; TP + cultivar = both TP and cultivar; Adapted = the best among four options above in each prefecture.

In the upper graph, T_{50} was set at 36.6 °C. Predictions at Sapporo showed that the combination of change in both the transplanting date and cultivar would increase rice yield by 70-80% under the future climate. At Sendai, rice yield was slightly increased by climate change, irrespective of climate scenarios and production technologies. At Nagoya, one-month-earlier transplanting was effective for avoiding high temperatures at flowering, although it was difficult to increase rice yield under the CGCM scenario. At Kumamoto, earlier transplanting made matters worse. The adoption of late-maturing cultivars was effective, although cultivars with such phenological traits do not exist currently. The weighted mean of yield increases by climate change in all prefectures in Japan was also calculated for each production technology (the bottom of Fig. 10). The improvement in high-temperature tolerance was effective for all cases. Predicted total rice production in Japan was almost unchanged under the CCSR climate with the current production technology and $T_{50} = 36.6$ °C and decreased by about 12% under the CGCM scenario. Predicted total rice production was increased by about 10% to 20% by selecting the best combination of technologies in each prefecture. The potential advantage of elevated CO_2 will be realized by mitigating the negative effects of global warming with adapted technologies in irrigated conditions with high inputs, like in Japan.

Effects of climate change on double cropping with rice and barley

Apart from the damage caused by extreme temperature, elevated temperature often reduces crop yield by shortening the growth period. However, high-temperature conditions extend the periods during which crops can be grown or increase the remaining periods for other crops to grow. Thus, the effects of climate change on the total cropping system are more important when considering food security. Here, we predicted the effects of climate change on the rice-barley double-cropping system in Japan (Table 1). Rice-barley or rice-wheat systems had been widely practiced in the central and southern part of Japan until barley and wheat production were minimized because of the increase in imports of wheat and barley. These cropping systems are also popular in many regions in monsoon Asia.

Rice yield under the current and future climate was predicted by SIMRTW at three locations in Japan. Barley yield was predicted by a barley simulation model, whose structure is similar to that of SIMRIW, and was parameterized by the data set for two-row barley cultivar Amagi-Nijo (Nakagawa et al 1993a,b). Sowing dates of barley were fixed at the current standard in the respective prefectures. We assumed that rice could be transplanted 2 weeks after the maturation of barley. Under the CCSR climate, two transplanting dates were used: the same date as that under the current climate and the advanced date (2 weeks after the predicted maturity date of barley). It was predicted that even late-maturing rice cultivar Mizuho finished its growth more than 2 weeks before the sowing of barley under the CCSR climate. Predicted yield increases in barley by climate change were 27%, 18%, and 8% at Utsunomiya, Nagoya, and Saga, respectively, under the CCSR climate. Changes in rice yield were 17%, –7%, and 15%, respectively, in the same order, when the current transplanting dates were used. The sums of potential yields of barley and rice increased similarly by 22%, 5%, and 12% at the three locations. The advanced transplanting date increased rice yield markedly at Utsunomiya, especially with the adoption of the late-maturing cultivar Mizuho, while it did not at Nagoya and Saga. The annual total productivity of the double-cropping system will improve significantly in the regions close to the northern limit of possible double-cropping areas in Japan.

Table 1. Effects of climate change on a double-cropping system with rice and barley at three locations in Japan. Yp denotes potential yield (rough grain with 14% moisture) predicted by SIMRIW and a barley growth model.

Location	Climate scenario[a]	Two-row barley			Rice				Barley + rice
		Sowing date	Maturity date	Yp (t ha^{-1})	Cultivar	Transplanting date	Maturity date	Yp (t ha^{-1})	Yp (t ha^{-1})
Utsunomiya	Current climate	9 Nov	11 Jun	7.0 (100)	Koshihikari	25 Jun	24 Oct	6.2 (100)	13.1 (100)
(36°33'N)					Koshihikari	25 Jun	2 Oct	7.2 (117)	16.1 (122)
	CCSR98 209099	9 Nov	14 May	8.9 (127)	Koshihikari	28 May	8 Sep	7.6 (123)	16.5 (126)
					Mizuho	28 May	30 Sep	9.0 (147)	17.9 (136)
Nagoya	Current climate	17 Nov	1 Jun	6.9 (100)	Nipponbare	15 Jun	2 Oct	7.1 (100)	14.0 (100)
(35°10'N)					Nipponbare	15 Jun	22 Sep	6.6 (93)	14.7 (105)
	CCSR98 209099	17 Nov	9 May	8.1 (118)	Nipponbare	23 May	3 Sep	5.7 (78)	13.8 (99)
					Mizuho	23 May	22 Sep	6.6 (93)	14.7 (105)
Saga	Current climate	26 Nov	30 May	6.4 (100)	Mizuho	13 Jun	14 Oct	8.3 (100)	14.7 (100)
(33°16'N)	CCSR98 209099	26 Nov	10 May	6.9 (108)	Mizuho	13 Jun	2 Oct	9.6 (115)	16.5 (112)
					Mizuho	24 May	15 Sep	8.0 (96)	15.0 (102)

[a] CCSR = Center for Climate Research Studies, Japan.

Conclusions

Averaged over several different studies, season-long doubling of CO_2 increased rice biomass production under field conditions by about 25% over a relatively wide range of air temperatures. There are considerable intraspecific differences in the response of biomass production and yield to CO_2. Although what traits contribute to breeding optimum cultivars under an increase in CO_2 remains a question, the high responsiveness of spikelet production to CO_2 may be one of the traits worth further investigating. High temperatures above about 35 °C markedly reduce rice yield because of spikelet sterility. Rice genotypes differ in their ability to tolerate or avoid high-temperature-induced spikelet sterility. CO_2 enrichment increased susceptibility to high-temperature-induced spikelet sterility in some cultivars.

The effects of climate change on rice production in Japan were predicted by using the rice growth simulation model SIMRIW, which included recent research findings as parameters, and four climate scenarios with doubled CO_2. The predicted relative change in total rice production in Japan in the 2090s ranged from -10% to 7% under current technologies, depending on climate scenarios. High-temperature-tolerant cultivars markedly mitigate negative effects on rice yield in southern Japan. Also, the best combination of cropping season and adoption of later-maturing cultivars in each prefecture can exploit the potential advantage of elevated CO_2 environments in northern Japan, but only maintain current yield levels in southern Japan. The predicted increase by climate change in total productivity of a double-cropping system with rice and barley was about 36% around the northern limit of double-cropping area in Japan, but only slight in southern Japan.

References

Akita S. 1980. Studies on the difference in photosynthesis and photorespiration among crops. II. The differential response of photosynthesis, photorespiration and dry matter production to carbon dioxide concentration among species. Bull. Natl. Inst. Agric. Sci. Ser. D 31:59-94.

Baker J, Allen L Jr, Boote K, Jones P, Jones J. 1990a. Rice photosynthesis and evapotranspiration in subambient, ambient and supraambient carbon dioxide concentrations. Agron. J. 82:834-840.

Baker J, Allen L Jr, Jones P, Jones J. 1990b. Developmental responses of rice to photoperiod and carbon dioxide concentration. Agric. Forest Meteorol. 50:201-210.

Baker J, Allen L Jr, Boote K. 1990c. Growth and yield responses of rice to carbon dioxide concentration. J. Agric. Sci. 115:313-320.

Baker J, Boote K, Allen L Jr. 1995. Potential climate change effects on rice: carbon dioxide and temperature. In: Rosenzweig C et al, editors. Climate change and agriculture: analysis of potential international impacts. ASA Special Publication No. 59. Madison, Wis. (USA): American Society of Agronomy. p 31-47.

Baker J, Allen L Jr, Boote K, Pickerings N. 1997. Rice responses to drought under carbon dioxide enrichment. 2. Photosynthesis and evapotranspiration. Global Change Biol. 3:129-138.

Enomoto C, Yamada I, Hozumi K. 1956. Artificial germination of pollens in rice. IV. Critical temperatures for the germination of pollens of rice cultivars. Jpn. J. Crop Sci. 25:69.

Homma K, Nakagawa H, Horie T, Ohnishi H, Kim HY, Ohnishi M. 1999. Energy budget and transpiration characteristics of rice grown under elevated CO_2 and high temperature conditions as determined by remotely sensed canopy temperatures. Jpn. J. Crop Sci. 68:137-145.

Horie T. 1994. Crop ontogeny and development. In: Boote KJ et al, editors. Physiology and determination of crop yield. Madison, Wis. (USA): CSSA-ASA-SSSA. p 153-180.

Horie T, Nakagawa H, Nakano J, Hamotani K, Kim HY. 1995a. Temperature gradient chambers for research on global environment change. III. A system designed for rice in Kyoto, Japan. Plant Cell Environ. 18:1064-1069.

Horie T, Nakagawa H, Ohnishi M, Nakano J. 1995b. Rice production in Japan under current and future climates. In: Matthews RB et al, editors. Modelling the impact of climate change on rice in Asia. Oxon (UK): CAB International. p 143-164.

Horie T, Matsui T, Nakagawa H, Omasa K. 1996. Effects of elevated CO_2 and global climate change on rice yield in Japan. In: Omas K et al, editors. Climate change and plants in East Asia. Tokyo (Japan): Springer-Verlag. p 39-65.

Horie T, Baker J, Nakagawa H, Matsui T, Kim HY. 2000. Crop ecosystem responses to climate change: rice. In: Reddy K, Hodges H, editors. Climate change and global crop productivity. Oxon (UK): CAB International. p 81-106.

Imai K, Murata Y. 1978. Effect of carbon dioxide concentration on growth and dry matter production of crop plants. IV. After-effects of carbon dioxide-treatments on the apparent photosynthesis, dark respiration and dry matter production. Jpn. J. Crop Sci. 47:330-335.

Imaki T, Tokunaga S, Obara S. 1987. High temperature-induced spikelet sterility of rice in relation to flowering time. Jpn. J. Crop Sci. 56(extra issue2):209-210.

Kim HY, Horie T, Nakagawa H, Wada K, Seo T. 1993. Effects of elevated CO_2 concentration and high temperature on growth and nitrogen use efficiency of rice. In: Crop production and improvement technology in Asia. Korea: KCSC. p 205-211.

Kim HY, Horie T, Nakagawa H, Wada K. 1996a. Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. I. The effect on development, dry matter production and some growth characters. Jpn. J. Crop Sci. 65:634-643.

Kim HY, Horie T, Nakagawa H, Wada K. 1996b. Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. II. The effect on yield and its components of Akihikari rice. Jpn. J. Crop Sci. 65:644-651.

Kim HY. 1996. Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. PhD thesis submitted to Graduate School of Agriculture, Kyoto University, Kyoto (Japan). p 1-90.

Kim HY, Lieffering M, Miura S, Kobayashi K, Okada M. 2001. Growth and nitrogen uptake of CO_2-enriched rice under field conditions. New Phytol. 150:223-229.

Kropff M, Matthews R, van Laar H, ten Berge H. 1995. The rice model ORYZA1 and its testing. In: Matthews R et al, editors. Modelling the impact of climate change on rice in Asia. Oxon (UK): CAB International. p 27-50.

Lin W, Ziska L, Namuco O, Bai K. 1997. The interaction of high temperature and elevated CO_2 on photosynthetic acclimation of single leaves of rice *in situ.* Physiol. Plant. 99: 178-184.

Long S. 1991. Modification of the response of photosynthetic productivity to rising temperaare by atmospheric CO_2 concentration: Has its importance been underestimated? Plant Cell Environ. 14:729-739.

Makino A, Shimada T, Takumi S, Kaneko K, Matsuoka M, Shimamoto K, Nakano H, Miyao-Tokutomi M, Mae T, Yamamoto N. 1997. Does decrease in ribulose-1,5-bisphosphate carboxylase by antisense *RbcS* lead to a higher N-use efficiency of photosynthesis under conditions of saturating CO_2 and light in rice plants? Plant Physiol. 114:483-491.

Makino A, Harada M, Kaneko K, Mae T, Shimada T, Yamamoto N. 2000. Whole-plant growth and N allocation in transgenic rice plants with decreased content of ribulose-1,5-bisphosphate carboxylase under different CO_2 partial pressures. Aust. J. Plant Physiol. 27:1-12.

Matsui T, Omasa K, Horie H. 1997a. High temperature-induced spikelet sterility of japonica rice at flowering in relation to air temperature, humidity and wind velocity. Jpn. J. Crop Sci. 66:449-455.

Matsui T, Namuco O, Ziska L, Horie T. 1997b. Effects of high temperature and CO_2 concentration on spikelet sterility in indica rice. Field Crops Res. 51:213-219.

Matsui T, Omasa K, Horie H. 1999. Rapid swelling of pollen grains in response to floret opening unfolds anther locule in rice (*Oryza sativa* L.). Plant Prod. Sci. 2:196-199.

Matsui T, Omasa K, Horie T. 2000. High temperature at flowering inhibits swelling of pollen grains, a driving force for thecae dehiscence in rice (*Oryza sativa* L.), Plant Prod. Sci. 3:430-434.

Matsui T, Omasa K, Horie T. 2001a. Comparison between anthers of two rice (*Oryza sativa* L.) cultivars with tolerance to high temperatures at flowering or susceptibility. Plant Prod. Sci. 4:36-40.

Matsui T, Omasa K, Horie T. 2001b. The difference in sterility due to high temperatures during the flowering period among japonica-rice varieties. Plant Prod. Sci. 4:90-93.

Matsushima S. 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice. Bull. Natl. Inst. Agric. Sci. Ser. A 5:1-271.

Matthews R, Horie T, Kropff M, Bachelet D, Centeno H, Shin J, Mohandas S, Singh S, Zhu D, Lee M. 1995. A regional evaluation of the effect of future climate change on rice production in Asia. In: Matthews RB et al, editors. Modelling the impact of climate change on rice in Asia. Oxon (UK): CAB International. p 95-139.

Morison J, Gifford R. 1983. Stomatal sensitivity to carbon dioxide and humidity: a comparison of two C_3 and two C_4 grass species. Plant Physiol. 71:789-796.

Morison J, Gifford R. 1984a. Plant growth and water use with limited water supply in high CO_2 concentrations. I. Leaf area, water use and transpiration. Aust. J. Plant Physiol. 11:361-374.

Morison J, Gifford R. 1984b. Plant growth and water use with limited water supply in high CO_2 concentrations. 11. Plant dry weight, partitioning and water use efficiency. Aust. J. Plant Physiol. 11:375-384.

Moya T, Ziska L, Namco O, Olszyk D. 1998. Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. Global Change Biol. 4545-656.

Nakagawa H, Horie T, Nakano J, Kim HY, Wada K, Kobayashi M. 1993. Effect of elevated CO_2 concentration and high temperature on growth and development of rice. J. Agric. Meteorol. 48:799-802.

Nakagawa H, Horie T, Kim HY. 1994. Environmental factors affecting rice responses to elevated carbon dioxide concentrations. Int. Rice Res. Notes 19:45-46.

Nakagawa H, Horie T. 1995. Modelling and prediction of developmental process in rice. 2. A model for simulating panicle development based on daily photoperiod and temperature. Jpn. J. Crop Sci. 64:33-42.

Nakagawa H, Horie T, Kim HY, Ohnishi H, Homma K. 1997. Rice responses to elevated CO_2 concentrations and high temperatures. J. Agric. Meteorol. 52:797-800.

Nakagawa H, Oh H, Endo N, Horie T. 1993a. Modelling and prediction of growth and yield in two-rowed barley. I. A model for predicting ontogenic development process. Jpn. J. Crop Sci. 62(extra issue2):77-78.

Nakagawa H, Fukui K, Ito A, Endo N, Horie T. 1993b. Modelling and prediction of growth and yield in two-rowed barley. II. Modelling of dry matter production and leaf area growth. Jpn. J. Crop Sci. 62(extra issue2):79-80.

Nakagawa H, Horie T. 2000. Rice responses to elevated CO_2 and temperature. Global Environ. Res. 3:101-113.

Nakagawa H, Takahashi W, Hasegawa T, Watanabe T, Horie T. 2001. Development of a three-dimensional simulator for rice growth and development. II. Accuracy of a rice phenology model to simulate heading stage and plant age in leaf number. Jpn. J. Crop Sci. 70(extra issue2):125-126.

Nakano H, Makino A, Mae T. 1997. The effect of elevated partial pressures of CO_2 on the relationship between photosynthetic capacity and N content in rice leaves. Plant Physiol. 115:191-198.

Nishida H, Okumoto Y, Nakagawa H, Ichitani K, Inoue H and Tanisaka T. 2001. Analysis of tester lines for rice (*Oryza sativa* L.) heading-time genes using reciprocal photoperiodic transfer treatments. Ann. Bot. 88:527-536.

Rowland-Bamford A, Baker J, Allen L Jr, Bowes G. 1991. Acclimation of rice to changing atmospheric carbon dioxide concentration. Plant Cell Environ. 14:577-583.

Satake T, Yoshida S. 1978. High temperature-induced sterility in Indica rice at flowering. Jpn. J. Crop Sci. 47:6-17.

Ueda T, Nakagawa H, Okada K, Horie T. 2000. Varietal differences in yield and spikelet fertility of rice in response to elevated CO_2 concentration and high temperature. Jpn. J. Crop Sci. 69(extra issue 1):112-113. (In Japanese.)

Wada G. 1969. The effect of nitrogenous nutrition on the yield-determining process of the rice plant. Bull. Natl. Inst. Agric. Sci. Ser. A 16:27-167.

Wada K, Horie T, Nakagawa H, Kim HY, Nakano Y. 1993. Effects of elevated CO_2 concentration and high temperature on water use efficiency of rice. Report of the Society of Crop Science and Breeding in Kinki 38:49-50.

Yin X, Kropff M, McLaren G, Visperas R. 1995. A nonlinear model for crop development as a function of temperature. Agric. For. Meteorol. 77:1-16.

Yin X, Kropff M, Goudriaan J. 1996. Differential effects of day and night temperature on development to flowering in rice. Ann. Bot. 77:203-213.

Yokozawa M, Goto S, Hayashi Y, Seino H. 2002. Mesh climate data for evaluating climate change impacts in Japan under gradually increasing CO_2. J. Agric. Meteorol. (In press.)

Ziska L, Manalo P, Ordonez R. 1996a. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J. EXP. Bot. 47:1353-1359.

Ziska L, Weerakoon W, Namuco O, Pamplona R. 1996b. The influence of nitrogen on the elevated CO_2 response in field-grown rice. Aust. J. Plant Physiol. 23:45-52.

Ziska L, Namuco O, Moya T, Quilang J. 1997. Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. Agron. J. 89:45-53.

Notes

Authors' address: Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Photosynthetic acclimation of rice to global climate change will a same-cell C_4 system help?

G. Bowes, S.K. Rao, and J.B. Reiskind

Photosynthesis, water-use efficiency, and growth of rice (*Oryza sativa*) should increase as atmospheric CO_2 doubles, but higher temperatures could reduce yields. Also, ribulose bisphosphate carboxylase-oxygenase (Rubisco) in rice is down-regulated by CO_2 enrichment, so photosynthesis and yield level off at 500 µbar CO_2. Yield increases from climate change are thus unlikely to keep pace with population growth. Molecular engineering of a C_4 system could enhance the C_3 photosynthesis of rice, but adverse temperature effects on reproduction must still be countered. Engineering C_4 biochemistry and Kranz anatomy into rice is a daunting task. However, the facultative C_4 monocot *Hydrilla verticillata* serves as a model because it lacks Kranz anatomy. Instead, the C_4 and Calvin cycles coexist and operate in series in the same cell, rather than in separate cells. Cytosolic phospho*enolypyruvate* carboxylase (PEPC) is segregated from Rubisco and the decarboxylase (NADP malic enzyme) in the chloroplasts, where CO_2 is concentrated. A specific PEPC isoform (*Hvpepc4*) is induced, along with other C_4 cycle enzymes, and functions in photosynthesis of the C_4 leaf.

Rising atmospheric CO_2, like the C_4 cycle, is a CO_2 concentrating mechanism (CCM) for Rubisco. Consequently, we review the responses of rice grown at elevated CO_2 and temperatures, as might be experienced in future climate scenarios. We also describe the *Hydrilla* CCM and discuss whether, in a CO_2-enriched atmosphere, its "minimalist" C_4 system could enhance yields of a transgenic rice cultivar.

According to FAO records, over the past 40 years, grain yields for Asian paddy rice (*Oryza sativa*) have doubled from around 2 to 4 t ha^{-1}, although the rate of increase has now declined (Dawe 2000, Doberman 2000). Over this time frame, the Keeling curve shows that atmospheric CO_2 has risen from 316 µbar in 1960 to 370 µbar in 2000 (Keeling and Whorf 2001). Because rice has C_3 photosynthesis, which is thus not saturated by current atmospheric CO_2, part of the yield increase is likely attributable to the additional CO_2. However, to meet the demand for food imposed by population growth, it is estimated that further increases of 40% to 50% are needed before the middle of this century. There is anticipation that the production of transgenic C_4 rice varieties could enhance future yields (Sheehy 2000) given that C_4 photosynthesis is generally more effective than C_3 at current CO_2. This hope is bolstered by the report that transgenic rice lines with one or two overexpressed C_4 enzymes, including phospho*enol*pyruvate carboxylase (PEPC), the initial fixation enzyme of C_4 plants, have increased photosynthesis, growth, and yield (Murphy et al 2001). But not all growth and yield results for transgenic rice have been as positive (Miyao-Tokutomi et al 2001).

Engineering into rice the multigenic traits for a full C_4 system like that of maize (*Zea mays*), including all C_4 cycle enzymes and their regulation and cell-specific expression along with the genes for C_4 (Kranz) leaf anatomy, is a daunting task. In this regard, over two decades ago, we made the first discovery of a plant that performs C_4 photosynthesis without Kranz anatomy-*Hydrilla verticillata* (Bowes et al 1978, Holaday and Bowes 1980, Salvucci and Bowes 1981, 1983a,b). In *Hydrilla,* the C_4 and Calvin cycles coexist and operate in series in the same cell, rather than in separate cell types as in other C_4 species. The PEPC in the cytosol is segregated from ribulose bisphosphate carboxylase-oxygenase (Rubisco) and the decarboxylase (NADP malic enzyme, NADP-ME) that are localized in the chloroplasts. In this manner, futile cycling of CO_2 is minimized and the chloroplast is the specific site where CO_2 is concentrated for assimilation by Rubisco (Reiskind et al 1997). Because it does not require a specialized leaf anatomy, *Hydrilla* has been proposed as a model for engineering a C_4 cycle-based CO_2 concentrating mechanism (CCM) in rice (Edwards 1999).

An important factor when considering molecular engineering of rice is the inexorable rise in atmospheric CO_2, along with the attendant, but less predictable, increases in temperature and changes in precipitation patterns. Anthropogenic CO_2 production is concentrating CO_2 in the atmosphere and at the Rubisco fixation site of C_3 plants. This resembles the CCM of C_4 species and could mitigate the need for a C_4 system in rice. Consequently, in this paper, we review the responses of rice when grown season-long at elevated CO_2 and temperatures, as might be experienced in future global climate change scenarios. We also describe the components of the *Hydrilla* CCM and discuss whether a similar "minimalist" C_4 system in rice could achieve higher-yielding cultivars.

Rice responses to growth under elevated CO_2 and temperature

Several studies have examined how rice responds when it is grown at elevated CO_2 and/or temperature (reviewed by Horie et al 2000, Sage 2000, Gesch et al 2001). As with other C_3 plants, it is well established that rice responds positively to CO_2 in terms of photosynthesis, growth, and yield. This is mainly attributable to the competition between CO_2 and O_2 for the active site of Rubisco (Bowes and Ogren 1972). Elevated CO_2 reduces O_2 inhibition and the oxygenase activity of Rubisco, which then reduces the loss of photorespiratory CO_2 and thereby enhances net CO_2

assimilation. Baker et al (1990a,b) conducted a rather rare dose-response study, in which rice (cv. IR30) was grown season-long under subambient, ambient, and superambient CO_2, from 160 to 900 µbar, in outside sunlit chambers that mimicked agricultural paddy-culture conditions. Canopy photosynthesis rates rose as CO_2 increased, but leveled off at about 500 µbar, while water-use efficiency (WUE) continued to increase up to 900 µbar (Baker et al 1990a). Concomitantly, shoot and root biomass, tillering, and grain yield increased, but again only up to about 500 µbar CO_2, even though NPK fertilizer was applied regularly to minimize photosynthetic acclimation (Baker et al 1990b). These results for rice differ from those of soybean (*Glycine max*), which continued to respond positively up to 990 µbar CO_2 (Gesch et al 2001). Ziska et al (1996) have shown in pot experiments that rice cultivars differ in the degree to which CO_2 and temperature influence growth and yield. Even so, by extrapolating from several data sets, Horie et al (2000) concluded that an overall 30% increase in rice grain yield is a reasonable estimate with a doubling in CO_2. However, the gains caused by such a rise still fall short of what are required to keep pace with projected population increases in the next half century.

The major reason why IR30 rice has minimal increases above 500 µbar CO_2 is because Rubisco amount and activity are down-regulated in a linear fashion with increasing growth in CO_2 (Rowland-Bamford et al 1991). Thus, gains from more substrate CO_2 are negated by the loss of Rubisco capacity. However, in an optimization process, the ability to handle the extra leaf carbohydrate may be aided by the up-regulation of enzymes such as sucrose phosphate synthase (Hussain et al 1999). In contrast to rice, soybean typically exhibits little acclimation in photosynthesis and Rubisco activity, possibly because it is able to create sinks for the additional photosynthate (Campbell et al 1988, Gesch et al 2001).

Elevated temperatures can increase the CO_2 enhancement of C_3 photosynthesis and growth because Rubisco's oxygenase activity and photorespiration increase markedly with temperature (Long 1991). In the case of soybean, doubling the CO_2 enhanced photosynthesis linearly from 32% to 95% over a growth temperature range of 28 to 40 °C (Vu et al 1997). In contrast, rice (cv. IR72) did not follow the theoretical pattern; the CO_2 enhancement was relatively constant at about 60% from 32 to 38 °C, but clearly CO_2 enrichment can offset to some extent negative effects of high temperatures on rice photosynthesis (Vu et al 1997). However, this benefit does not extend to reproduction. Even though rice photosynthesis has a high temperature optimum for a C_3 plant (35 °C), high temperatures are deleterious to its reproductive processes and cause reduced grain yields even under elevated CO_2. Yields of an indica rice declined by 10% for every 1 °C over 26 °C, reaching zero at 36 °C, and similar outcomes occur with other cultivars, including japonica types (Baker and Allen 1993, Ziska et al 1996, Horie et al 2000). If temperatures rise in rice-growing regions, especially during the flowering period, sterility, abortion, or poor grain-fill will become serious problems that cannot be solved by engineering a C_4 photosynthetic system into the plant.

Elevated CO_2 and temperatures have opposing effects on water use. The WUE of a rice crop is enhanced as CO_2 increases, mainly because assimilation is greater, but evapotranspiration is also lower because of decreased stomatal conductance (Horie et al 2000). The difference in WUE because of a doubling of CO_2 can be as much as 26% to 50% (Nakagawa et al 1997, Vu et al 1998). Furthermore, CO_2 enrichment delays the effects of severe drought on rice plants and minimizes a drought-induced down-regulation of Rubisco amount and activity that would otherwise impair CO_2 assimilation (Vu et al 1998). However, air temperatures above 26 °C diminish these enhancement effects of CO_2 on rice WUE (Horie et al 2000). The positive effects of CO_2 enrichment on water use by rice would be most obvious in upland regions, less so for paddy-grown crops.

Same-cell (Kranz-less) C_4 systems

Until recently, it was considered dogma that C_4 photosynthesis functioned fully only when Kranz anatomy was present, with the carboxylases and decarboxylase segregated in mesophyll and bundle sheath cells to prevent futile CO_2 cycling. That view has now changed. Since our discovery of the *Hydrilla* C_4 system, other Kranz-less C_4 systems have been reported. There is substantial evidence for a C_4-based CCM in the marine macroalga *Udotea flabellum,* derived from techniques using gas exchange, enzymes, and isotopic labeling, and inhibitor studies (Reiskind and Bowes 1991). The marine diatom *Thalassiosira weissflogii* may perform C_4 photosynthesis in a single cell (Reinfelder et al 2001), but it is not established if it concentrates CO_2 for Rubisco. The presence of C_4 photosynthesis in organisms other than angiosperms indicates that its origins predate them.

There art reports of C_4 photosynthesis in freshwater monocots that lack Kranz anatomy, in addition to *Hydrilla,* including *Egeria densa* (Casati et al 2000) and *Sagittaria subulata* (Bowes et al 2002). The grasses (Poaceae) contain more than 60% of C_4 species (Sage 2001) and in almost all the C_4 cycle is associated with Kranz anatomy. Aquatic *Orcuttia* species are an exception; they are C_4 NADP-ME species, as evidenced by ^{14}C-pulse-chase labeling and enzyme studies, but the submersed leaves lack Kranz anatomy (Keeley 1998). The sedges (Cyperaceae) also contain a substantial number of C_4 Kranz species (Sage 2001), but one, *Eleocharis acicularis,* has Kranz-less submersed leaves that produce C_4 acids. Whether this constitutes a C_4-based CCM remains to be seen.

The ability to perform C_4 photosynthesis in the absence of Kranz anatomy is not confined to submersed leaves. The terrestrial halophyte *Borszczowia aralocaspia* (Chenopodiaceae) lacks Kranz anatomy but is a C_4 NAD-ME species, on the basis of $d^{13}C$, gas exchange, enzyme activity, and localization studies (Voznesenskaya et al 2001). Its carboxylases and decarboxylase are spatially separated in a cell containing dimorphic chloroplasts. Similarly, the terrestrial plant *Bienertia cycloptera* is described as a facultative C_4 system that operates with the Calvin cycle in the same chlorenchyma cells (Freitag and Stichler 2002).

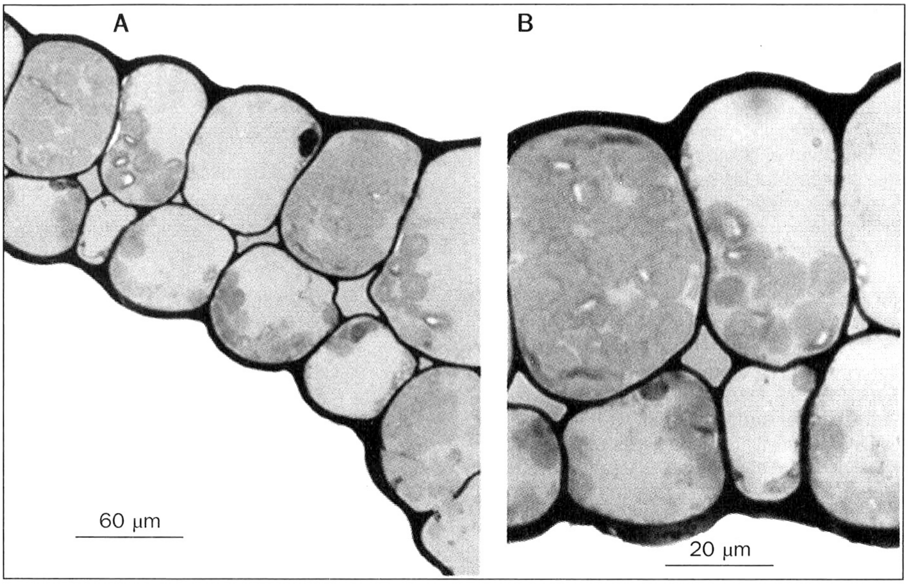


Fig. 1. Light micrograph of a cross section of part of a *Hydrilla verticllilata* C_4 leaf. (A) Lamina (which is the major photosynthetic region) and part of the midrib (which lacks Kranz anatomy and contains few chloroplasts). (B) An enlargement of part of the lamina to show the many small chloroplasts in both the adaxial and lower abaxial cells.

The facultative C_4 system of *Hydrilla*

Hydrilla verticillata is a tropical submersed monocot that was introduced as an aquarium plant into Florida around 1960, but it escaped, and its rapid distribution and growth soon made it a major weed problem. *Hydrilla* has a small leaf, about 14 mm long × 3 mm wide, with a single vein (midrib), and there is no differentiation into mesophyll and bundle sheath cells (Kranz anatomy) as normally occurs in a C_4 plant. The anatomy of part of a C_4 *Hydrilla* leaf is shown as a cross section in Figure 1. The C_3 leaf (not shown) is essentially the same. The lamina, where photosynthesis occurs, is composed of just two cell layers (Fig. 1A). The upper adaxial layer has larger cells, with more prominent vacuoles, than the lower, abaxial layer. There are no stomata. The midrib is only 5-6 cells thick and part of it is shown at the right of Figure 1A. It contains relatively few chloroplasts compared with the lamina that extend on either side of it. The lamina adaxial and abaxial cells contain many small chloroplasts (Fig. 1B), like terrestrial leaf cells, and not one or a few large chloroplasts as found in many algae with CCMs. The chloroplasts in both C_3 and C_4 leaves are granal and presumably have a competent PSII that produces NADPH. Immunocytochemical gold labeling shows that the adaxial and abaxial cells contain Rubisco in their chloroplasts and PEPC in the cytosol (Reiskind et al 1989). Thus, the C_4 and Calvin cycles are not segregated between the adaxial and abaxial cells; instead, the

Table 1. Photosynthesis-related characteristics of C_3 and C_4 leaves of *Hydrilla*.

Parameter and (reference) [a]	C_3 leaf	C_4 leaf
Kranz anatomy (1)	None	None
CO_2 compensation point (µbar) (2)	>40	<10
O_2 inhibition of photosynthesis (%) (2)	>28	<5
Net photosynthesis rate (µmol mg^{-1} Chl h^{-1}) (2)	5	15
Ratio internal/external inorganic carbon (3)	0.8	4.2
Estimated chloroplast CO_2 (µM) (3)	7	400
Leaf abaxial surface (pH) (3)	3.6	4.7
Rubisco activity (µmol g^{-1} fresh wt h^{-1}) (4)	45	36
Rubisco location: adaxial and abaxial cells (1,4)	Chloroplasts	Chloroplasts
PEPC activity (µmol g^{-1} fresh wt h^{-1}) (4)	<10	>150
PEPC location: adaxial and abaxial cells (1,4)	Cytosol	Cytosol
Induced PEPC isoform (5)	None	*Hvpepc4*
Ratio PEPC/Rubisco activity (4)	0.2	>4.2
PPDK activity (µmol g^{-1} fresh wt h^{-1}) (2)	3	35
NADP-ME activity (µmol g^{-1} fresh wt h^{-1}) (2)	16	44
^{14}C pulsechase: 50% mal + asp turnover(s) (6)	None	<180

[a] (1) Reiskind et al (1989), (2) Salvucci and Bowes (1981), (3) Reiskind et al (1997), (4) Magnin et al (1997), (5) Rao et al (2002), (6) Salvucci and Bowes (1983b).

compartmentation is between the chloroplasts and the cytosol (Magnin et al 1997, Reiskind et al 1997). *Hydrilla* represents a "minimalist" C_4 system and, even though the vast majority of C_4 plants exhibit Kranz anatomy, this feature is not a sine qua non for C_4 photosynthesis; neither does it differentiate terrestrial from submersed C_4 plants (Bowes et al 2002).

Terrestrial C_4 species are obligate, whereas *Hydrilla* has a facultative C_4 system. From ecological, physiological, and biochemical perspectives, *Hydrilla's* C_4 photosynthesis is one of the most thoroughly documented and is clearly in the C_4 NADP-ME subgroup, not in the C_3-C_4 intermediate or CAM categories. Evidence that it is a facultative C_4 plant, despite its lack of Kranz anatomy, is shown in Table 1, which compares some characteristics of C_3 and C_4 *Hydrilla* shoots. C_4 photosynthesis is induced by low CO_2, which in nature usually occurs in dense vegetation in summer (Holaday et al 1983, Spencer et al 1994), but is also inducible in the laboratory. Thus, shoots with previously high, C_3-like CO_2 compensation points (an indicator of substantial photorespiration) exhibit low, C_4-like values (Table 1). Concomitantly, the O_2 inhibition of photosynthesis declines and net photosynthesis at limiting CO_2 increases. The photosynthetic temperature optimum is high (35 °C), as in other C_4 species (Bowes and Salvucci 1989). Perhaps the best evidence that the system is an effective CCM comes from measurements of internal inorganic-C in the leaves (Table 1). With an external solution of 0.5 mM, the inorganic-C in C_3 leaves was 0.4 mM, but it was fivefold higher (2.1 mM) in C_4 leaves (Reiskind et al 1997), akin to the situation in terrestrial C_4 leaves (Furbank and Hatch 1987). The high CO_2 is mainly confined to the C_4 leaf chloroplasts and is far greater than in the surrounding medium. The CCM is able to operate in a low pH medium, where HCO_3^- is negligible, showing that it is independent of the uptake of HCO_3^-. In fact, the active secretion of H^+ causes the abaxial leaf surface to become acidified (Table 1), which facilitates the diffusion of CO_2 into the leaf. Thus, *Hydrilla's* CCM is not located at the plasma membrane nor is it dependent on HCO_3^- use (Reiskind et al 1997). Consequently, dissolved CO_2 enters *Hydrilla* leaf cells, which is the same situation as in terrestrial plants whose mesophyll cell walls are wet with an acidic solution.

Biochemical changes accompany physiological changes. C_4 cycle enzyme activities increase in *Hydrilla* leaves concomitant with the induction of C_4 gas exchange characteristics, but Calvin cycle and photorespiratory enzymes do not increase (Holaday and Bowes 1980, Salvucci and Bowes 1981). C_4 enzymes that are up-regulated include PEPC, NADP-malic enzyme (NADP-ME) and NAD-ME, NAD and NADP malate dehydrogenases (MDH), aspartate and alanine aminotransferases, pyrophosphatase, adenylate kinase, and pyruvate orthophosphate dikinase (PPDK). An activity of PPDK equivalent to the photosynthetic rate is significant as it plays a major role in the light-dependent conversion of pyruvate to PEP in C_4 photosynthesis. In terms of a decarboxylase, NADP-ME increases tenfold during C_4 induction (Salvucci and Bowes 1981, Magnin et al 1997). Western analysis time courses for PEPC, NADP-ME, and PPDK show that these enzyme proteins increase as the C_4 cycle is induced (Magnin et al 1997). There is a 10- to 15-fold increase in PEPC activity, which becomes the predominant carboxylase, while Rubisco is essentially unchanged and the PEPC:Rubisco activity ratio increases 20-fold (Table 1).

We have recently identified a specific PEPC isoform (*Hvpepc4*) whose transcript is induced as the leaf becomes C_4, and which is responsible for the initial photosynthetic carboxylation reaction (Rao et al 2002). The PEPC activities in C_4 and C_3 *Hydrilla* leaf extracts exhibit very different properties. In C_4 extracts, PEPC is light-activated in vivo, with daytime values 53% higher than at night, and it thus resembles a terrestrial C_4-PEPC isoform (Bowes et al 2002). Sensitivity to malate inhibition is also less during the day. In contrast, PEPC in C_3 leaf extracts shows no light activation and little malate inhibition day or night. Unlike *Hvpepc4,* another PEPC isoform (*Hvpepc3*) may have an anapleurotic function in *Hydrilla* leaves or recycle respiratory CO_2 at night.

For C_4 *Hydrilla* leaves, malate and aspartate are major products initially labeled with ^{14}C in the light, and, as Table 1 indicates, the label is rapidly turned over into Calvin cycle compounds and carbohydrates (Holaday and Bowes 1980, Salvucci and Bowes 1983b). These kinetic characteristics, like those of a terrestrial C_4 plant, demonstrate that C_4 acids are photosynthetic intermediates. In contrast, C_3 *Hydrilla* leaves do not turn over ^{14}C-malate during a 2-h chase period. Carbon flow through photorespiratory compounds is reduced in C_4 leaves, which is consistent with an effective CCM (Salvucci and Bowes 1983b).

Under inorganic carbon-limited conditions, the C_4 shoots have O_2-insensitive relative growth rates that are up to 60% greater than those of their C_3 counterparts, and higher photosynthetic nitrogen-use efficiency (Spencer et al 1994). These features are like those of terrestrial C_4 plants. However, the C_4 cycle has an energy cost, perhaps more than a terrestrial C_4 plant. Field studies suggest that the quantum yield may be half that of the C_3 shoots (Spencer et al 1994).

Will a C_4 system be effective in rice?

Most researchers agree that a well-designed and optimized C_4 system in rice could increase CO_2 assimilation, biomass production, and grain yield. It should also improve crop water, and possibly nitrogen, use efficiency. The same is true for rising atmospheric CO_2. However, extrapolating from the current increase of about 2 μbar CO_2 y^{-1}, atmospheric CO_2 would be around 470 μbar by 2050, which is insufficient to saturate the photosynthesis of C_3 rice and increase yields to satisfy the projected needs. Moreover, if temperatures rise, an engineered C_4 system may also show positive responses to [CO_2], especially in dry upland areas where stomatal conductance is reduced (Sage 2000). Adverse temperature effects on reproduction need to be examined, but this important subject is separate from attempts to engineer a more effective CO_2 assimilation system.

The evidence from *Hydrilla* and *Borszczowia,* that C_4 systems can function without Kranz anatomy, increases the likelihood that a minimalist system could be realized in rice. However, several subjects need to be examined when creating such a system, some of which are described as follows.

It has been suggested that the *Hydrilla* C_4 CCM may not work in a terrestrial plant if the diffusion resistance of water around the submersed leaf retards leakage of the high internal CO_2. But this ignores the observation that the high CO_2 is in the chloroplasts, not in the cytosol or at the cell surface where the aqueous resistance would be operative (Reiskind et al 1997). The "same-cell'' C_4 systems in terrestrial plants also undermine the "aqueous resistance" argument. However, a valid criticism is that we do not know how *Hydrilla* chloroplasts minimize CO_2 leakage, especially given that, as in terrestrial plants, they are small and mobile, with a greater surface area than a single, large chloroplast. Until this is resolved, it is difficult to predict whether rice mesophyll chloroplasts could retain a high CO_2 and prevent excessive leakage and futile cycling.

The PEPC reaction produces OAA, but malate and aspartate are the stable products observed in studies with *Hydrilla.* It is important to identify the major C_4 acid transported into the chloroplast. This is because *Hydrilla* chloroplasts, unlike the bundle-sheath chloroplasts of most NADP-ME C_4 plants, have grana like those of rice, and presumably produce NADPH. The direct import of malate, as in other C_4 NADP-ME species, could decrease the NADP+/NADPH ratio and exacerbate photoinhibition. In contrast, if OAA is imported, the coupling of the NADPH-MDH and NADP-ME reactions in the chloroplast could recycle NADPH. This would reduce the potential for photoinhibition and eliminate the need to down-regulate PSII activity. *Hydrilla* is not especially prone to photoinhibition, which lends weight to the argument that OAA and/or aspartate, rather than malate, are the major imported acids. We are searching for chloroplast transporters that may be induced along with *Hydrilla's* C_4 system. An up-regulated chloroplast transporter may be crucial to direct C_4 acids produced in the cytosol to the chloroplasts, rather than to the mitochondria where they would fuel a futile cycle.

Carbonic anhydrase (CA) catalyzes the interconversion of HCO_3^- and CO_2 in the stroma of C_3 chloroplasts. However, preliminary data suggest that it may not be present in *Hydrilla* chloroplasts, just in the cytosol. At a stromal pH of 8, the CA-catalyzed conversion of CO_2 to HCO_3^- should compete with Rubisco for CO_2 and be counterproductive for the *Hydrilla* CCM. This concept needs to be verified, but, if true, it may require that the stromal CA be down-regulated in rice by antisense technology to maximize the effectiveness of a C_4 CCM.

Attention must be given to Rubisco and its activase because they can be rate-limiting in a C_4 system (von Caemmerer et al 1997, Spreitzer and Salvucci 2002). In C_4 plants, Rubisco typically has a higher $K_m(CO_2)$ and 20% to 50% greater turnover capacity (k_{cat}) than in C_3 species. The C_4 CCM enables Rubisco to operate closer to CO_2 saturation and places a premium on maximum rate, rather than on CO_2 affinity. A high k_{cat} enables rapid photosynthesis rates to be maintained with less Rubisco protein, which enhances the nitrogen-use efficiency. The downside is that the C_4 leaf may have less nitrogen available for remobilization and this might affect seed yield (Sage 2000). Rice Rubisco, with its lower k_{cat}, may be limited in its ability to respond to a C_4-based CCM. In addition, if Rubisco protein and activity are down-regulated when a CCM is inserted, as they are when IR30 rice is grown at elevated atmospheric CO_2, then this would further reduce the effectiveness of a C_4 system. It is worth noting that *Hydrilla* Rubisco shows minimal down-regulation when the C_4 cycle is induced (Magnin et al 1997). A reduction in leaf Rubisco protein might also compromise the subsequent protein content of the rice grain, which is already lower than that of other grains. The acclimation response may be linked to sink limitations, in which case the best candidates for a transgenic C_4 system would be cultivars that have the capacity to handle the additional carbohydrate loading. They could be selected from plants that exhibit the least acclimation of Rubisco when grown at twice-ambient atmospheric CO_2 with natural sunlight and adequate nitrogen.

Various isoforms of PEPC are found in C_3, CAM, and C_4 species, which differ in function and in regulatory and kinetic characteristics (Chollet et al 1996). We have found several isoforms in *Hydrilla.* Curiously, phylogenetic sequence analyses indicate that all the Hydrilla isoforms resemble "C_3" rather than other monocot "C_4" forms (Rao et al 2002). However, one of them, *Hvpepc4,* is inducible and functions as the photosynthetic isoform (Rao et al 2002). A C_4 signature serine residue (Ser-770 or -772) that is ubiquitous in other C_4 isoforms, and influences the kinetics of PEPC, is absent from *Hvpepc4* and is replaced by alanine, which is typical of C_3 sequences (Rao et al 2002). We are investigating the regulation and kinetics of PEPC to determine how a "C_3" sequence can function in C_4 photosynthesis. Similarly, the decarboxylase in *Hydrilla* and *Egeria,* NADP-ME, resembles kinetically and in molecular mass a nonphotosynthetic isoform (Casati et al 2000, Bowes et al 2002). A detailed understanding of how specific isoforms of key enzymes are tailored to function in *Hydrilla's* C_4 photosynthesis should enable us to better predict the properties needed for these components to operate optimally in a C_4 rice system.

In summary, the CO_2 component of climate change will be positive for rice yields, whether rice is upland- or paddy-grown. In contrast, if the predicted increases in air temperatures occur, their detrimental effects on reproduction must be countered. However, even if they can be offset, rising atmospheric CO_2 over the next 25 to 50 years will not increase rice yields enough to meet the predicted needs, especially given the substantial Rubisco acclimation that rice displays: better-yielding cultivars will still be required. Improved cultivars may be engineered to have less down-regulation of Rubisco, a Rubisco that has a greater specificity for CO_2 relative to O_2 (Evans and von Caemmerer 2000), or a C_4 system similar to that of *Hydrilla* (Bowes et al 2002).

References

Baker JT, Allen LH Jr, Boote KJ, Jones P, Jones JW. 1990a. Rice photosynthesis and evapotranspiration in subambient, ambient and superambient carbon dioxide concentrations. Agron. J. 82:834-840.

Baker JT, Allen LH Jr, Boote KJ. 1990b. Growth and yield responses of rice to carbon dioxide concentration. J. Agric. Sci. 115:313-320.

Baker JT, Allen LH Jr. 1993. Contrasting crop species responses to CO_2 and temperature: rice, soybean and citrus. Vegetatio 104/105:239-260.

Bowes G, Ogren WL. 1972. Oxygen inhibition and other properties of soybean ribulose 1, 5-diphosphate carboxylase. J. Biol. Chem. 247:2171-2176.

Bowes G, Holaday AS, Van TK, Haller WT. 1978. Photosynthetic and photorespiratory carbon metabolism in aquatic plants. In: Hall DO, Coombs J, Goodwin TM, editors. Photosynthesis 77. Proceedings of the Fourth International Congress on Photosynthesis. The Biochemical Society, London. p 289-298.

Bowes G, Salvucci ME. 1989. Plasticity in the photosynthetic carbon metabolism of submersed aquatic macrophytes. Aquat. Bot. 34:233-266.

Bowes G, Rao SK, Estavillo GM, Reiskind JB. 2002. C_4 mechanisms in aquatic angiosperms: comparisons with terrestrial C, systems. Func. Plant Biol. 29:379-392.

Campbell WJ, Allen LH Jr, Bowes G. 1988. Effects of CO_2 concentration on Rubisco activity, amount, and photosynthesis in soybean leaves. Plant Physiol. 88:1310-1316.

Casati P, Lara MV, Andreo CS. 2000. Induction of a C_4-like mechanism of CO_2 fixation in *Egeria densa,* a submersed aquatic species. Plant Physiol. 123:1611-1621.

Chollet R, Vidal J, O'Leary MH. 1996. Phospho*enol*pyruvate carboxylase: a ubiquitous highly regulated enzyme in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47:273-298.

Dawe D. 2000. The contribution of rice research to poverty alleviation. In: Sheehy JE, Mitchell PL, Hardy B, editors. Redesigning rice photosynthesis to increase yield. Makati City (Philippines): International Rice Research Institute and Amsterdam (Netherlands): Elsevier Science. p 3-12.

Dobermann A. 2000. Future intensification of irrigated rice systems. In: Sheehy JE, Mitchell PL, Hardy B, editors. Redesigning rice photosynthesis to increase yield. Makati City (Philippines): International Rice Research Institute and Amsterdam (Netherlands): Elsevier Science. p 229-247.

Edwards GE. 1999. Tuning up crop photosynthesis. Nat. Biotechnol. 17:22-23.

Evans JR, von Caemmerer S. 2000. Would C_4 rice produce more biomass that C_3 rice? In: Sheehy JE, Mitchell PL, Hardy B, editors. Redesigning rice photosynthesis to increase yield. Makati City (Philippines): International Rice Research Institute and Amsterdam (Netherlands): Elsevier Science. p 53-71.

Freitag H, Stichler W. 2002. *Bienertia cycloptera* Bunge ex Boiss., Chenopodiaceae, another C_4 plant without Kranz tissues. Plant Biol. 4: 121-132.

Furbank RT, Hatch MD. 1987. Mechanism of C_4 photosynthesis: the size and composition of the inorganic carbon pool in bundle sheath cells. Plant Physiol. 85:958-964.

Gesch RW, Vu JCV, Allen LH Jr, Boote KJ. 2001. Photosynthetic responses of rice and soybean to elevated CO_2 and temperature. Recent Res. Dev. Plant Physiol. 2:125-137.

Holaday AS, Bowes G. 1980. C_4 acid metabolism and dark CO_2 fixation in a submersed aquatic macrophyte (*Hydrilla verticillata*). Plant Physiol. 65:331-335.

Holaday AS, Salvucci ME, Bowes G. 1983. Variable photosynthesis/photorespiration ratios in *Hydrilla* and other submersed aquatic macrophyte species. Can. J. Bot. 61:229-236.

Horie T, Baker JT, Nakagawa H, Matsui T. 2000. Crop ecosystem responses to climatic change: rice. In: Reddy KR, Hodges HF, editors. Climatic change, plant productivity and global implications. New York, N.Y. (USA): CABI Publishing. p 81-106.

Hussain MW, Allen LH Jr, Bowes G. 1999. Up-regulation of sucrose phosphate synthase in rice grown under elevated CO_2 and temperature. Photosyn. Res. 60:199-208.

Keeling CD, Whorf TP. 2001. Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Carbon Dioxide Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., USA.

Keeley JE. 1998. C_4 photosynthetic modifications in the evolutionary transition from land to water in aquatic grasses. Oecologia 116:85-97.

Long SP. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? Plant Cell Environ. 14:729-739.

Magnin NC, Cooley BA, Reiskind JB, Bowes G. 1997. Regulation and localization of key enzymes during the induction of Kranz-less, C_4-type photosynthesis in *Hydrilla verticillata.* Plant Physiol. 115:1681-1689.

Miyao-Tokutomi M, Fukayama H, Matsuoka M. 2001. High level of expression of C_4 photosynthesis enzymes in transgenic rice. In: PS2001 Proceedings. 12th International Congress on Photosynthesis. CSIRO Publishing, Australia. S39-001.

Murphy LR, Huang XQ, Li X, Jiao DM, Cho D, Pinto M, Wong D, Li C, Yang J, Matsuoka M, Ku MSB. 2001. Improved photosynthetic performance and grain yield in transgenic rice expressing maize C_4 photosynthetic enzymes. In: PS2001 Proceedings. 12th International Congress on Photosynthesis. CSIRO Publishing, Australia. S39-011.

Nakagawa H, Horie T, Kim HY, Ohnishi H, Homma K. 1997. Rice responses to elevated CO_2 concentrations and high temperatures. J. Agric. Meteorol. 52:797-800.

Rao SK, Magnin NC, Reiskind JB, Bowes G. 2002. Photosynthetic and other phospho*enol*pyruvate carboxylase isoforms in the single-cell, facultative C_4 system of *Hydrilla verticillata.* Plant Physiol. 130:876-886.

Reinfelder JR, Kraepiel AML, Morel FMM. 2001. Unicellular C_4 photosynthesis in a marine diatom. Nature 407:996-999.

Reiskind JB, Berg RH, Salvucci ME, Bowes G. 1989. Immunogold localization of primary carboxylases in leaves of aquatic and a terrestrial C_3-C_4 intermediate species. Plant Sci. 61:43-52.

Reiskind JB, Bowes G. 1991. The role of phospho*enol*pyruvate carboxykinase in a marine macroalga with C_4-like photosynthetic characteristics. Proc. Natl. Acad. Sci. USA 88:2883-2887.

Reiskind JB, Madsen TV, Van Ginkel LC, Bowes G. 1997. Evidence that inducible C_4-type photosynthesis is a chloroplastic CO_2-concentrating mechanism in *Hydrilla,* a submersed monocot. Plant Cell Environ. 20:211-220.

Rowland-Bamford AJ, Baker JT, Allen LH Jr, Bowes G. 1991. Acclimation of rice to changing atmospheric carbon dioxide concentration. Plant Cell Environ. 14:577-583.

Sage RF. 2000. C_3 versus C_4 photosynthesis in rice: ecophysiological perspectives. In: Sheehy JE, Mitchell PL, Hardy B, editors. Redesigning rice photosynthesis to increase yield. Makati City (Philippines): International Rice Research Institute and Amsterdam (Netherlands): Elsevier Science. p 13-35.

Sage RF. 2001. Environmental and evolutionary preconditions for the origin and diversification of the C_4 photosynthetic syndrome. Plant Biol. 3:202-213.

Salvucci ME, Bowes G. 1981. Induction of reduced photorespiratory activity in submersed and amphibious aquatic macrophytes. Plant Physiol. 67:335-340.

Salvucci ME, Bowes G. 1983a. Ethoxyzolamide repression of the low photorespiration state in two submersed angiosperms. Planta 158:27-34.

Salvucci ME, Bowes G. 1983b. Two mechanisms mediating the low photorespiratory state in submersed aquatic angiosperms. Plant Physiol. 73:488-496.

Sheehy JE. 2000. Limits to yield for C_3 and C_4 rice: an agronomist's view. In: Sheehy JE, Mitchell PL, Hardy B, editors. Redesigning rice photosynthesis to increase yield. Makati City (Philippines): International Rice Research Institute and Amsterdam (Netherlands): Elsevier Science. p 39-52.

Spencer WE, Teeri J, Wetzel RG. 1994. Acclimation of photosynthetic phenotype to environmental heterogeneity. Ecology 75:301-314.

Spreitzer RJ, Salvucci ME. 2002. Rubisco: structure, regulatory interactions, and possibilities for a better enzyme. Annu. Rev. Plant Biol. 53:449-475.

von Caemmerer S, Millgate A, Farquhar GD, Furbank RT. 1997. Reduction of ribulose-1,5-bisphosphate carboxylase/oxygenase by antisense RNA in the C_4 plant *Flaveria bidentis* leads to reduced assimilation rates and increased carbon isotope discrimination. Plant Physiol. 113:469-477.

Voznesenskaya EV, Franceschi VR, Kiirats O, Freitag H, Edwards GE. 2001. Kranz anatomy is not essential for C_4 plant photosynthesis. Nature 414:543-546.

Vu JCV, Allen LH Jr, Boote KJ, Bowes G. 1997. Effects of elevated CO_2 and temperature on photosynthesis and Rubisco in rice and soybean. Plant Cell Environ. 20:68-76.

Vu JCV, Baker JT, Pennanen AH, Allen LH Jr, Bowes G, Boote KJ. 1998. Elevated CO_2, and water deficit effects on photosynthesis, ribulose bisphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. Physiol. Plant. 103:327-339.

Ziska LH, Manalo PA, Ordonez RA. 1996. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J. Exp. Bot. 47:1353-1359.

Notes

Authors' address: Department of Botany, 220 Bartram Hall, University of Florida, Gainesville, Florida 32611, USA.

Acknowledgments: We thank Drs. L.H. Allen Jr. (USDA-ARS, Gainesville, Fla.) and J.T. Baker (USDA-ARS, Bethesda, Md.) for their insights on rice yields and climate change. Part of this work was supported by the U.S. Department of Agriculture, National Research Initiatives Competitive Grants Program (No. 98-35306-6449), and the National Science Foundation (No. IBN-9604518).

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Rubisco and photosynthesis in rice: coarse and fine control of Rubisco activity *in vivo*

T. Mae and A. Makino

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in a leaf is regulated by multiple mechanisms from coarse to fine levels. The contribution of each mechanism to the regulation of Rubisco activity *in vivo* may vary with the developmental stage of the leaf, the environmental conditions it is under, and the plant species. Synthesis and degradation of Rubisco protein, which may be a coarse control of the activity *in vivo,* were examined in leaves of rice throughout their life spans using ^{15}N as a tracer. Synthesis of Rubisco peaked during leaf expansion, became quite low at the time of full expansion, and then declined further during senescence. The sum of Rubisco synthesized up to the time when Rubisco content reached its maximum was 80-90% of the total Rubisco synthesized during the life span of leaves. The changes in the levels of *rbc*S and *rbc*L mRNAs were approximately coordinated with those in the amount of Rubisco synthesized throughout the life span of leaves. Thus, it is indicated that the amount of Rubisco synthesized in leaves is primarily determined by the levels of *rbc*S and *rbc*L mRNAs throughout their life spans. Degradation of Rubisco started just before the time of full expansion and became far more active than its synthesis during senescence. Since the synthesis of Rubisco during senescence contributed little to its amount, we concluded that the degradation of Rubisco is the major determinant for the amount of Rubisco in senescent leaves. The amount of Rubisco per unit leaf area in fully expanded leaves varied with growth conditions such as nitrogen nutrition, temperature, irradiance, and CO_2 partial pressure, but the ratio of Rubisco to total leaf nitrogen (leaf-N) was constant for a given leaf-N content, irrespective of the growth conditions.

An important fine control of Rubisco activity *in vivo* may be the modulation of this enzyme by reversible carbamylation or tight binding of 2-carboxyarabinitol 1-phosphate (CA1P) and other sugar phosphate inhibitors to its catalytic sites. The proportion of activated (carbamylated) Rubisco to the total (nonactivated, activated, and deactivated) Rubisco in leaves increased with increasing irradiance, from 20% in the dark to 90% at an irradiance of 900 µmol quanta m^{-2} s^{-1} under low CO_2 partial pressure (pCa = 36 Pa). The proportion of deactivated Rubisco was 70-80% in the dark and less than 10% at an irradiance of 900 µmol quanta $m^{-2}s^{-1}$. These results suggest that deactivation, rather than decarbamylation, of Rubisco comes into play as one of the regulatory mechanisms of Rubisco *in vivo* in leaves of rice exposed to weak light.

Ribulose- 1,5-bisphosphate carboxylase/oxygenase (Rubisco; EC4.1.1.39) is a key enzyme of photosynthetic carbon fixation. Rubisco is a bifunctional enzyme and it catalyzes two competing reactions, namely, the carboxylation and oxygenation of ribulose-l,5-bisphosphate (RuBP); the former initiates the primary step of the photosynthetic carbon reduction cycle and the latter initiates the primary step of photorespiration. Rubisco has an extraordinarily low catalytic rate and the net rate of carboxylation *in vivo* is further reduced by its poor affinity for CO_2 and the competing reaction with O_2. Probably because of these catalytic properties of Rubisco, plants must invest a huge amount of nitrogen in Rubisco to support their photosynthetic function. The amount of Rubisco accounts for about 10-30% of leaf nitrogen in mature leaves of C_3 plants (Evans 1989) and Rubisco is the most abundant protein in leaves and is probably the most abundant protein on Earth.

Rubisco activity *in vivo* is regulated at multiple steps from coarse to fine levels (Stitt and Schulze 1994). The amount of Rubisco in leaves changes dramatically throughout the life of a leaf. Rubisco content in a leaf increases during leaf expansion and reaches the maximum around the time of full expansion. Thereafter, it continuously decreases with the progression of leaf senescence and reaches a nondetectable level when leaves are fully senescent. The amount of Rubisco in a leaf is the result of a balance between its synthesis and degradation. Therefore, synthesis and degradation of Rubisco protein throughout the life span of a leaf may be the major coarse control of the activity *in vivo.*

It is known that the *in vivo* activity of Rubisco is modulated in response to changes in light and CO_2 levels by reversible carbamylation of lysine 201 of the large catalytic subunit or tight binding of 2-carboxyarabinitol 1-phosphate (CAlP) and other sugar phosphate inhibitors to its catalytic sites (Makino 1994). Rubisco activase mediates this modulation by removing sugar-phosphate inhibitors from the catalytic sites and by promoting carbamylate formation (Salvucci et al 1985, Portis et al 1986, Portis 1990). As the modulation of Rubisco by reversible carbamylation and deactivation generally occurs within a relatively short time, it can be regarded as a fine-tuning mechanism of Rubisco activity *in vivo.*

Rice is the staple food grain for more than half of the world's population. It is estimated that the world's population will increase to a level 1.4-1.5 times the present population by 2025, and this projected increase will be mostly in Asia (IRRI 1995). It is therefore crucial to increase rice production within a relatively short period. With little scope for expanding land area, the increase in rice production must be achieved by an increase in yield from the land currently used for rice cultivation. To achieve this, a better understanding of the characteristic nature of photosynthesis in rice is a fundamental requirement for further improvement of its yield potential.

Here, we first describe the relationship between the amount of Rubisco and leaf photosynthesis in rice leaves, and the effect of environmental factors on the amount of Rubisco and its proportion to total leaf nitrogen (leaf-N). Then, as a coarse control of Rubisco activity *in vivo,* changes in the synthesis and degradation of Rubisco throughout the life span of a leaf and their molecular basis are described. Finally, fine-tuning of Rubisco activity *in vivo,* as shown by changes in the proportion of activated and deactivated Rubisco in rice leaves exposed to different irradiances, is described.

Rubisco and photosynthesis

Is Rubisco in excess for photosynthesis in rice leaves?

In the early 1980s, it was not clear whether Rubisco was a limiting factor of photosynthesis in leaves. For example, in the late 1970s, no correlation between the photosynthetic rate and RuBP carboxylase activity was found in flag leaves of wheat (Hall et al 1978). Furthermore, Camp et al (1982) reported that RuBP carboxylase activity decreased at a much faster rate than the photosynthetic rate during senescence. Contrary to those reports, it was reported that the loss of RuBP carboxylase activity during senescence was caused by a loss of enzyme protein in leaves of barley (Friedrich and Huffaker 1980) and wheat (Peoples et al 1980).

In rice, it was initially indicated that the level of Rubisco protein could be a limiting factor in photosynthesis throughout the life span of a leaf (Makino et al 1983). This indication was based on the high correlation between RuBP carboxylase activity and the light-saturated rate of CO_2 assimilation under existing ambient CO_2 concentrations and a constant value of the specific activity of RuBP carboxylase throughout the life span of the leaf. Thereafter, the relationship between the amount of Rubisco and the photosynthetic rate in leaves of rice was further examined according to the biochemical model of C_3 photosynthesis by Farquhar et al (1980).

According to their model, the photosynthetic rate at low CO_2 partial pressure under light-saturated conditions is limited by Rubisco capacity, whereas the rate at high CO_2 is limited by electron transport capacity, which reflects the capacity of RuBP regeneration. Sharkey (1985) modified this model and added a limitation, namely, the availability of Pi (inorganic phosphate) in the chloroplast for ATP synthesis. Changes in gas-exchange rates during the life span of the leaves of rice were analyzed quantitatively by measuring changes in the carboxylation/oxygenation and regeneration of RuBP at an irradiance of 2,000 μmol quanta m^{-2} s^{-1} (saturating irradiance) under ambient air conditions (Makino et al 1984b, 1985). The RuBP level was always higher than the active-site concentrations of RuBP carboxylase. Analysis of the CO_2-assimilation rate as a function of intercellular CO_2 concentration indicated that RuBP regeneration does not limit CO_2 assimilation. The estimated RuBP-carboxylase/oxygenase activity *in vivo* was linearly correlated with the rate of CO_2 assimilation. The enzyme activity was just enough to account for the rate of CO_2 assimilation. These results indicated that the light-saturated rate of CO_2 assimilation in rice leaves under ambient air conditions is limited during the entire life span of a leaf by the RuBP-carboxylation/oxygenation capacity (Makino et al 1985).

Recently, their conclusion was further verified by using transgenic rice plants, in which the proportion of Rubisco to leaf nitrogen was specifically reduced by introducing an *rbc*S antisense gene into the plants under the control of the rice *rbc*S promoter (Makino et al 1997b). The rate of CO_2 assimilation under light-saturated conditions at low intercellular CO_2 partial pressure (pCi = 20 Pa) in leaves of transgenic rice declined almost proportionally to the amount of reduced Rubisco, and there was no difference in the relationship between light-saturated photosynthesis at pCi = 20 Pa and Rubisco content between the antisense and wild-type plants. These results strongly support their previous conclusion. Similar results have been obtained in tobacco (Hudson et al 1992, von Caemmerer et al 1994).

Under nonlight-saturated (suboptimal) conditions, the amount of Rubisco reaches a level in excess of the actual rate of CO_2 assimilation and a certain proportion of Rubisco exists as its nonactivated and/or deactivated form(s) (see the section on "The activation and inhibition of Rubisco *in vivo* ").

Effects of environmental conditions on the proportion of Rubisco to leaf nitrogen

The amount of Rubisco per unit leaf area is a potent determinant of the rate of photosynthetic CO_2 assimilation in leaves. Effects of various growth conditions on the amount of Rubisco and its proportion to leaf-N were examined in young fully expanded leaves of rice.

Nitrogen nutrition. The amount of Rubisco per unit leaf area in young fully expanded leaves of rice was strongly influenced by the level of nitrogen supplied to the plants during leaf expansion. Higher amounts of nitrogen supply resulted in higher amounts of Rubisco and leaf-N per unit leaf area. The proportion of Rubisco-N to leaf-N depended on the amount of leaf-N per unit leaf area. It increased from 22% in leaves of nitrogen-deficient plants to 34% in leaves of nitrogen-sufficient plants. The light-saturated rate of CO_2 assimilation at an intercellular CO_2 partial pressure of 20 Pa (CO_2-limited photosynthesis) was linearly dependent on the amount of leaf-N per unit leaf area, but curvilinearly correlated with the amount of Rubisco per unit leaf area. This difference was due to a greater increase than the proportional increase in the amount of Rubisco relative to leaf-N and a CO_2 transfer resistance between the intercellular air spaces and the carboxylation sites. The proportion of Rubisco-N to leaf-N also increased in spinach and bean leaves with increasing amounts of leaf-N per unit leaf area, but it was constant in wheat, irrespective of leaf-N contents (Makino et al 1994a).

Temperature, irradiance, and partial pressure of CO_2. Rice was grown with different amounts of nitrogen supply under ambient air conditions at different irradiances or temperatures, or under light-saturated conditions at different partial pressures of CO_2. The proportion of Rubisco-N relative to leaf-N was examined in just expanded leaves with concomitant measurements of the amounts or activities of chlorophyll, cytochrome *f,* fructose bisphosphatase, ATPase, and sucrose phosphate synthase (Makino et al 1994a,b, 1997a,b, Nakano et al 1997). Surprisingly, the relationship between Rubisco and leaf-N was almost the same among all the treatments and fell on one regression line. These results strongly indicate that the amount of Rubisco per unit leaf area is solely determined by the amount of leaf nitrogen per unit leaf' area, irrespective of the growth conditions in rice.

One exception to this relationship was found in rice grown under sulfur-deficient conditions. The proportion of Rubisco-N to leaf-N was specifically lowered in the leaves of sulfur-deficient plants, most probably because of the limited availability of sulfur-containing amino acids for protein synthesis (Resurreccion et al 2001, 2002).

Unlike that of Rubisco, the relationship between chlorophyll and leaf-N varied depending on growth conditions (Makino et al 1994b,1997a, Nakano et al 1997, Ohashi et al 1998). A higher proportion of chlorophyll relative to leaf-N was observed in the leaves of rice plants grown under lower irradiance or higher temperature conditions, while the relationship was the same between plants grown under high CO_2 and low CO_2. Chlorophyll content in leaves is a determinant of the ability of light capture. Rice probably adjusts its amount to suit a given growth environment to maintain high photosynthetic efficiency and/or to avoid damage from excess light.

The relationship between the amount of cytochrome *f* and leaf-N also varied depending on growth conditions. The proportion of cytochrome *f* to leaf-N was lower in leaves grown under low-light conditions than those grown under high-light conditions in rice. The amount of cytochrome *f* per unit leaf area is thought to be a determinant of photosynthetic electron transport capacity.

Synthesis and degradation of Rubisco throughout the leaf's life and their relation to changes in the levels of mRNAs of *rbc*S and *rbc*L

The amount of Rubisco in leaves changes greatly from leaf emergence through senescence. Rubisco is degraded during senescence and its degradation products are reused as a source of N for developing tissues. Recycled N from Rubisco accounts for about 30-40% of total remobilized N in senescent leaves (Makino et al 1984a).

The amount of Rubisco in leaves is the result of a balance between its synthesis and degradation. Therefore, synthesis and degradation .of Rubisco in leaves during the life span of the leaf are directly related to carbon and nitrogen economy in plants (Mae 1997). Although synthesis and degradation of Rubisco throughout the life span of the leaf are important subjects to be studied, available information has been limited because of the difficulty of estimating this synthesis and degradation simultaneously.

Changes in the amount of Rubisco protein synthesized and degraded throughout the life span of leaves were first examined in rice by using ^{15}N as a tracer (Mae et al 1983, Makino et al 1984a). Synthesis of Rubisco peaked during leaf expansion, became quite low at the time of full expansion, and then further declined during senescence. Changes in the amount of Rubisco synthesized paralleled changes in the N influx to the leaves throughout the life span of the leaves. The sum of Rubisco synthesized up to the time when Rubisco content reached its maximum was 80-90%

of the total Rubisco synthesized during the life span of the leaves. The molecular basis for such changes in synthesis and degradation of Rubisco, however, has not been studied until recently.

In higher plants, Rubisco is composed of two distinct subunits. The large subunit is encoded on the plastid genome (*rbc*L) and synthesized on plastid ribosomes in the stroma, where it aggregates as octametric cores with the aid of chaperonins. Each core associates with eight small subunits that are encoded on the nuclear genome (*rbc*S), synthesized on cytoplasmic ribosomes, and subsequently imported into the chloroplast. The molecular basis for Rubisco synthesis in young leaves during expansion or in etiolated leaves during greening has been extensively studied during the past two decades (Gatenby and Ellis 1990, Gutteridge and Gatenby 1995, Rodermel, 1999), whereas less attention has been paid to that in senescent leaves.

Recently, changes in the levels of *rbc*S and *rbc*L mRNAs and their relationship to the synthesis of Rubisco have been examined in the leaf blades of rice from emergence to senescence (Suzuki et al 2001a,b). Synthesis of Rubisco protein was found to be most active during leaf expansion. It had already declined, however, to about one-fifth of the maximum amount at the time of full expansion. Thereafter, it further declined to about one-tenth of the maximum amount during leaf senescence. The amount of total RNA increased rapidly soon after leaf emergence, reached its maximum during leaf expansion, and then gradually declined. On the other hand, the amount of total DNA increased during leaf expansion, peaked at around the time of full expansion, and then declined slightly during senescence. The levels of mRNAs for *rbc*S and *rbc*L increased rapidly after leaf emergence and peaked during leaf expansion. Thereafter, the levels of *rbc*S and *rbc*L mRNAs declined quickly to about one-third and one-fifth of their maximums, respectively, at the time of full expansion, and declined further to less than one-tenth during senescence. These changes in the levels of both mRNAs were approximately parallel with the changes in the amount of Rubisco synthesized throughout the life span of the leaf. The level of *rbc*S DNA increased after leaf emergence and remained almost constant thereafter. The level of *rbc*L DNA increased gradually after leaf emergence, reached its maximum just before full expansion, and then declined to about half of its maximum during senescence. However, the decline in the level of *rbc*L DNA started later and proceeded much slower than that of *rbc*L mRNA.

These results indicate that the synthesis of Rubisco is determined primarily by the levels of *rbc*S and *rbc*L mRNAs throughout the life span of the leaf, and that the level of *rbc*L DNA is not a major determinant for the level of *rbc*L mRNA in senescent leaves of rice. When more nitrogen was supplied to the plant during the expansion of rice leaves, the levels of *rbc*S and *rbc*L mRNAs in the leaves increased roughly in parallel to the increase in the amount of synthesized Rubisco (Imai K, Makino A, Mae T, unpublished data).

Degradation of Rubisco had already started at the time of full expansion and became far more active than synthesis during leaf senescence. Since the synthesis of Rubisco during senescence contributed little to its amount, we concluded that the degradation of Rubisco is the major determinant for the amount of Rubisco in senescent leaves of rice.

Changes in the levels of *rbc*S and *rbc*L mRNAs and their relationship to the synthesis of Rubisco have been studied in amaranth leaves at various times from emergence to senescence (Nikolau and Klessig 1987) and in bean (*Phaseolus vulgaris* L.) leaves during senescence (Bate et al 1991). These observations suggest that the rate of synthesis of the large and small subunits of Rubisco is controlled not only at the transcriptional level, but also at the translational level (at least in part) during senescence. However, changes in the absolute amount of Rubisco synthesized and degraded were not examined simultaneously with changes in the levels of both mRNAs from leaf emergence to senescence in these studies. Therefore, it has remained unclear how changes in the balance between synthesis and degradation of Rubisco determine the amount of Rubisco during senescence. The *in vivo* observed decline in the synthesis of Rubisco has been shown to correlate with a declining population of mRNAs for each subunit in the leaves of wheat, placing the point of control at either transcription or at mRNA stability (Brady 1988). In leaves of soybean (Jiang et al 1993), *Arabidopsis* (Hensel et al 1993), and *P. vulgaris* (Craft-Brandner et al 1996), the decreases in the levels of Rubisco protein were correlated with decreases in the levels of mRNAs for both subunits during senescence. All these studies indicate that transcription of *rbc*S and *rbc*L may play a primary role in the determination of mRNA abundance in senescent leaves. However, analysis of mRNA levels and transcription rates has also provided evidence that plastid mRNA stability might be an important factor determining the level of mRNA (Deng and Gruissem 1987, Mullet and Klein 1987, Kim et al 1993, Rapp et al 1992). Transcriptional activity in plastids varies during chloroplast development. Plastid transcriptional activity and the DNA copy number increased early in chloroplast development and transcriptional activity per template varied up to 5-fold during barley leaf biogenesis (Baumgartner et al 1989).

Mechanisms of Rubisco degradation in senescent leaves have been studied in many plants (Huffaker 1990). Many studies have indicated that a majority of Rubisco can be degraded within chloroplasts during leaf senescence because the decrease in the amounts of Rubisco occurs much earlier than the decrease in the number of chloroplasts in leaves during leaf senescence (Wardley et al 1984, Mae et al 1984). Other studies have indicated that Rubisco could be degraded outside of the chloroplasts after secretion from chloroplasts or in vacuoles after the incorporation of whole chloroplasts into vacuoles (Wittenbach et al 1982).

It is evident that chloroplasts contain a variety of proteases (Adam 2001). This is true of rice leaves as well (Mae et al 1985). However, it is still not known which protease triggers the initial event of Rubisco degradation and how the degradation proceeds in chloroplasts during senescence. Recent studies have also suggested another mechanism that possibly triggers Rubisco degradation in chloroplasts. Under light-stress conditions, the large subunit of Rubisco can be modified or directly fragmented by reactive oxygen species mediated by a Fenton-type reaction in chloroplasts (Desimone et al 1996, Ishida et al 1997,1998, 1999). Some modification or conformational change of Rubisco protein during senescence may trigger the degradation by changing the susceptibility of Rubisco to proteases existing in chloroplasts.

The activation and inhibition of Rubisco *in vivo*

The fine-tuning of Rubisco activity *in vivo* may involve the activation and deactivation of the enzyme by reversible carbamylation at its activation site of lysine 201 followed by the binding of Mg^{2+} to form a ternary complex, namely, enzyme-CO_2-Mg^{2+} (Miziorko and Lorimer 1983). Reversible binding of sugar phosphates such as RuBP (Brooks and Portis 1988) and/or 2-carboxy-D-arabinitol- 1-phosphate (CA1P) (Gutteridge et al 1986, Berry et al 1987, Servaites 1990) to the enzyme or its ternary complex may be a fine-tuning of Rubisco activity *in vivo.* Although not all plant species produce a significant amount of CAlP (Moore et al 1991, Parry et al 1997), it was shown that rice belongs to the group of plants that has enzyme activity regulated by CAlP (Makino et al 1994b, Vu et al 1997).

The catalytically active form of Rubisco is a ternary complex of enzyme-CO_2-Mg^{2+} (ECM form). Rubisco alone is not an active form (E form). RuBP is known to tightly bind to the nonactive form of Rubisco (ER form) and it inhibits the formation of the ECM form. A naturally occurring inhibitor, CA1P, and some other sugar phosphates bind tightly to the ECM at its catalytic sites (ECMI form) and deactivate the ECM. CAlP is thought to be important in the diurnal regulation of photosynthesis, particularly during periods of low irradiance or darkness in some species (Kobza and Seeman 1989). On transition from dark to light, Rubisco activase promotes the release of CA1P, RuBP, and/or other inhibitory sugar phosphates from the catalytic site of Rubisco (Portis 1990). Free CA1P is rendered noninhibitory by the action of a light-activated CA1P phosphatase (Holbrook et al 1989). Recently, the existence of a daytime inhibitor of Rubisco was suggested (Parry et al 1997), although its chemical form has not yet been definitely identified.

The activation state of Rubisco *in vivo* can be deduced by the ratio of the activity measured immediately in rapidly prepared extracts (ECM form; activated Rubisco) to the activity measured following incubation with saturating concentrations of CO_2 and Mg^{2+} (E + ECM forms; nonactivated and activated Rubisco). These measurements are so-called "initial" and "total" activities, and the ratio of the initial activity to the total activity [E/(E + ECM)] is termed "activation state" or "carbamylation ratio." Exactly speaking, however, this so-called total activity does not actually reflect real total activity because it does not include the activity blocked by inhibitors such as RuBP (ER form) and CA1P (ECMI form). Total activity measurements often underestimate the potential activity of Rubisco. This means that such an "activation state" does not necessarily indicate the "true" activation state of Rubisco. Parry et al (1997) reported methods for determining the potential activity of Rubisco after removal of inhibitors with high concentrations of sulfate, the activity thus being termed "maximal" activity (E + ECM + ER + ECMI forms; total Rubisco).

When rice was placed in the dark at a low CO_2 partial pressure (pCa = 36 Pa), the activated Rubisco (ECM form) accounted for about 20% of the total Rubisco

(E + ECM + ER + ECMI forms) in the young fully expanded leaves. The proportion increased with increasing irradiance to 40% at an irradiance of 100 μmol quanta m^{-2} s^{-1}, 60% at an irradiance of 300 μmol quanta m^{-2} s^{-1}, and 90% at an irradiance of 900 μmol quanta m^{-2} s^{-1}. The proportion of deactivated Rubisco (ER and ECMI forms) was about 70-80% in the dark, 25-30% at an irradiance of 100 μmol quanta m^{-2} s^{-1}, 20% at an irradiance of 300 μmol quanta m^{-2} s^{-1}, and less than 10% at an irradiance of 900 μmol quanta m^{-2} s^{-1}. The proportion of nonactivated Rubisco (E) was estimated to be quite low in the dark, about 35% at an irradiance of 100 μmol quanta m^{-2} s^{-1}, 15% at an irradiance of 300 μmol quanta m^{-2} s^{-1}, and less than 10% at an irradiance of 900 μmol quanta m^{-2} s^{-1}.

The results suggest that deactivation, rather than decarbamylation, of Rubisco comes into play as one of the regulatory mechanisms of Rubisco *in vivo* in leaves of rice exposed to weak light.

References

Adam Z. 2001. Chloroplast proteases and their role in photosynthesis regulation. In: Aro E, Anderson B, editors. Regulation of photosynthesis. Dordrecht (Netherlands): Kluwer Academic Publishers. p 265-276.

Bate NJ, Rothstein SJ, Thompson JE. 1991. Expression of nuclear and chloroplast photosynthesis-specific genes during leaf senescence. J. Exp. Bot. 42:801-811.

Baumgartner BJ, Rapp JC, Mullet JE. 1989. Plastid transcription activity and DNA copy number increase early in barley chloroplast development. Plant Physiol. 89: 1011-1018.

Berry JA, Lorimer GH, Pierce J, Seeman JR, Meek J, Freas S. 1987. Isolation, identification, and synthesis of 2-carboxyarabinitol- 1-bisphosphate, a diurnal regulator of ribulose-bisphosphate carboxylase activity. Proc. Natl. Acad. Sci. USA 84:734-738.

Brady CJ. 1988. Nucleic acid and protein synthesis. In: Nooden LD, Leopold AC, editors. Senescence and aging in plants. San Diego, Calif. (USA): Academic Press Inc. p 147-179.

Brooks A, Portis AR. 1988. Protein-bound ribulose bisphosphate correlates with deactivation of ribulose bisphosphate carboxylase in leaves. Plant Physiol. 87:244-249.

Camp PJ, Huber SC, Burke JJ, Moreland DE. 1982. Biochemical changes that occur during senescence of wheat leaves. 1. Basis for the reduction of photosynthesis. Plant Physiol. 70:1641-1646.

Craft-Brandner SH, Klein RR, Klein P, Holzer R, Feller U. 1996. Coordination of protein and mRNA abundance of stromal enzymes and mRNA abundances of the Clp protease subunits during senescence of *Phaseolus vulgaris* (L.) leaves. Planta 200:312-318.

Deng XW, Gruissem W. 1987. Control of gene expression during development: the limited role of transcriptional regulation. Cell 49:379-387.

Desimone M, Henke A, Wagner E. 1996. Oxidative stress induces partial degradation of the large subunit of ribulose-l,5-bisphosphate carboxylase/oxygenase in isolated chloroplasts of barley. Plant Physiol. 111:789-796.

Evans J. 1989. Photosynthesis and nitrogen relationship in leaves of C_3 plants. Oecologia 78:9-19.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 148:78-90.

Friedrich JW, Huffaker RC. 1980. Photosynthesis, leaf resistance and ribulose-1,5-bisphosphate carboxylase degradation in senescing barley leaves. Plant Physiol. 65:1103-1107.

Gatenby AA, Ellis RJ. 1990. Chaperone function: the assembly of ribulose-1,5-bisphosphate carboxylase/oxygenase. Annu. Rev. Cell Biol. 6:125-149.

Gutteridge S, Gatenby AA. 1995. Rubisco synthesis, assembly, mechanism and regulation. Plant Cell 7:809-819.

Gutteridge S, Pany MAJ, Burton S, Keys AJ, Mudd A, Feeney J. Servaites J, Pierce J. 1986. A nocturnal inhibitor of carboxylation in leaves. Nature 324:274-276.

Hall NP, Keys AJ, Merrett MJ. 1978. Ribulose-1,5-diphosphate carboxylase protein during flag leaf senescence. J. Exp. Bot. 29:31-37.

Hensel LL, Grbic V, Baumgarten DA, Bleecker AB. 1993. Developmental and age-related processes that influence the longevity and senescence of photosynthetic tissues in *Arabidopsis*. Plant Cell 5:553-564.

Holbrook GP, Bowes G, Salvucci ME. 1989. Degradation of 2-carboxy arabinitol 1-phosphate by a specific chloroplast phosphatase. Plant Physiol. 90:673-678.

Hudson GS, Evans J, von Caemmerer S, Arvidsson YBC, Andrews TJ. 1992. Reduction of ribulose-1,5-bisphosphate carboxylase/oxygenase content by antisense RNA reduces photosynthesis in transgenic plants. Plant Physiol. 98:294-302.

Huffaker RC. 1990. Proteolytic activity during senescence of plants. New Phytol. 116:199-231.

IRRI (International Rice Research Institute). 1995. Rice facts. Manila (Phillippines): IRRI. p 2.

Ishida H, Nishimori Y, Sugisawa M, Makino A, Mae T. 1997. The large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase is fragmented into 37-kD and 16-kDa polypeptides by active oxygen in the lysates of chloroplasts from primary leaves of wheat. Plant Cell Physiol. 38:471-479.

Ishida H, Shimizu S, Makino A, Mae T. 1998. Light dependent fragmentation of the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase in chloroplasts isolated from wheat leaves. Planta 204:305-309.

Ishida H, Makino A, Mae T. 1999. Fragmentation of the large subunit of ribulose-1,5-bisphosphate carboxylase by reactive oxygen species occurs near Gly-329. J. Biol. Chem. 274:5222-5226.

Jiang C, Rodermel SR, Shibles RM. 1993. Photosynthesis, Rubisco activity and amount, and their regulation by transcription in senescing soybean leaves. Plant Physiol. 101:105-112.

Kim M, Christopher DA, Mullet JE. 1993. Direct evidence for selective modulation of *psb* A, *rpo* A, *rbc* L and 16S RNA stability during barley chloroplast development. Plant Mol. Biol. 22:447-463.

Kobza J, Seeman JR. 1989. Light-dependent kinetics of 2-carboxy arabinitol 1-phosphate metabolism and ribulose-1,5-bisphosphate carboxylase activity *in vivo.* Plant Physiol. 89:174-179.

Mae T. 1997. Physiological nitrogen efficiency in rice: nitrogen utilization, photosynthesis, and yield potential. Plant Soil 196:201-210.

Mae T, Hoshino T, Ohira K. 1985. Proteinase activities and loss of nitrogen in the senescing leaves of field-grown rice (*Oryza sativa* L.). Soil Sci. Plant Nutr. 31:589-600.

Mae T, Kai N, Makino A, Ohira K. 1984. Relation between ribulose bisphosphate carboxylase content and chloroplast number in naturally senescing primary leaves of wheat. Plant Cell Physiol. 25:333-336.

Mae T, Makino A, Ohira K. 1983. Changes in the amount of ribulose bisphosphate carboxylase synthesized and degraded during life span of rice leaf (*Oryza sativa* L.). Plant Cell Physiol. 24:1079-1086.

Makino A. 1994. Biochemistry of C_3-photosynthesis in high CO_2. J. Plant Res. 107:79-84.

Makino A, Mae T, Ohira K. 1983. Photosynthesis and ribulose 1,5-bisphosphate carboxylase in rice leaves: changes in photosynthesis and enzymes involved in carbon assimilation from leaf development through senescence. Plant Physiol. 73: 1002-1007.

Makino A, Mae T, Ohira K. 1984a. Relationship between nitrogen and ribulose-1,5-bisphosphate carboxylase in rice from emergence through senescence. Plant Cell Physiol. 25:429-437.

Makino A, Mae T, Ohira K. 1984b. Changes in photosynthetic capacity in rice leaves from emergence through senescence: analysis from ribulose-1,5-bisphosphate carboxylase and leaf conductance. Plant Cell Physiol. 25:511-521.

Makino A, Mae T, Ohira K. 1985. Photosynthesis and ribulose-1,5-bisphosphate carboxylase/oxygenase in rice leaves from emergence through senescence: quantitative analysis by carboxylation/oxygenation and regeneration of ribulose 1,5-bisphosphate. Planta 166:414-420.

Makino A, Nakano H, Mae T. 1994a. Responses of ribulose-1,5-bisphosphate carboxylase, cytchrome *f*, and sucrose synthesis enzymes in rice leaves to leaf nitrogen and their relationships to photosynthesis. Plant Physiol. 105: 173-179.

Makino A, Nakano H, Mae T. 1994b. Effect of growth temperature on the responses of ribulose-1,5-bisphosphate carboxylase, electron transport components, and sucrose synthesis enzymes to leaf nitrogen in rice, and their relationships to photosynthesis. Plant Physiol. 105:1231-1238.

Maluno A, Sato T, Nakano H, Mae, T. 1997a. Leaf photosynthesis, plant growth and nitrogen allocation in rice under different irradiances. Planta 203:390-398.

Makino A, Shimada T, Takumi S, Kaneko K, Matsuoka M, Shimamoto K, Nakano H, Miyao-Tokutomi M, Mae T, Yamamoto N. 1997b. Does decrease in ribulose-1,5-bisphosphate carboxylase by antisense *rbc*S lead to a higher N-use efficiency of photosynthesis under conditions of saturating CO_2 and light in rice plants? Plant Physiol. 114:483-491.

Miziorko HM, Lorimer GH. 1983. Ribulose-1,5-bisphosphate carboxylase-oxygenase. Annu. Rev. Biochem. 52:507-523.

Moore BD, Kobza J, Seeman JR. 1991. Measurement of 2-carboxyarabinitol I-phosphate in plant leaves by isotope dilution. Plant Physiol. 96:208-213.

Mullet JE, Klein RR. 1987. Transcription and RNA stability are important determinants of higher plant chloroplast RNA levels. EMBO J. 6:1571-1579.

Nakano H, Makino A, Mae T. 1997. The effect of elevated partial pressures of CO_2 on the relationship between photosynthetic capacity and N content in rice leaves. Plant Physiol. 115:191-198.

Nikolau BJ, Klessig DE 1987. Coordinate, organ-specific and developmental regulation of ribulose- 1,5-bisphosphate carboxylase gene expression in *Amaranthus hypochondriacus.* Plant Physiol. 85:167-173.

Ohashi K, Makino A, Mae T. 1998. Gas exchange characteristics in rice leaves grown under the conditions of physiologically low temperature and irradiance. Plant Cell Physiol. 39:1384-1387.

Parry MAJ, Andralojc PJ, Parmar S, Keys AJ, Habash D, Paul MJ, Alred R, Quick WP, Servaites JC. 1997. Regulation of Rubisco by inhibitors in the light. Plant Cell Environ. 20:528-534.

Peoples MB, Belzharz VC, Water SP, Simpson RJ, Darling MJ. 1980. Nitrogen redistribution during grain growth in wheat (*Triticum aaestivum* L.). II. Chloroplast senescence and the degradation of ribulose-l,5-bisphosphate carboxylase. Planta 149:241-254.

Portis AR. 1990. Rubisco activase. Biochem. Biophys. Acta 1015: 15-28.

Portis AR, Salvucci ME, Ogren WL. 1986. Activation of ribulose bisphosphate carboxylase/ oxygenase at physiological CO_2 and ribulose bisphosphate concentrations by Rubisco activase. Plant Physiol. 82:967-972.

Rapp JC, Baumgartner BJ, Mullet JE. 1992. Quantitative analysis of transcription and RNA levels of 15 barley chloroplast genes: transcription rates and mRNA levels vary over 300-fold; predicted mRNA stabilities vary 30-fold. J. Biol. Chem. 267:21404-21411.

Resurreccion AP, Makino A, Bennett J, Mae T. 2001. Effects of sulfur nutrition on the growth and photosynthesis of rice. Soil Sci. Plant Nutr. 47:611-620.

Resurreccion AP, Makino A, Bennett J, Mae T. 2002. Effects of light intensity on the growth and photosynthesis of rice under different sulfur concentrations. Soil Sci. Plant Nutr. 48:71-77.

Rodermel S. 1999. Subunit control of Rubisco biosynthesis: a relic of an endosymbiotic past? Photosyn Res. 59:105-123.

Salvucci ME, Portis AR, Ogren WL. 1985. A soluble chloroplast protein catalyzes activation of ribulosebisphosphate carboxylase/oxygenase *in vivo.* Photosyn Res. 7:193-201.

Servaites JC. 1990. Inhibition of ribulose 1,5-bisphosphate carboxylase/oxygenase by 2-carboxyarabinitol-1-phosphate. Plant Physiol. 92:867-870.

Sharkey TD. 1985. Photosynthesis in intact leaves of C_3 plants: physics, physiology and rate limitations. Bot. Rev. 51:51-105.

Stitt M, Schulze D. 1994. Does Rubisco control the rate of photosynthesis and plant growth? An exercise in molecular ecophysiology. Plant Cell Environ. 17:465-487.

Suzuki U, Makino A, Mae T. 2001a. An efficient method for extraction of RNA from rice leaves at different ages using benzyl chloride. J. Exp. Bot. 47:1845-1852.

Suzuki Y, Makino A, Mae T. 2001b. Changes in the turnover of Rubisco and levels of mRNAs of *rbc*L and *rbc*S in rice leaves from emergence to senescence. Plant Cell Environ. 24:1353-1360.

von Caemmerer S, Evans JR, Hudson GS, Andrews TJ. 1994. The kinetics of ribulose-1,5-bisphosphate carboxylase/oxygenase *in vivo* inferred from measurements of photosynthesis in leaves of transgenic tobacco. Planta 195:88-97.

Vu JCV, Allen Jr LH, Boote KJ, Bowes G. 1997. Effects of elevated CO_2 and temperature on photosynthesis and Rubisco in rice and soybean. Plant Cell Environ. 20:68-76.

Wardley TA, Bhalla PL, Dalling MJ. 1984. Changes in the number and composition of chloroplasts during senescence of mesophyll cells of attached and detached primary leaves of wheat (*Triticum aesrivum* L.). Plant Physiol. 75:421-424.

Wittenbach VA, Lin W, Heber RR. 1982. Vacuolar localization of proteases and degradation of chloroplasts in mesophyll protoplasts from senescing primary wheat leaves. Plant Physiol. 69:98-102.

Notes

Authors' address: Department of Applied Plant Science, School of Agricultural Science, Tohoku University, 1-1 Tsutsumidori-Amamiyaachi, Sendai 981-8555, Japan; fax: (+81) 22 7 17 8765, E-mail: hikomae@ biochem.tohoku.ac.jp.

Acknowledgement: This work was supported in part by the Bio-Design-Program (BDP-02-1-1) of the Ministry of Agriculture, Forestry, and Fisheries, Japan, and in part by Grants-in-Aid for Scientific Research (Nos. 12460028 and 11460029) from the Ministry of Education, Science, Sport, Technology, and Culture of Japan.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Mechanization and nonfood use of rice

Rice quality management through better drying, storage, and milling practices

R.R. Bakker, J.F. Rickman, and O.W. Kim

This paper gives an overview of the research and development program in rice handling and processing that is carried out by IRRI in collaboration with its partner organizations in Asia. The overall objective of this research program is to improve the efficiency and profitability of rice production by improving rice grain quality at the consumer's end and reducing physical losses. Attempts are made to improve rice handling and processing by focusing on the entire production-postproduction system rather than on component technologies alone. Recent research activities include an in-country assessment of bottlenecks in rice-processing systems, evaluation of newly developed postproduction technologies, and development of appropriate technology and knowledge dissemination strategies. The ultimate goal of IRRI and its partners is to facilitate an active, international Rice Postharvest Consortium with the objective of taking a more comprehensive approach to rice postproduction research, with the active participation of the private sector.

During the past three to four decades, Asian farmers have dramatically raised rice yields by adopting modern rice varieties. During this time, Asian consumers have also become more discriminating in terms of rice quality. In many countries in the region, consumers are now willing to pay a higher price for the specific rice quality that they desire. However, the adoption of modern postharvest technologies and practices that are needed to produce better-quality rice has not kept pace with the increased demand for high-quality rice. Inappropriate technologies, unsuitable management techniques, and lack of knowledge during grain harvesting, drying, storage, and milling often result in quality deterioration and physical losses. Rice quality deterioration can be in the form of high grain breakage, incomplete milling, yellowing or discoloration, impurities, or undesirable odors or taste.

Historically, research on rice quality improvement has largely focused on changing quality characteristics by means of genetic improvement and evaluating the effect of component technologies on qualitative changes in the grain. So far, research on grain quality management throughout the entire postproduction system has taken a backseat (Bell et al 2000). As stated by De Datta (1981) more than two decades ago, attempts that have been made to improve rice processing have often not focused on the total system but have taken a piecemeal approach, resulting in little effect on the quality of the rice that arrives at the consumer's table. It is therefore important to consider the entire postproduction system and its various players as a system, an approach taken in most temperate-climate rice-growing countries. Furthermore, it is recognized that, while much of the research on genetic improvement of rice is carried out through various collaborative research partnerships and consortia, much of the research on rice grain quality management is conducted in a rather isolated manner, prompting the need for more international collaboration and exchange. Given its mandate, IRRI is in the best position to facilitate such collaborative research activities.

Recognizing the need for more systems-based and collaborative postproduction research (see also Bell and Dawe 1998), IRRI, in association with primary research organizations and private-sector participants, began a collaborative research program to improve rice grain quality and reduce physical grain losses. Important characteristics of this program are that all research activities take on a systems-based approach, that is, research focuses on the entire production-postproduction system rather than on component technologies alone. In addition, private-sector companies involved in rice processing or manufacturing are engaged as true collaborating partners as they are considered a legitimate beneficiary of public-sector research. Rice farmers will benefit indirectly through higher farm income because of higher yields, more efficient postproduction facilities, and professionally managed trading and processing services.

Recent research activities on rice postproduction systems can be broadly divided into three groups: (1) in-country assessment of bottlenecks in rice handling and processing systems, (2) evaluation of newly developed postproduction technologies, and (3) development of appropriate technology and knowledge dissemination strategies. The objective of this paper is to give an overview of the current research activities to draw out interests from other organizations and potential private-sector partners.

Assessment of bottlenecks in the rice production-postproduction system

Rice quality evaluation

Evaluation of rice quality in the market is important as it can provide crucial information as to where and how rice quality in the postproduction sector can be improved. In 2000, IRRI, in association with the National Food Authority of the Philippines, launched a nationwide grain quality study (Bakker et al 2001). The objective was to evaluate milled rice quality characteristics of rice sold in the Philippine retail market. Laboratory analysis of some 937 rice samples taken from both urban and rural markets revealed that, in general, the head rice percentage of rice sold in the Philippines is low (67% on a total milled rice basis), with a relatively high percentage of small brokens (>1%). The study also revealed a high percentage of chalky and immature grains (>5% on a total milled rice basis) in the milled rice, as well as a high incidence of discolored (i.e., yellowing) and insect-damaged grain (Table 1). These findings indicate a general low quality of rice brought about by a host of problems, such as poor seed quality and improper harvesting procedures at the farm level, a lack of adequate drying and storage facilities during grain handling, low milling recovery because of inefficient milling systems, and a virtual absence of grading systems for both rough and milled rice. Furthermore, a survey of 279 retailers indicated that consumers select rice primarily based on whiteness, a quality characteristic that is not included in the current standards for milled rice and for which no simple and low-cost evaluation methods exist. An additional market study in 2002 of 200 large retail outlets showed a strong correlation among price, whiteness, and broken kernels. In general, there was no correlation between rice variety and retail price, whereas a strong correlation was found between retail price and the grade written on the bag. Laboratory analysis of these samples showed that none of the rice in the bags met the Philippine national standard for that grade: 80% of the rice was off-grade and only 2% of the rice actually met a grade standard above the lowest grade, grade 3. Similar surveys of rice quality in the market are currently being done in Bangladesh and Indonesia.

Rice mill performance studies

Performance studies of rice mills are useful to determine opportunities to increase milling recovery and head rice yield during milling. The performance evaluation is carried out by processing a known quantity of rice through a commercial rice mill that is operated at steady state by its owner or designated operator. During the milling process, all products and by-products are collected and specifics of the milling system are recorded, such as the number of stages, energy consumption, and maintenance status. Subsequently, efficiencies of each unit operation are calculated in addition to overall milling recovery and rice quality. A performance survey in Cambodia carried out by the Cambodia-IRRI-Australia project revealed that milling recovery and head rice yield of rice mills are low and highly variable (Table 2). At the village level, one-pass rice mills had throughputs of 200 kg h^{-1} of paddy and an average milling recovery of 53% (i.e., 53 kg total milled rice produced out of 100 kg rough rice). Commercial mills (0.6 to 2 t h^{-1} capacity) that use rubber roll huskers with abrasive-type whiteners showed slightly better milling and head rice recovery (60% milling recovery or higher; head rice recovery 40% on a rough rice basis). Improvements in the performance of existing machinery could be made as rubber rolls were used well beyond their design life and milling stones were not maintained on a regular basis. In addition, millers did not monitor grain moisture during storage and milling and many mill operators seemed unaware of the effect of moisture on head rice recovery.

An in-depth performance evaluation of five commercial rice mills in the Philippines and Indonesia was undertaken in 2002. These mills were evaluated on a total mass basis where a known amount of rice was milled and the weight of the rice

Table 1. Means and standard errors of milled rice quality parameters for rlce purchased from retailers in 18 rural and 16 urban municipalities in the Philippines, sampling period September-October 2000 (adapted from Bakker et al 2001).

Rice grade indicated on price tag	Retail price[a] kg^{-1}	% Head rice	% Large brokens	% Small brokens	% Insect-damaged grains	% Heat-damaged grains	% Red grains	%Red-streaked grains	% Chalky or immature grains	% Foreign matter
Total (n = 365)	0.41	67.24	31.53	1.24	1.04	2.64	0.02	0.68	5.89	0.01
	± 0.01	± 2.2	± 2.1	± 0.2	± 0.1	± 0.8	± 0.01	± 0.18	± 0.4	± 0.00
Premium grade	0.46	75.60	23.91	0.49	0.53	1.37	0.03	0.72	5.05	0.01
	± 0.02	± 5.0	± 4.9	± 0.2	± 0.2	± 0.4	± 0.03	± 0.40	± 0.6	± 0.01
Grade 1	0.42	70.23	28.84	0.93	1.01	1.62	0.03	0.68	5.96	0.00
	± 0.01	± 4.3	± 4.2	± 0.3	± 0.2	± 1.1	± 0.03	± 0.32	± 0.8	± 0.01
Grade 2	0.39	62.57	36.03	1.42	1.08	1.58	0.01	0.79	6.07	0.01
	± 0.01	± 3.8	± 3.8	± 0.6	± 0.3	± 0.5	± 0.02	± 0.35	± 0.9	± 0.01
Grade 3	0.36	64.79	33.62	1.59	1.46	6.53	0.01	0.38	6.53	0.01
	± 0.01	± 5.1	± 4.7	± 0.6	± 0.5	± 2.9	± 0.02	± 0.41	± 0.8	± 0.01
No grade	0.41	63.76	34.55	1.69	1.06	1.96	0.02	0.85	5.76	0.03
	± 0.01	± 4.7	± 4.5	± 0.5	± 0.2	± 1.4	± 0.03	± 0.53	± 0.8	± 0.02

[a] Price in US$: US$1 = 45 Phil. pesos; all % on a total milled rice basis.

Table 2. Performance of rice mills in Cambodia, the Philippines, and Indonesia (data partly adapted from Rickman et al 2000).

Country	Theoretical yield	Cambodia		Philippines	Indonesia
Mill		Village	Commercial	Commercial	Commercial
Capacity (t h^{-1} paddy)		0.20	1.35	0.73	0.75
Husk (%)	19	31	24	24	19
Brown rice (%)	81	69	76	75	81
Bran (%)	8.5	16	11	8	8.5
Milled rice (%)	72	53	65	63[b]	72
Head rice[a] (%)	50	–	40	38	50
Broken kernels + brewers (%)	22	–	25	27	22

[a] Head rice yield on % total milled rice basis. [b] 2.5% unaccounted losses attributed to change in moisture content, dust, and grain retained in the mill.

and by-products was measured at each stage of the milling process. Grab samples of grain and by-products were also taken to determine the theoretical or potential efficiency of each process in the rice mills. Results from the mass analysis (Table 2) show that milling efficiency in the Philippines is similar to that in the commercial mills in Cambodia, with an average milling recovery of 63%. The potential yield study showed that the low recovery was a result of high levels of foreign matter and cracked kernels in the paddy, in addition to the loss of milled rice at the husking and polishing stages. It also highlighted that damage was occurring to the kernel during the polishing process, often caused by the rice being overmilled. By analyzing rice samples from before and after each mechanical operation, cleaning, husking, paddy separation, and hull aspiration efficiencies were also determined. During the performance tests, interaction with rice millers indicated further that there is a general lack of simple and affordable tools for quality evaluation of rice. Therefore, developing low-cost quality evaluation tools (e.g., moisture content, head rice, and milling degree) would help millers, traders, and retailers to evaluate and improve quality. IRRI is in the process of developing a low-cost moisture meter and color chart for monitoring grain-milling degree.

Evaluation of postproduction technologies

Hermetic storage

Good grain quality management relies heavily on the ability to safely store grain for extended periods. Moisture content (MC) is the major factor determining the storage behavior of grain. Rice quality is often severely affected by mold development during storage, a process generally associated with moisture remigration in the grain. Even if grain is kept sufficiently dry to avoid molding, however, insects survive and cause damage to the grain. Periodic control measures are therefore required to prevent loss of grain quality and quantity. Hermetic or airtight storage provides an excellent opportunity to control insects in stored grain, without the use of chemical pesticides. The principle of hermetic storage is based on traditional underground storage pits found in semiarid climates where insects that are enclosed in the stored grain die off naturally because of a lack of oxygen. Stored grain protection through hermetic storage is enabled by the use of an artificial seal that provides an airtight environment in which insect pests are unable to develop because of an oxygen-deficient atmosphere. Recent technological advances in plastic manufacturing have led to the development of PVC liners that provide the required durability for climate, gas permeability, and physical properties that enable airtight storage for extended periods of time. Evaluation studies conducted by IRRI focus on two hermetic storage technologies: commercial plastic envelopes (e.g., Volcani cubes, grain cocoons) and storage technologies for small farmers based on recycled containers and drums. The goal of the research is to provide feasible technologies at a competitive cost that preserve both grain and seed quality in rough rice.

Research on hermetic storage of rough rice consists of evaluating plastic enclosures, including a 4.2-ton (rough rice basis) capacity unit for bag storage and a 750-kg unit for bulk storage. The units are for storage at ambient tropical conditions and results are compared with those for unsealed, open-bag storage at ambient and artificially cooled conditions (air-conditioned room). A controlled trial of 15 months' duration was conducted at IRRI's experiment station. The grain was mechanically dried to 11-12% MC (wet basis) and cleaned through a conventional scalper-blower, resulting in an average purity of 90.3%, which is believed to be comparable to farm-level stored grain. Samples were taken at 0, 24, 36, 43, 56, and 70 weeks and grain was analyzed for moisture content, seed germination (at 10 d), and insect infestation and a milling analysis was subsequently performed. Results indicate that there is a significant reduction in insects in the hermetically stored grain and that seed viability can be maintained for at least 12 mo compared with seed viability in the unsealed ambient environment, which starts to decline after approximately 6 mo of storage (Fig. 1). In addition, hermetic storage did not lead to a decline in milling recovery and head rice yield vis-à-vis the grain stored in the artificially cooled environment.

Many farmers rely on their own seed reserves and store seed in clay pots or fertilizer bags, which are prone to insect and pest damage, reentry of moisture into the grain, and spoilage. At IRRI, low-cost sealed storage devices are being evaluated that hold from 25 kg up to 250 kg of seed. Figure 2 presents the results of a controlled trial of insect-infested grain (100 live insects 500 g^{-1}) and shows that a rapid decline in oxygen can be maintained in sealed containers, resulting in a rapid decline in insects. In addition to controlled trials, on-farm hermetic storage trials are conducted in Bangladesh, Indonesia, and Cambodia in collaboration with partner organizations. Preliminary results showed an improvement of 30% to 70% in germination of seed stored by farmers for a 7-mo period vis-à-vis the traditional storage method. Therefore, results for grain quality and seed viability are comparable with the results of the controlled trials; however, field trials provide evidence of practical problems that prompt the need for improvements in user friendliness of the technology. For instance,

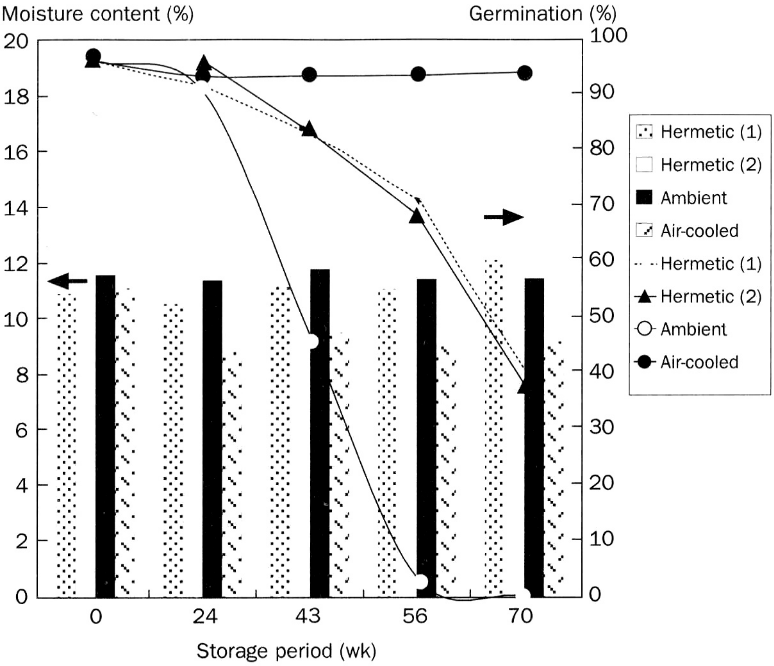


Fig. 1. Moisture content and seed viability of rough rice stored under airtight, ambient, and air-cooled conditions.

intermittent opening of the storage bags (e.g., to till or remove part of the stored grain or to perform a visual check for insect infestation) is a common procedure in farming communities, but this is not desirable from a hermetic storage point of view as it may replenish oxygen inside the stored grain. On one occasion, reopening of the bag led to rapid reinfestation of grain with lesser grain borer (*Rhizopertha dominica*), resulting in replenishment of oxygen inside the bag and even piercing of *Rhizopertha* through the plastic liner.

Low-cost quality evaluation tools

Studies in the Philippines have highlighted that rice is often overmilled, which reduces the head rice recovery and increases the volume of broken kernels. Overmilling occurs because few mills have a whiteness meter or any means other than visual inspection to determine the degree of milling. Whiteness meters are expensive (US$5,000–6,000) and are used only in very large commercial mills. The whiteness meter gives a reflective reading of whiteness, indexed from 0 to 100. The whiteness index is an international standard that uses complete darkness as zero and the reflective index (whiteness) of the pure white of a surface on which white fume produced by burning magnesium has been adhered as 100. The operation of common commercial whiteness meters (e.g., KETT, Satake) is based on this principle. The indexed number

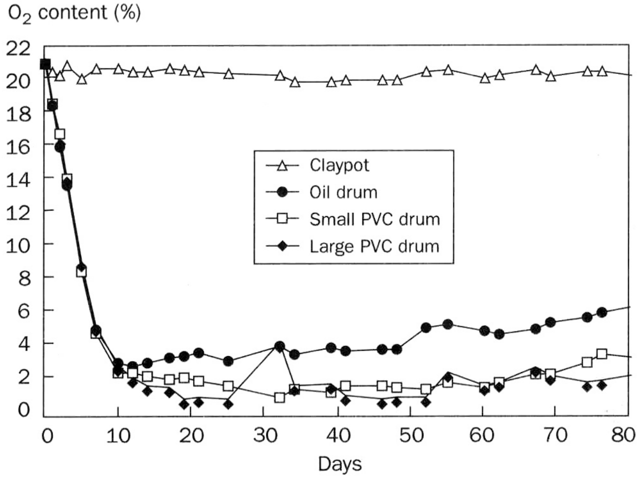


Fig. 2. Oxygen content in low-cost sealed storage devices.

that is often quoted as an acceptable guideline for whiteness is the "Whiteness of brown rice +20."

A research project was undertaken at IRRI in 2001-02 to develop a simple visual color check based on the actual color seen by the naked eye to predict the color change of rice according to the degree of milling. The color standard used for this study was taken from the CIE color model (International Commission on Illumination) and uses the CIELAB system. The CIELAB system distinguishes color on the basis of light and dark (L), red and green (a), and blue and yellow (b). These values can then be expressed as the Hunter whiteness.

The development process required that a model be established that could predict the change in the color value according to a change in the degree of milling. Milling degree was established by measuring the weight difference of 1,000 kernels before and after milling. A Satake whiteness meter and Minolta CR-300 colorimeter were used to determine the whiteness and color coordinates. The testing was undertaken using an abrasive and friction mill and three different rice varieties. The relationship was consistent for the three varieties and was best represented by a sigmoid curve, which can be expressed by the following algorithm:

$$\begin{array}{c}\text{Milled Rice}\\ \text{Hunter Whiteness}\end{array} = \begin{array}{c}\text{Brown Rice}\\ \text{Hunter Whiteness}\end{array} + \frac{a}{1+\exp-^{(\text{Milling degree} - x_0)}}$$

where a, b, and x_0 are constants (Fig. 3).

From the sigmoid curve, the upper and lower limitations of the degree of milling were established. The upper limitation was established by using chemical staining techniques, mathematically differentiating whiteness, and determining the upper limit

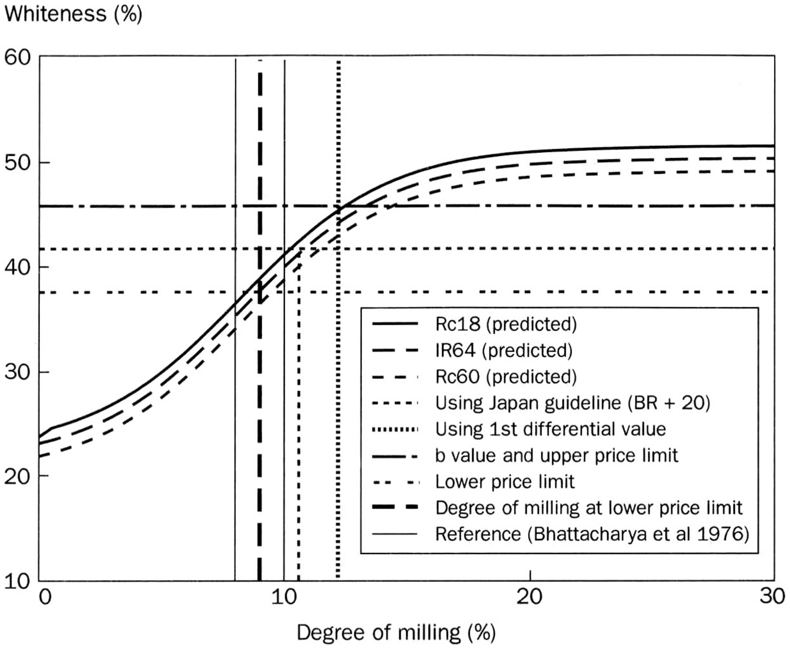


Fig. 3. Whiteness as affected by the degree of milling (note: Rc18 stands for PSBRc18).

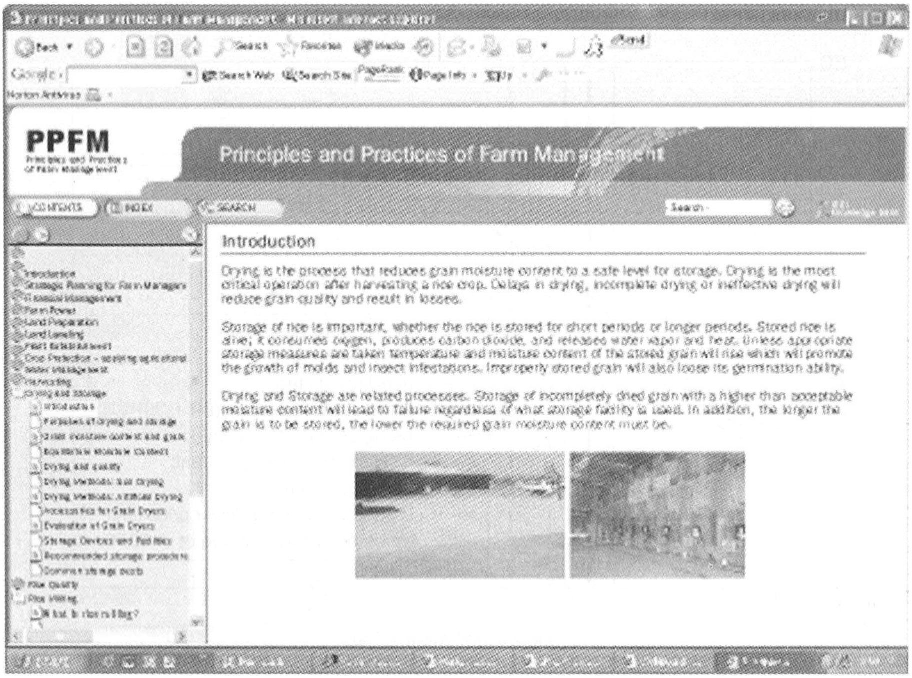
of whiteness of rice found in the marketplace. The lower limit was more difficult to establish. Factors used were the lower limitation of whiteness of rice found in the market, researchers' experience, and earlier published reports.

The upper and lower limits for the degree of milling for the three varieties tested were calculated to be 44% whiteness and 12% milling degree and 36% whiteness and 8% milling degree, respectively. There was a very strong correlation between the Hunter whiteness and whiteness from the Satake whiteness meter (r^2 = 0.93).

By determining the upper and lower limits for the degree of milling, it was possible to establish the color coordinates and then process the actual color that would represent the categories for the degree of milling. A color chart has been developed that differentiates among the following categories of milling degree (indicated in parentheses):

- Husked or unmilled rice (0-2.5%)
- Undermilled rice (2-5%)
- Lightly milled rice (5-7.5%)
- Reasonably well-milled rice (7.5-10%)
- Well-milled rice (10-12.5%)
- Overmilled rice (12.5% and above)

The milling degree chart will then be verified through further research and evaluated through panel tests.



Introduction

Drying is the process that reduces grain moisture content to a safe level for storage. Drying is the most critical operation after harvesting a rice crop. Delays in drying, incomplete drying or ineffective drying will reduce grain quality and result in losses.

Storage of rice is important, whether the rice is stored for short periods or longer periods. Stored rice is alive; it consumes oxygen, produces carbon dioxide, and releases water vapor and heat. Unless appropriate storage measures are taken temperature and moisture content of the stored grain will rise which will promote the growth of molds and insect infestations. Improperly stored grain will also loose its germination ability.

Drying and Storage are related processes. Storage of incompletely dried grain with a higher than acceptable moisture content will lead to failure regardless of what storage facility is used. In addition, the longer the grain is to be stored, the lower the required grain moisture content must be.

Fig. 4. Detail of IRRI's principles and practices of farm management training.

Knowledge dissemination strategies

Before embarking on a quality management program, it is important to identify who is involved along the postproduction chain and what are the incentives of each to maintain quality. If incentives exist to maintain quality, then awareness of the general principles of grain quality management should be raised, regardless of the technology that is used. Field experience (see also Bell et al 2000) shows that many knowledge gaps exist among key players in postproduction with respect to maintaining grain quality; therefore, the challenge is how information can be appropriately packaged and distributed to bridge these knowledge gaps. In an attempt to overcome these knowledge gaps, IRRI has launched several activities that are designed to disseminate common principles of rice quality management.

An entirely new three-week training course titled "Principles and Practices of Farm Management" was designed to target those that manage a farm, extension station, or grain-processing facility. The course focuses on producing rice and managing grain throughout the entire production cycle, including postharvest handling and processing, and consists of intensive hands-on instruction modules. The course is organized according to the modular format promoted in the IRRI Knowledge Bank (Fig. 4; see also www.knowledge.irri.org), which enables easy adaptation of course content depending on the needs and demands of the trainees. A second training course deals specifically with all aspects of rice grain quality, such as quality characteristics, quality evaluation procedures, and common international and national standardization programs. Finally, principles and practices of good grain quality management are incorporated in Troprice, IRRI's decision-support tool for rice producers.

References

Bakker RR, Jarcia EA, Jawili MCE, Billate RD, Barredo IR, de Padua DB, Mangaoang CC. 2001. Assessment of milled rice quality in the Philippines retail market. Paper presented at the 20th ASEAN/2nd APEC Seminar on Postharvest Technology, Chiang Mai, Thailand, September 2001. (In press.)

Bell MA, Dawe D, Douthwaite MB, editors. 1998. Increasing the impact of engineering in agricultural and rural development. IRRI Discussion Paper Series No. 30. Los Baños (Philippines): International Rice Research Institute. 108 p.

Bell MA, Bakker RR, De Padua DB, Rickman J, 2000. Rice quality management: principles and some lessons. In: Johnson GI, Le Van To, Nguyen Duy Doc, Webb MC, editors. Quality assurance in agricultural produce. ACIAR Proceedings No. 100. Canberra (Australia): Australian Centre for International Agricultural Research.

De Datta SK. 1981. Principles and practices of rice production. New York, N.Y. (USA): John Wiley and Sons,

Rickman JF, Som Bunna, Poa Sinath. 2000. Rice milling in Cambodia. In: Johnson GI, Le Van To, Nguyen Duy Doc, Webb MC, editors. Quality assurance in agricultural produce. ACIAR Proceedings No. 100. Canberra (Australia): Australian Centre for International Agricultural Research.

Notes

Authors' addresses: R.R. Bakker and J.F. Rickman, Agricultural Engineering Unit, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; R.R. Bakker, currently Institute for Agrotechnological Research (ATO B.V.), Wageningen University and Research Center, Netherlands; O.W. Kim, Korean Food Research Institute (KFRI), Seoul, Republic of Korea.

Acknowledgments: Many organizations are collaborating in postharvest research at IRRI. These include the Bangladesh Rice Research Institute, Rural Development Academy, Rangpur Dinajpur Development Service (Bangladesh), Karawang Research Institute for Paddy Rice (Indonesia), and the Cambodia Agricultural Research and Development Institute. The technical assistance of Haogenplast Inc. and the Satake Corporation is gratefully acknowledged as well.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Using power tillers for rice cultivar in Southeast Asia

V.M. Salokhe

The power tiller is one of the most important pieces of multipurpose equipment used for cultivation in many Southeast Asian countries. Because of the lack of capital, limited land reform, poor land layout, and smaller holdings in these countries, the breakeven area and other positive factors such as multipurpose applications, versatility, simplicity, and ability for use in difficult conditions have justified the use of the power tiller for crop cultivation. The power tiller population has grown exponentially, thus improving the productivity of medium- and small-scale farms in the region. The main advantages are the availability of attachments for use in every stage of crop cultivation as well as postharvest processing applications and transportation. During the past few decades, the applicability spectrum of the power tiller for a variety of operations has been extended with the development of new implements and attachments. This paper summarizes recent developments in the use of the power tiller, especially for rice production in selected Southeast Asian countries.

Agriculture is one of the most important economic sectors for many developing countries of Southeast Asia. A large proportion of the population is involved in agriculture. However, this number has declined in the last five to ten years because of the rapid expansion in the industrial, construction, and tourism sectors. As a consequence, labor has been drawn from the agricultural sector to others, which has resulted in labor shortages during the peak farming seasons. Undoubtedly, agricultural machinery plays an important role in the current agricultural systems of the region. The number of pieces of agricultural machinery used has increased rapidly. Most of these agricultural machines are manufactured locally in some of the developing countries in the region, first by copying the popular brands and then modifying them to make them appropriate for local working conditions.

Rice is one of the major economic crops and is also the staple food in most Asian countries. World rice production increased from 170 to 573 million tons from 1957 to 1997 (FAO 1997) and the largest harvested area of 134 million hectares was in Asia. This constituted 90% of the total. Southeast Asia has the major rice producers and suppliers in the world (Prempridi 1994). Mechanization and improvements in the quality of agricultural inputs such as irrigation, fertilizer, and technologies may be the reason for the consistent rice production growth of 1.5% over the past decades (FAO 1999).

Rice can be cultivated in many different ways: upland, rainfed, irrigated, or deep-water conditions. Agricultural workers in different areas employ different techniques and use a variety of tools. The agricultural work carried out in these countries varies from manual or animal power to mechanized, with machines and equipment for activities from land preparation to postharvest. In a peak season, some of these activities overlap. As a result, agricultural workers are lacking to carry out these tasks in time. Harvesting and postharvest activities usually have to be done simultaneously, followed by land preparation in a short period for multiple cropping. Rice-based cultivation varies from region to region and so does the level of mechanization. In most developed or partially developed countries in the region, power-intensive operations such as water pumping, soil tillage, or threshing are being mechanized but other operations are not much mechanized yet as wages are still relatively low for performing these operations.

Agriculture in the tropics depends heavily on the input of human energy. Work demands high levels of human effort, making health especially an important subject, particularly as agricultural tasks are often performed in an open area. Climatic conditions such as extreme temperature, humidity, and solar radiation impose stress on an individual's homeostatic and working efficiency (Choudhry 1989). Meteorological conditions not only reduce working capacity but may also affect workers' health (International Labor Organization 1979). To create safe and satisfactory working conditions and prevent problems of unnecessary fatigue because of some hazardous processes, most of these countries have considered appropriate mechanization by using aids such as power tillers (Elgstrand 1979).

Agricultural workers in developing countries rarely have modern tools and equipment. Workers tend to use traditional tools and methods, which require a high human energy input. FAO statistics (FAO 1999) demonstrate that human effort provides more than 70% of the energy required for crop production tasks in developing countries. However, the trend is decreasing in the agricultural population in Asian countries, which dropped from 62.9% to 59.3% from 1988 to 1997 in Asia-Pacific and from 47.3% to 43.9% in the rest of the world. Consequently, the number of agricultural tractors has shown an increasing trend in Asia-Pacific, with a 2.6% average annual growth, while this growth for the rest of the world was -0.5% (FAO 1999).

The power tiller is a common name for a two-wheel tractor guided and supported by hand. In rice-growing regions of Southeast Asia, hand tractors are equipped with a rotary tiller; hence, the name became power tiller. Figure 1 shows the early version of the power tiller. Japanese power tiller designs evolved from rotary tillers used for garden work in the Western world during the 1920s. The Japanese adapted this for rice mechanization with simplified designs and engine power ranging from 2 to 12

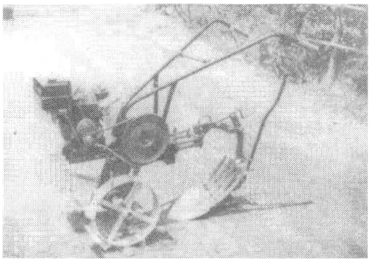


Fig. 1. Early version of the power tiller.

Table 1. Power tiller production in and exports from Japan from 1990 to 2000.

Year	Production (units)	Shipment (units)
1990	269,027	205,944
1992	245,675	199,141
1994	212,539	172,471
1995	205,758	163,323
1996	214,702	173,894
1997	225,229	174,004
1998	212,551	173,397
1999	253,817	180,511
2000	243,995	169,996

Source: Shin-Norinsha (2002).

kW (Sakai 1978). However, recent statistics have shown a slight decline in power tiller production in and exports from Japan. This may not be due to the reduction in use, but to the improved production capability in other regional countries such as China (including Taiwan Province), Thailand, Indonesia, Malaysia, and India. Table 1 shows the reduction in Japanese exports from 1990 to 2000 (Shin-Norinsha 2002). By 2000, the number of household walking-type tractors in Japan reached 2,028,000 units.

Multipurpose applications

The tractor is the most important machine in modern agriculture. Power tillers are the most used machines in Southeast Asia because of their suitability in varying field conditions. The recent trend is such that most power tillers are produced in Southeast Asian countries using local material although the designs used are mostly a copy from other countries. Currently, millions of power tillers are produced and are in active use in Southeast Asian countries such as Japan, Korea, China (including Taiwan Province), Thailand, Indonesia, and Malaysia. They suit both the economic and physical conditions associated with rice production in these countries. Because

Table 2. Power tiller use for different operations in various regions of Thailand.

Use	Northern (%)	Northeastern (%)	Central Plain (%)	Southern (%)	Av (%)
Land preparation	99	100	99	99	99
Transportation	33	39	53	6	33
Irrigation	55	53	83	25	54
Threshing	1	9	11	18	10
Weed control	1	1	4	–	2
Planting	4	1	–	–	1
Ridging	17	36	2	6	15

Source: Office of Agricultural Economics, Thailand (1997).

of their light weight and the use of cage wheels, power tillers are used in wetland cultivation as well as dryland conditions on small farms. In addition, they are used for transportation and to power stationary pumps or other machines such as planters, fertilizer applicators, reapers, threshers, or winnowers.

Power tillers originally came with a rotary tiller or rotavator attachment connected via a PTO shaft. However, modified and simplified versions of power tillers manufactured in most Southeast Asian countries don't have a PTO shaft for driving the rotary cultivator. On a few machines, diesel, gasoline, or kerosene engines are fitted on the locally fabricated frame. They have steering clutches and gears for power trains. The operating speed can be adjusted by positioning the acceleration lever and shifting the gear lever. Engagement or disengagement of power to be transmitted is done with the help of an idler pulley (Roy 1994).

Thailand, the number-one rice producer in the world, has shown a steady increase in the use of the "walking tractor," with annual local production of 50,000 units from 33 local manufacturers. More than 1,500,000 units are now used in the country (Office of Agricultural Economics, Thailand, 1997). Table 2 shows the use of power tillers for different operations in various regions in the country.

Land preparation and planting

The power tiller is the highest contributor of mechanical power in land preparation in the developing countries of Southeast Asia (Figs. 2 and 3). Because of the low breakeven area and lower capital requirement, it can be used in any terrain. For land preparation, these power tillers are commonly used for providing draft to tillage implements as well as puddling. Labor savings in land preparation by using the power tiller is about 63% compared to the labor input required for land preparation by buffalo, or 16 labor-days per hectare per season (Salokhe and Mamansari 1995). Farmers generally use the moldboard plow, disc plow, puddler, and rake attachments with the power tiller. The disc plow attachment is commonly used in dryland conditions, whereas the moldboard, rake, and puddler are used for wetland conditions (Roy 1994).

Fig. 2. Puddling under flooded conditions.

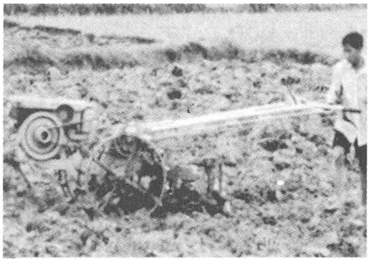


Fig. 3. Power tiller in dryland tillage.

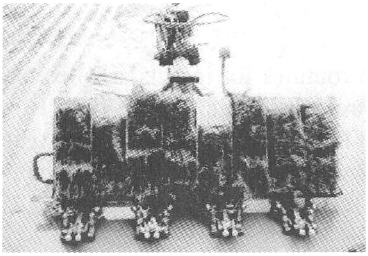


Fig. 4. Transplanter attachment.

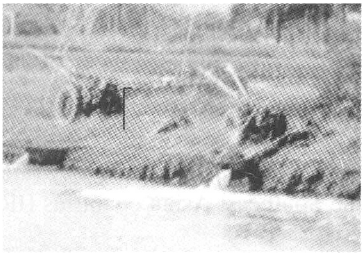


Fig. 5. Pump powered by a power tiller.

Another critical operation in association with land preparation under paddy cultivation is planting. Planting has different techniques: direct sowing to manual planting or with machine aids. Direct sowing has many disadvantages when other subsequent operations are involved because of the nonuniform placing of plants and growth, and manual planting is very labor-intensive and ergonomically uncomfortable. Conversely, rice transplanters have shown their advantages in precision and easy maintainability of the crop in subsequent operations (Fig. 4). All these attachments are available with power tillers in most Southeast Asian countries.

Irrigation

Irrigation of paddy fields is one of the most important steps in paddy cultivation except for upland or rainfed varieties. Irrigation has a very clear correlation with the yield of rice and an annual growth of 2.0% has been reported for the Asia-Pacific region and 1.0% for the rest of the world for 1988 to 1997. In Asia-Pacific, the percentage of irrigated land is 31.6% and for the rest of the world it was 10.5% in 1997 (FAO 1999). Most power tiller models available can power irrigation pumps (Fig. 5). The power tiller makes a significant contribution to increasing irrigated land for rice cultivation. Especially in Southeast Asia, the reason for increased power tiller usage is its ability to do multipurpose work.

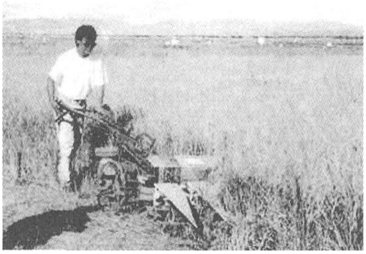


Fig. 6. Single-row reaper attachment.

Fig. 7. Stripper attachment.

Crop protection and maintenance

It has been found that better crop protection routines for insects and diseases and also proper nutritional practices and weed control would enhance rice yield. However, the contribution of the power tiller is limited (Table 1) in these processes except that some power tiller attachments are available for weed control and fertilizer application in some Southeast Asian countries (IRRI 2002).

Harvesting and processing

Manual harvesting of rice with sickles in the traditional way is a time-consuming and labor-intensive job. In an unfavorable climate with less labor, losses may be unavoidable. Combine harvesters have been in use in most developed countries to cope with this problem. With cheaper and freely available labor, most developing countries have mechanized some labor-intensive and hazardous operations in rice cultivation.

Figures 6 and 7 show reaper and stripper attachments developed to work with the power tiller (IRRI 2002), thus improving timeliness in operations. Most power tillers available in Southeast Asian countries are of simple design and power can be taken out by using a belt-drive system or through the PTO shaft for operating the cutter-bar system and even to operate a thresher or a winnowing fan. Most postharvest processes are handled by the power drawn from a power tiller using the attachments originally developed by the Japanese manufacturers and regional research institutions such as IRRI, the Asian Institute of Technology, and other organizations located in most countries in the region.

Transportation

After harvesting or in-field postharvest processing, the final product needs to be transported to a proper shelter to protect it from any unfavorable climate or from insects and birds. To cope with this labor-consuming job in most developing countries, power tillers play a big role. Trailer-mounted power tillers can be seen even transporting people in rural areas, thus justifying their versatility, popularity, and multipurpose handling of agriculture-related work (IRRI 2002).

Fig. 8. Walking behind the power tiller is often hard work from an ergonomic point of view.

Applicability under different operating conditions and drawbacks

The power tiller can be used in any soil condition for different crop production applications. Land preparation under wet or dry conditions is important as it relieves humans and animals from labor-intensive operations. The hand tractor is popular for its contribution to tillage operations with the rotary tiller, but other operations with moldboard or disc plows for primary tillage and seedbed preparation under dry-soil conditions can also be seen. The power tiller can be adapted to most farming and land conditions in Southeast Asian countries. With recent modifications, power tiller operation in weak soils such as peat soils in Indonesia is being investigated (Hendriadi 2002).

Ergonomic considerations

Contrary to its economic and technical advantages, the power tiller has some disadvantages from the operator's point of view. Controlling it while walking behind this machine is often hard work from an ergonomic point of view (Fig. 8). Some studies showed, in terms of physiological responses, hazardous effects over long-term usage associated with working outdoors in tropical conditions, which are hot and humid and may affect the physical working capacity of the operator (Salokhe and Mamansari 1995, Mamansari 1993, Kathirvel et al 1991, Rijk 1991).

Safety and health concerns associated with the use of this machine have not been well documented. The majority of agricultural workers depend on their physical strength and energy reserves to perform agricultural tasks. Because many agricultural tasks are seasonal, workers often have to perform the same operations for extended periods of time. When performing these agricultural tasks, the tools they use determine the workers' posture. It is desirable that the posture of the body not cause strain and that the work allow some change of position (Salokhe and Mamansari 1995).

Farmer complaints and frequent problems

One of the main problems found with the power tiller when working in remote and rural areas is the scarcity of maintenance facilities, spare parts, or availability of

Table 3. The difficulties encountered by farmers during the use of power tillers.

Type of difficulty	Frequency	Distribution (%)
Power tiller is too heavy to handle	5	12.5
Breakdown of transmission system	10	25.0
Breakdown of engine	15	37.5
Steering clutch-lever is too hard to press	7	17.5
Breakdown of steering clutch mechanism	3	7.5

Source: Hendriadi (1993).

Table 4. The average working life of locally made power tillers in Thailand.

Working life (years)	Region				Total number
	Northeastern	Northern	Central	Southern	
<2	25	30	38	27	110
2–5	37	37	89	25	188
5–8	27	15	57	16	115
8-10	16	15	45	11	87
10-15	5	1	28	6	20
> 15	5	0	10	1	16
Av	7.9	5.5	10.3	6.8	5.6

Source: Tanatas (1991).

skilled mechanics to take care of regular or urgent repairs. It is evident that on some occasions farmers need to wait for months to complete a job. This may be a serious problem for a farmer surviving on a marginal income. Some of the difficulties reported by farmers and their frequency distribution are shown in Table 3 (Hendriadi 2002).

Though most power tillers have been developed and produced to suit rural and low-tech conditions, as farmers themselves can take care of most maintenance problems, the locally manufactured power tillers had an average life of 8 to 10 years or 6,400 to 8,000 h or 800 to 900 h y^{-1} (Tanatas 1991). Table 4 shows the average power tiller life in different regions in Thailand.

Modifications made to improve working efficiency

Developments in rotary tillers for land preparation

In paddy land preparation, puddling destroys weeds completely and facilitates the transplanting of paddy seedlings. Rautary et al (1997) stated that puddling up to a 10–15-cm depth is adequate to disperse organic matter at the bottom of the puddle. Rotary tillers attached to a power tiller can be used to prepare the seedbed in a fundamentally different method than the conventional method of plowing. Deep rotary tillage provides a better mixing of the soil (Salokhe and Ramlingam 2001). The soil is pulverized by the cutting and chopping action of several blades that receive energy from the engine of the prime mover. For quality of the seedbed, one pass of the rotary tiller is equivalent to several conventional tillage operations (Mandang et al 1993). Shibusawa (1993) found that the reverse-rotary tiller cuts and throws the soil backward, in the form of large sliced soil clods, causing a reduction in retillage of tilled soil and the power requirement. Salokhe and Ramlingam (2001) reported that shear strength decreased after every pass for all forward speeds for both the rotary tiller with reverse rotation having scoop-type blades and the rotary tiller with C-type blades in wetland and dryland conditions. The rotary tiller with C-type blades produced clods of a larger size than the rotary tiller with reverse rotation having scoop-type blades at all passes.

Sakai (1978) observed that soil slices of paddy fields couldn't be thrown by one cutting pass of the blade. The action of a rotary machine on the soil and plant roots is mostly by impact, during which there is a sudden concentration of stresses in the soil being tilled because of the machine's inertia. This considerably changes the picture of fragmentation of the soil compared to when the external load is applied slowly. That is why the knives of a rotary cultivator can pulverize hard clods on the field surface and till highly soddy peat and mineral soils without getting clogged (Bernacki et al 1972).

Kosutic et al (1997) found that the best combination for minimum energy requirement and highest rate of work for a rotary tiller was 4.87 km h^{-1} working velocity, 12-cm depth of tillage, and 5.91 m s^{-1} peripheral tine velocity. Shibusawa (1993) stated that a noticeable reduction in power requirement was achieved during a reverse-rotary tillage. The soil movement depended upon the direction of rotation and the ratio of the tilling depth to blade radius. Kataoka et al (1995) stated that reverse-rotary tillers equipped with special blades called "Sukui-zume" brought about successful deep rotary tillage with a reduced power requirement because of superior backward throwing of the tilled soil.

Development of a PTO for the power tiller

For stationary machines, such as water pumps and threshers, the power from a small engine flywheel is used for pumping and threshing. Farmers usually disengage the V-belt drive between the engine flywheel and transmission gearbox and arrange another V-belt to power the equipment. But this method reduces the efficiency because of the excessive belt slippage, as belt tightening cannot be done properly. A PTO shaft similar to the one on 4-wheel tractors was successfully designed and developed to cope with this energy waste (Bunyawanichakol 1998). By connecting the PTO shaft, rotary power could be obtained with minimum losses for many operations.

Use of cage wheels on power tillers

To optimize the lug spacing and angle, Jayasundara (1980) investigated using an 11-kW tractor and changing the lug angle and number of lugs on a 1-m-diameter cage wheel for optimum draft conditions. The lug spacings of 23 cm and 29 cm were found to be optimum (Fig. 9). The highest drawbar power was obtained for the lug

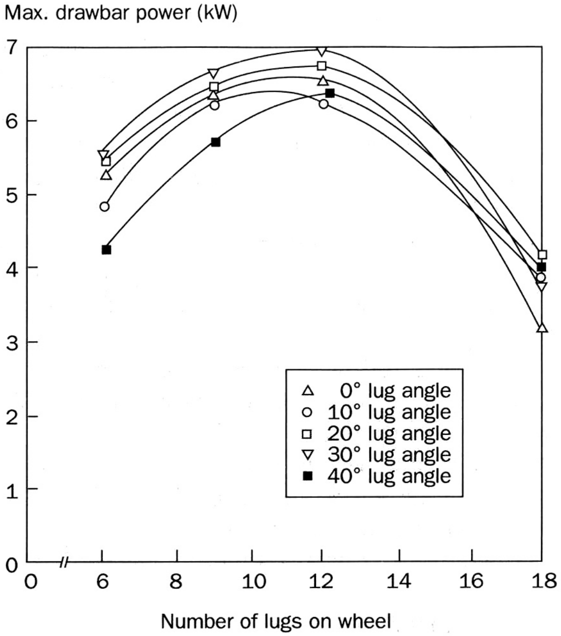


Fig. 9. Effect of lug angle and number of lugs on power transmissibility.

angle of 30°. Cage-wheel developments for power tiller applications have shown significant improvements in wetland mobility and traction (Salokhe and Gee-Clough 1988).

Table 5 shows the performance improvement by cage wheels under different moisture components. Maximum power transmitted and tractive efficiency could be increased significantly by using cage wheels.

Soil adhesion under paddy soil conditions was severe when operating with machinery in rainfed areas where water sometimes becomes scarce during seedbed preparation. Operations without standing water or at the moisture content between plastic and liquid limits become extremely difficult for this reason. To cope with this problem, Salokhe and Gee-Clough (1988) investigated tines and implements with different coating materials. Out of several materials tested, Teflon and enamel coating (the latter is normally used in many kitchen utensils) showed promising results. To consider cost-effectiveness, the enamel coating was tested for several types of agricultural tools and applications. These coating treatments were used for cage-wheel lugs and for floats successfully. When working with enamel-coated surfaces, a significant reduction in adhesive resistance and tool wear was observed. Figure 10 shows the improvement of the power tiller pull because of enamel-coated plates on

Table 5. Power tiller (4.74 kW) performance with cage wheels and rubber tires.

Moisture content (%)	With rubber tires		With cage wheels	
	Max. power transmitted (kW)	Max. tractive efficiency (%)	Max. power transmitted (kW)	Max. tractive efficiency (%)
20	1.74	46.4	2.00	52.8
27	1.40	37.1	1.46	42.5
34	1.07	25.5	1.27	34.6

Source: Hossain (1981).

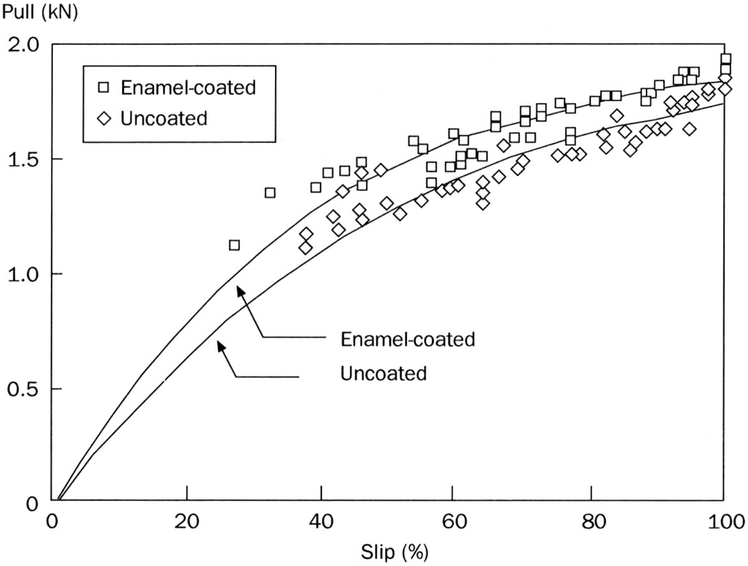


Fig. 10. Performance of enamel-coated lugs.

the cage wheel. Because of the enamel coating, drag force was reduced by 11% to 45% depending on soil moisture conditions.

Developments in handling deep sinkage problems

For incorporating with the deep sinkage (deep hardpan) problem in paddy field conditions in which conventional power tillers or 4-wheel tractors may not be able to work, some appropriate and practical solutions are developed in a few countries. The "Turtle Tiller" (Fig. 11) from the Philippines is one of them (Salokhe and Gee-Clough 1988). The buoyancy effect coming from the turtle-shaped cover provides the necessary flotation with a "nose-up" condition for the vehicle.

Fig. 11. Turtle tiller from the Philippines.

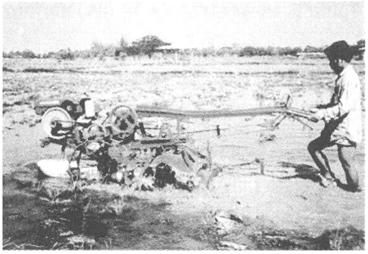


Fig. 12. Power tiller with a float.

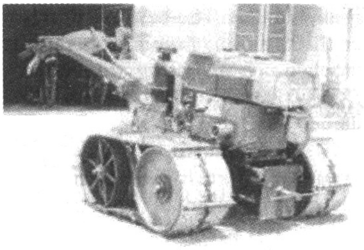


Fig. 13. Power tiller with rubber track.

With the turtle tiller, puddling is done by the rotor/drive wheel itself attached in front and depth and speed can be controlled by pushing the handle up or down. A similar attempt was made for conventional power tillers having a float attached at the bottom-front area with the float center aligning with the axle of the drive wheels (Fig. 12). The float cultivator combination as shown in Figure 12 improved the performance of the power tiller (Ghazalis 1989).

Recent developments to improve traction of the power tiller

Recent studies have revealed that the traction of the power tiller could be further improved by different methods. The tractive efficiency was affected by the ground drive system and ground support. Kathirvel et al (2002) reported that the use of a track system for a power tiller could provide a 50% reduction in specific fuel consumption and a 40% increase in tractive efficiency over conventional lug tires. The track system used in the experiment consisted of a winged chain, sprockets, pulley lugs, and an 8-ply fabric-reinforced canvas endless belt track (Fig. 13).

Future trends of applications and research and development

The agricultural machines and equipment used in most Southeast Asian countries are locally made. However, the basic design of the machine and equipment may have been adopted from other developed countries within the region or from outside. As Western agriculture is governed by precision and high-tech mechanization to cover the labor shortage created by rapid industrialization and huge landholdings, agricultural mechanization in Southeast Asia need not use the same techniques or technologies. Technology dealing with medium or lower-medium levels, which contributes to the development of small-scale equipment and implements suitable for prime movers such as 2-wheel tractors, would be sufficient. This level will enhance the optimum use of surplus labor or will also fit the scarcity of labor in some cases.

The replacement of traditional methods with modern ones in some agricultural activities affects agricultural workers in most developing countries. Because agricultural activities are becoming more mechanized, it is expected that agricultural workers will be affected. The absence of standards in the modification of or new developments in agricultural machines has led to nonuniformity in the machines produced, leading to various problems for operators.

Concluding remarks

The following conclusions can be made:

- Asia was found to be having the most suitable paddy cultivation conditions adaptable to appropriate mechanization with low-tech equipment and implements.
- The adoption of power tillers apart from economics depends on social and cultural factors in Southeast Asia.
- Power tillers are comparatively cheaper, need less skill to operate and for maintenance, and are suitable for the conditions of paddy farming with rough terrain and smaller landholdings.
- The easy maneuverability of the power tiller and its versatility in use for multipurpose activities, including goods or human transportation in rural areas, have increased its popularity over that of many other mechanical inputs.
- However, factors such as poor ergonomic conditions, initial investment (still appearing to be high for most farmers in Southeast Asia), less efficiency in wetland, mobility, development of matching and suitable implements and attachments, etc., need to be further investigated.

References

Bernacki H, Haman J, Kanfojki CZ. 1972. Agricultural machines: theory and construction. Vol. 1. Warsaw (Poland): Center of Central Institute for Scientific Technical Information. p 382-387.

Bunyawanichakol P. 1998. Development of power take-off for Thai power tiller. M. Eng. thesis no. AE 98-6, Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Choudhry AW. 1989. Occupational health in agriculture. East Afr. Newsl. Occup. Health Safety 3:393-401.

Elgstrand K. 1979. Teaching ergonomics in tropical countries. Proceedings of the Fifth Joint Ergonomics Symposium in Ergonomics in Tropical Agriculture and Forestry. Wageningen, Netherlands. p 81-87.

FAO (Food and Agriculture Organization). 1997. Selected indicators of food and agriculture development in Asia-Pacific region, 1987-97. FAO of the United Nations, Regional Office, Bangkok.

FAO (Food and Agriculture Organization). 1999. Selected indicators of food and agriculture development in Asia-Pacific region, 1988-98. FAO of the United Nations, Regional Office, Bangkok.

Ghazali A. 1989. Development of a float attachment for power tiller. M. Eng. thesis no. AE 89-8. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Hendriadi A. 2002. Tractive performance of a power tiller in swampy peat soils. Dr. Eng. dissertation no. AE 2002-1. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Hossain M. Md. 1981. Field performance evaluation of a power tiller manufactured in Thailand. M. Eng. thesis no. AE 81-9. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

IRRI (International Rice Research Institute). 2002. www.irri.org/, homepage of the International Rice Research Institute, Philippines.

Jayasundara L. 1980. Study of factors affecting the design of flat lugged cage wheels in paddy soils. M. Eng. thesis no. AE 80-15. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Kanai K. 1980. Performance of rice transplanter as evaluated by the national test in Japan. Jpn. Agric. Res. Quart. 14(2):84-87.

Kataoka T, Onodera K, Shibusawa S, Ota Y. 1995. A model for backward throwing of sliced soil clods by a reverse-rotational rotary tiller using rigid body kinematics. Proceedings of the 4th Asia-Pacific Conference of the ISTVS, Okinawa, Japan, 20-22 Nov. p 339-346.

Kathirvel K, Job TV, Karunanithi R, Swaminathan KR. 1991. Energy expenditure pattern of power tiller operator. Agric. Mech. Asia Afr. L. Am. 22(4):18-20.

Kosutic S, Filipovic D, Gospodaric Z. 1997. Agro-technical and energetic characteristics of a rotary cultivator with spike tines in seedbed preparation. Agric. Eng. J. 6(3&4):137-144.

Mamansari DU. 1993. Anthropometry and physical work capacity of agricultural labor in Central Plain, Thailand. M. Eng. thesis no. AE-93-4. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Mandang T, AI F, Hayashi N, Watanabe K, Tojo S. 1993. Studies on the overturning properties of soil by rotary blade using CT image analyzer. ASAE Paper No. 93-3035. St. Joseph, Mich. (USA): American Society of Agricultural Engineers.

Prempridi T. 1994. Conventional farming systems and their evolution in Thailand: a study on conventional farming systems and their development in the case of Southeast Asia. Project report. Faculty of Bio-Resources, Mie University, Japan.

Rautary SK, Watts CW, Dexter AR. 1997. Puddling effects on soil physical parameters. Agric. Mech. Asia Afr. L. Am. 28(3):37-40.

Rijk A. 1991. The process of mechanization in historical context: utilization of farm machinery in Asia. Tokyo (Japan): Asian Productivity Organization.

Roy SK. 1994. Evaluation of the transmission system of a power tiller manufactured in Thailand. M. Eng. thesis no. AE-94-7. Asian Institute of Technology, Bangkok, Thailand. (Unpublished.)

Sakai J. 1978. Designing process and theories of rotary blades for better rotary tillage (part I). J. Agric. Res. Quart. 12(2).

Salokhe VM, Gee-Clough D. 1988. Working with Bangkok clay soil: some experience. Agric. Mech. Asia Afr. L. Am. 19(2):33-41.

Salokhe VM, Mamansari DM. 1995. Physical workload during selected farm operations. J. Human Ergol. 24(2):31-40.

Salokhe VM, Gee-Clough D. 1988. Wet clay soil behavior under multiple cage wheel lugs. J. Agric. Eng. Res. 39(1):57-70.

Salokhe VM, Ramlingam N. 2001. Effect of reverse-rotation on power and draft requirement of a rotavator. J. Terramechanics. (In press.)

Shibusawa S. 1993. Reverse rotational rotary tiller for reduced power requirement in deep tillage. J. Terramechanics 30(3):205-217.

Shin-Norinsha. 2002. The present status of farm machinery industry. Agric. Mech. Asia Afr. L. Am. 33(1):65-68.

Tanatas. 1991. Thailand country report: utilization of farm machinery in Asia. Tokyo (Japan): Asian Productivity Organization. p 267-282.

Notes

Author's address: Professor, Asian Institute of Technology, Bangkok, Thailand.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The challenges to and technical innovations in the mechanization of rice production in China

Wang Zhicai

Rice is the grain crop with the largest growing area and highest yield per unit area in China. The development of rice production mechanization is closely related to the Chinese economy. Mechanization can be adopted in land preparation, the seedling nursery, transplanting/seeding, irrigation, field management, harvesting, and drying. The level of mechanization is high in the north but low in the south, high on dry land but low in the paddy field, and high in wheat but low in rice. To meet the urgent demand of farmers for rice production machinery, the Chinese government made the "Study on appropriate technology and key implements for rice mechanization production" a national key project. The Ministry of Agriculture launched a 100-county demonstration project for rice production mechanization in the whole country. Mechanization for land preparation, irrigation, and field management is fairly high, but is rather low for rice planting and harvesting. To solve the key technological problems that limit rice planting mechanization, we made the "Study on the high-speed rice transplanter" a key project. The project aims to develop and manufacture a high-speed rice transplanter, highspeed seedling-throwing machine, and seeding machines. Ricegrowing areas in China can be divided into three kinds according to geographic location and cropping system: single-crop rice area in the cool temperate zone, rice and wheat rotation, and double-crop paddy rice area. The diversity in ecotype, crop species, and farming systems requires diversity in rice cultivation technology and farm implement system. China now mainly applies the technique of conventional seedling nursing and planting. Direct seeding provides convenient conditions for mechanization and has labor saving, reduced cost, and high production efficiency. The technology of raising potted rice seedlings in the greenhouse and surface planting was applied in the 1990s in China. Compared with the conventional technique of raising rice seedlings and transplanting, it has high operation efficiency, good quality of rice seedlings, fast regreening of seedlings, more low node-order tillers, a high degree of maturity, high yield, and ease of operation. Another key problem that restricts rice mechanization is the diversity in rice harvesting. The whole-feed combine harvester has strong adaptability but has high

energy consumption and stripping losses. The head-feed combine has strong suitability and good performance but has a higher cost and lower working efficiency. The stripping-type combine harvester has low energy consumption, high efficiency, and low cost but has a high loss rate, high breaking rate, and low adaptability and reliability. To speed up mechanization of rice production in China, we need to heighten technical innovation capability, strengthen international technical cooperation and exchange, extend the industrialization of agricultural machinery service, and develop strategies for implementation.

China is a vast agricultural country with a large population. Rice is the grain crop with the largest growing area and highest yield per unit area. The growing area of rice in 2001 was 28,812,000 hectares, with a total yield of 177.58 million tons, accounting for 27% of the crop cultivation area in China, 39% of the total national grain production, approximately one-fifth of the world's rice cultivation area, and about one-third of the world rice production. Rice production not only has a very important position in grain production in China but also has a great influence on rice production worldwide. The development of rice production mechanization has a close relationship with the Chinese rural economy and the overall development of agricultural mechanization in China.

Rice production mechanization includes the main operations: paddy land plowing, seedling nursing, transplanting (broadcasting), irrigating, field management, harvesting, and drying. Along with the upgrading of the overall level of agricultural mechanization in China, the mechanization of rice production developed very fast. But a large imbalance appeared in mechanization between the south and the north, between the paddy field and dry land, and between rice and wheat, forming a pattern of "north high, south low, dry land high, paddy field low, and wheat high and rice low." The area of wheat sown and harvested by machinery in 1995 was up to 1.658 million ha and 1.362 million ha and mechanization operations were 58% and 47%, respectively. The figures for rice in the same year were only 673,000 ha and 744,000 ha and mechanization was 2.2% and 2.4%, respectively.

To change the backward situation existing in the development of rice production mechanization and to meet the urgent demand of farmers for rice production machinery, the Chinese government has adopted a series of effective measures in recent years. Starting with the development of key technologies for rice production mechanization, the government added a "Study on appropriate technology and key implements for rice mechanization production" into the national key projects and obtained better results. The project provided applicable farm implements for rice mechanization as well as relevant production technologies. That promoted the development of rice production mechanization. The Ministry of Agriculture launched a 100-county demonstration project for rice production mechanization in the whole country, which pushed forward the extension and application of technology on rice production mechanization and stimulated farmer initiatives. Meanwhile, based on the actual situation of each region, the governments at all levels prepared a series of policies and measures to accelerate the development of rice production mechanization. Government guidance, coupled with the farmers' demand, speeded up the development of rice production mechanization. The area of rice transplanted by machines was 1,376,000 ha by 2001, an increase of two times over that of 1995; machine planting was 4.78%, 2.58% higher than in 1995; rice-harvesting area reached 5,193,000 ha, seven times that of 1995; and harvest mechanization went up to 18.02%, an increase of 15.62% over 1995, resulting in a large increase in rice production mechanization.

Mechanization varies with different operations: mechanization for paddy land plowing, irrigation, and field management is fairly high, while that of rice planting and harvesting is rather low. The reason relates to many factors such as the shortage of advanced and applicable farm implements, which results in inefficient coordination of agricultural machines and farming practices in rice production. The mechanization of rice planting and harvesting remains a bottleneck in the mechanization of rice production and is a key problem to be tackled now.

Technical features of and innovations in rice production mechanization in China

Rice is grown widely in China and covers all areas apart from Qinghai Province. The climate and geographic conditions vary greatly among different regions and so does economic development. The rice-growing area in China can be divided into three kinds according to the geographic location and cropping system. The first is the single-crop rice area in the cool temperate zone, also called the north rice area, which mainly involves Heilongjiang, Jilin, Liaoning, Inner Mongolia, Ningxia, Xinjiang, Gansu, Xannxi, Hebei, Tianjin, and Beijing. The second is the area of rotation of rice and wheat, mainly Jiangsu, Anhui, Hubei, Shandong, Heinan, Sichuan, Chongqing, Guizhou, and Shanghai. The third is the double-crop paddy rice area, mainly Hunan, Jiangxi, Guangdong, Guangxi, Fujian, Yunnan, and Hainan. Rice in China has developed into an extremely complicated farming and varietal system. Diversity in ecotype, crop species, and farming system cannot but require diversity in rice cultivation technology and farm implements. This characterizes rice production mechanization in China, with the feature of technical diversification. So, rice production mechanization in China developed distinctive Chinese features, applicable to the natural conditions as well as the economic development level in the local area and considering the target of high yield and high efficiency and combining environmental protection with sustainable development.

For the two key factors that restricted the development of rice production mechanization, rice seedling-nursing mechanization and the practices of rice cultivation are closely linked. For worldwide rice development, rice-growing practices can basically be divided into direct paddy-field seeding and rice seedling nursing and transplanting. Direct seeding is divided into dryland seeding and paddy-field seeding. Paddy-field seeding can be further broken down into dry seeding and germinated seeding. Rice seedling-nursing and transplanting practices include traditional practices and the newly developed one that involves potted seedlings and surface planting. China now mainly applies the technique of conventional seedling nursing and planting.

Since seeding saves the procedure of raising rice seedlings, it greatly simplifies the technical flow and provides convenient conditions for mechanization operations, possesses the advantage of labor savings, cost reduction, high production efficiency, etc., and therefore has developed very fast in China in the areas of single cropping and rotation of rice and wheat where the temperature accumulation is sufficient. It will have good prospects for developing as the problems of keeping a full stand of seedlings and weeding are solved. For the technology of raising rice seedlings and cultivation, potted seedling nursing and surface planting in the greenhouse are new techniques that were disseminated and applied in the 1990s in China. In comparison with the conventional technique of raising rice seedlings and transplanting, their advantages are high operational efficiency, good quality of rice seedlings, fast regreening of seedlings, more low-node tillers, a high degree of maturity and high yield, as well as ease of operation. The results in yield increase and cost savings are obvious. These techniques were extended to 7 million ha in all of China in 2000 and are predicted to develop much faster in the years to come. Since rice production is distributed widely across the country, no one kind of planting technology could dominate rice production. Rice planting mechanization practices will develop in the direction of the three practices: potted rice seedling nursing, traditional rice seedling nursing and transplanting, and direct seeding. These will complement each other and coexist.

To further solve the key technological problem that limits rice planting mechanization, we made the “Study on the High-speed Rice Transplanter” a key project to be developed in the Tenth Five-Year Plan Period. The project aims to develop and manufacture a high-speed rice transplanter equipped with a multifunction paddy-field chassis, high-speed seedling-throwing machine, and sit-on seeding machines. The result of the project can meet the different demands for farm implements from various cultivation practices and will have a positive effect on and play a large role in the development of rice planting machinery in China.

Another key problem that restricts rice planting mechanization—rice harvest mechanization technology—also features diversity. Technically, it is mainly divided into pickup harvesting and combine harvesting. Combine harvesters are basically classified into three kinds: the whole-feed, head-feed, and stripping-type combine harvester. The whole-feed combine harvester has strong adaptability, but, when harvesting rice, especially threshing and shelling grains under high humidity in South China, it is high in energy consumption and cleaning losses. The head-feed combine has strong suitability and a good performance, but it is complicated in structure, higher in cost, and lower in working efficiency. The stripping-type combine harvester has low energy consumption, high efficiency, and low cost, but there are still some problems that are neither completely solved nor experienced in a vast area of farmland, such as the high loss rate, high breaking rate, low adaptability, low reliability, etc. If the combine harvester could efficiently overcome the problems of wet rice threshing and cleaning losses, if the head-feed combine harvester could lower the price while maintaining good quality, and if the stripping-type combine harvester could improve its reliability and smoothness, the Chinese rice-harvesting machine market would have prospects for “three kinds of combines sharing the market.” For areas with less developed and poor paddy fields, it is best to use the pickup harvesting machinery to solve the problems of labor and low efficiency in rice harvesting first, and then use the thresher to finish subsequent operations. Even though the subsequent pickup harvest has a fairly low overall efficiency, the structure of the machine is simple and easy to operate, it has less downtime and a low cost, and it is easy for many farmers to accept and operate. It could be an effective way to solve the current problem of rice harvesting mechanization in China.

China’s rice cultivation area is vast. There are great differences in geography and economic conditions among the different areas of the country. Each place should develop its own way to promote rice production mechanization according to local conditions, to meet the requirements of farmers, to provide a technology guarantee for rice production, and to promote the fast development of rice production.

Guidelines for mechanization of rice production in China

In view of the problems in rice production mechanization in China, its development in the future should revolve around the key task of strategic regulation of agriculture and the structure of the rural economy. Based on the changing trend and characteristics of farming systems in the main rice cultivation areas, it is vital to develop forms of rice production mechanization to push forward the adjustment of the planting system and improve varietal structure. Research needs to focus on developing dry nursing and spaced planting and the technology of light-duty cultivation mechanization, and work on raising rice seedlings, transplanting, and combine-harvesting technology. Scientific research on advanced and applied technology also needs to be popularized and extended. We need to speed up the mechanization of rice production, achieve a better combination of technical innovation and organizational innovation, set up and improve the agricultural mechanization service system, improve the organizational level, promote the industrialization of the agro-machinery service, transform the way of economic growth, and raise the economic benefits. We should stress and do better in the following tasks:

(1) Heightening technical innovation capability

It is necessary to adopt system reforms by gradually building up multitechnique innovations and the extension system, which are market-oriented and involve the social forces of government support, scientific and research institutions, extension organizations, enterprises, and farmers. We need to heighten technical innovation capability; enforce system innovation to formulate a new system in keeping with the requirements of the market economy and the laws of science and technology development; promote a combination of production, study, and research work;

encourage scientific and technological organizations that engage in the application and development of science to enter into enterprises or transform their systems into enterprises; guide enterprises to establish research and development organizations; define the enterprises' position as a principal part in gradual technical innovation; and create conditions and an atmosphere that are advantageous for innovation for enterprises and scientific research institutes.

(2) Strengthening international technical cooperation and exchanges

It is necessary to implement the strategy of "go out" and strengthen international technical cooperation and exchanges in rice production mechanization and realize a technical jump forward. First, we should actively introduce, digest, and assimilate the advanced technology from other countries to promote our technology innovation. Second, we should enhance international cooperation and exchanges, that is, enhance exchanges and cooperation among governments on the one hand and strengthen exchanges and cooperation among enterprises, scientific research organizations, universities, and technological organizations on the other hand. We should use the successful experiences of other countries for reference in terms of management and servicing and follow up on the development of foreign advanced technology. Third, we should organize and guide the competitive technology and machinery of rice production mechanization to export them and encourage good agricultural machinery enterprises to take part in international competition and to innovate and develop during this process.

(3) Actively extending industrialization of agricultural machinery service

The industrialization of agricultural machinery service is an effective way to accelerate agricultural mechanization. It closely links the scattered individual agro-machinery special families with the agro-machinery operations market, combines mechanization production with family contracting operations, makes good use of agricultural machinery by way of markets and industrialization operations, lowers production costs, and increases the use of agro-machinery. We started rice transregional operation services in 2000. By 2001, the combine harvesters involved in transregional operations amounted to 25,000 and greatly advanced the technical extension of rice mechanization. Later, we will give active impetus to the mechanization of rice machinery service and promote the popularization of rice mechanization technology via this method.

(4) Conducting strategic implementation of project promotion

We should actively win over investments from multiple channels during the period of the Tenth Five-Year Plan and further advance the development of rice production mechanization. We should exert effort to implement well the key project "Study and Develop the Key Technology of Agricultural Mechanization" and other projects on drying, etc., integrate funds and projects, focus on the important points and do overall planning, and build a group of demonstration bases to play a promoting role. We should actively win over capital from the key projects of national science and technology, the “863” high-tech industrialization fund, the agricultural achievement transformation fund, and the important projects of science and technology and the extension of the “Leaping Forward Program,” “ Sparkling Plan,” and “Bumper-Harvest Plan” to speed up technical innovation and the application of rice production mechanization.

Notes

Author's address: Director of the Administration Bureau of Agricultural Mechanization, Ministry of Agriculture, Beijing, China.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Innovations in key technologies of rice mechanization in South China

Xiwen Luo and Xuecheng Zhou

Because of great efforts in the past 20 years, significant progress has been made in South China in the crucial processes of mechanization of paddy rice production such as planting, harvesting, and drying. Advances and innovations in the key technologies of these processes are summed up in this paper.

Paddy rice is the major crop in China, with a planting area of 31.2 million ha, and occupies second place in the world, covers 34% of Chinese grain crop planting area, and represents 2 I .4% of world paddy rice planting area. Annual production reaches 198.7 million t (first in the world) and represents 34.5% of the world paddy rice yield and 44% of Chinese grain yield. Southern China is the main paddy rice-producing area, with planting area reaching 27.3 million ha and annual production above 170 million t, representing more than 85% of nationwide paddy rice planting area and annual yield. Southern paddy rice production therefore plays an important role in China and globally.

The climate, soil, and irrigation conditions in South China are quite suitable to paddy rice growing. Because of more hilly country (above 90% of total land area), less crop land, lower economic benefit, and so on, however, the mechanization of paddy rice production in South China has lagged behind for a long time. After the reform and opening in China, with great efforts in the past 20 years, tillage in paddy rice fields has become mechanized. The crucial mechanization processes of paddy rice production are therefore planting, harvesting, and drying. Significant progress has also been made in these processes in China in the past 20 years, which played a significant role in promoting mechanization.

Mechanization of seedling raising

A common Chinese saying is, “good seedling stands lead to successful grain.” Seedling raising is an important process in paddy rice production. Rice seedling raising in

China went through three stages, from traditional field raising to field raising with plastic film mulching, and finally to industrial-like raising. Now, industrial-like seedling raising has become the most important method of seedling raising. It shows superiority in saving seedling land, ignoring climatic effects (especially the harmful influence of cold in early spring), and raising seedlings that are good, strong, and suitable for mechanized planting.

Industrial-like seedling raising in China has two main kinds: blanket-form (flat-plate) seedling raising and bowl-form (hill-plate) seedling raising. The seedling-raising process in the two forms is identical. It includes soil preparation (breaking and sieving), seed selection, soaking, sprouting, greening, and strengthening. The seedling plate and seeder, however, are different. Of these two, the seeder is more crucial.

Blanket-form (flat-plate) seedling raising meets the requirement of the ordinary rice transplanter and high-speed rice transplanter because the plastic flat plate is adapted for seedlings. Several kinds of rice seeders have been developed in China for blanket-form sowing. A typical one is the type 2SB-500, a model whose seed plate can be fed automatically. Its production efficiency can reach 500 plates h^{-1} and it requires 7–8 people. Each seeder can provide service for 200 ha each season. Its service cost is 30% lower than that of manual seedling raising in the field.

Bowl-form (hill-plate) seedling raising meets the requirement of hybrid seeds and has developed quickly in China. Hybrid rice has made the greatest contribution in China in the past 30 years to paddy rice breeding. Its yield is high, 6-8 t ha^{-1}, for each season, and more than 60% of the countrywide rice varieties are hybrid. A notable characteristic for hybrid rice planting is the requirement of expensive seedlings and shallow planting, which normally uses 1–3 seedlings per hill and a planting depth of 2–3 cm. Research institutes and universities have made many efforts to develop several kinds of seeders for bowl-form seedling raising, such as the vibration-type and vacuum-inhaling-type.

The 2BZ-330 vibration-type paddy seedling hill-plate combine-seeder can work continuously. The hill-plate combine makes a soil bed, sprays water, sows, and mulches. The major working parts are a metered seed supply and an electromagnetism-vibration sowing part. The amount of seeds to sow can be adjusted at any time according to production needs to meet the requirement of different applications or different kinds of seed. The electromagnetism-vibration sowing part is controlled by a computer, which can adjust the vibration frequency and amplitude in accordance with sowing amount. The sowing rate of the combine seeder can be 1–3,2-4, or 3–5 seeds per hill. Reliability reaches more than 90%. The rate of empty hills is lower than 2%. Productivity is 550 plates per hour. Its service cost is 50% lower than that of manual seedling raising in the field.

The vibrating and vacuum-inhaling-type bowl-form (hill-plate) seedling seeder has a tray supplier, conveyer, soil spreader, mulcher, sprinkler, and tray. The accuracy of this machine is high. Hybrid seeds sowed in each hill are 1-2, the empty hill rate is less than 4%, and the reliability is more than 90%. Production efficiency reaches 360–500 plates h^{-1}. The service area for each seeder in each planting season is 150 ha. The seedling cost is 40% lower than that of seedlings raised in the field by human labor.

Transplanting and planting mechanization

Transplanting and planting of paddy rice are processes that need the greatest labor intensity. Mechanization not only improves the quality of planting and efficiency of labor, but can also finish transplanting and planting operations on time. The level of paddy rice transplanting and planting mechanization in China increased to 3.96% in 1998 from 1.98% in 1991. The typical transplanting and planting machinery included the conventional transplanter, high-speed transplanter, seedling-row-throwing machine, and seedling broadcasting machine.

Transplanter

The 2ZT rice transplanter is the conventional model used in China. Its engine is a 2.2-kW air-cooled diesel engine. The action device is composed of a single wheel and a floating board. A longitudinal reciprocal-type crank fork control device and split needle-type seedling claw are adopted for the separating-planting mechanism. Planting depth can be adjusted easily by a lifting and lowering rod. Productivity is 0.13-0.2 ha h^{-1}. The high-speed transplanter is the new paddy rice transplanter introduced in the past few years from Japan. Its unique rotary mechanism is adapted for high-speed separating and planting. It can insert 2 seedlings per hill in each rotation. Its working efficiency is 1.5 times that of the conventional model of rice transplanter. The unique transplant claw can transplant rice seedlings accurately and with good quality. The running wheels can move along the plow bottom, and can keep the transplanting position horizontal. Because of the even depth in transplanting, much more uniform growth took place in the initial stage, and the management of fertilizer is also relatively easy. By using the automatically adjusting float body, the mud-sprouting phenomenon is reduced and the field of rice seedlings is very neat.

Shallow plant machinery

The 2ZPY C-type seedling braodcasting machine throws the bowl-form seedlings evenly from a certain altitude to scatter the plants on the field surface. Three people are needed for this operation and productivity is 0.671 ha h^{-1}. This machine is suitable for hill-plate seedlings with various kinds of specifications. The empty hill rate is less than 10%. The hill number can be controlled according to farming system, variety, and location and can be adjusted by the operator. Normally, 480-600 plates ha^{-1} are recommended.

Seedling-placement machine. The paddy rice seedling-placement machine uses a blanket-formed rice seedling. It cuts the seedling blanket into small pieces and places these pieces on the soil surface. Compared with the shallow plant machine, the seedling-placement machine places the seedlings both shallow and in order. These small seedlings are 10-15 days old, have 2-2.5 flat leaves, their height is 10-16 cm, and the soil depth in the seedbed is around 20 mm. The machine has a single driving wheel and flat board to aid flotation. Working efficiency is as high as 0.2-0.34 ha h^{-1}. The working principle of the major working parts is similar to that of the rice transplanter. The main difference is that the seedling claw speeds up after taking the seedling to throw on the soil surface. The seedling claw itself does not enter the soil and can therefore reach high speed for transplanting.

Seedling row-throwing machine. The 2ZHP-530Z type self-propelled seedling row-throwing machine is a newly designed machine. Its major working principle is that the seedling operator takes a spouted seedling tray from the tray carrier and feeds it into the seedling roller. The seedling roller holds and pulls the tray forward. The seedlings are pulled out from the plate hills and put into the seedling conductor in order. The seedlings fall into the mud along the seedling conductor because of gravity. The empty seedling tray is sent back to the empty tray collector. Two operators are required during operation. Productivity reaches 0.29-0.33 ha h^{-1}. Vis-à-vis the transplanter, the comprehensive working cost drops 20-40%.

Seed-sowing machine

The Hujia J-2BD-type paddy rice seed-sowing machine is the leading machine of its kind in China. The machine is composed of a running mechanism and drilling mechanism. For the running mechanism, a single driving wheel and floating board are used. The sowing mechanism has a seed box, sheave and driving shaft, feed hopper, ground wheel, and pilot bar. The ground wheel and sowing roller are fixed on the same shaft and the sowing roller is turning while the ground wheel is turning and the machine is moving forward. The working efficiency is 0.53-0.67 ha h^{-1}. The delivery rate can be adjusted from 0 to 300 kg ha^{-1}.

The bowl-form seedling-throwing technology is a new one for paddy rice planting in China, for which promotion and application started in the 1990s. It has been proved by practice that this technology has two great advantages. The first is that significant innovation has been made in the method of paddy rice seedling raising, overtaking the conventional system. By seedling raising in plastic hill plates, the seedling in one hill can be kept separate from the other, with no intervention. This is useful for decreasing seedling disease spread. The root system of such a seedling is strong and the quality of seedling raising can obviously be improved. This new technology reduces seedling damage. Thus, seedlings can grow immediately after the throwing operation, without an obvious regreening period. Paddy rice can have a longer growth duration, which is very important in paddy rice regions with a shorter nonfrost period. In addition, bowl-form seedling raising can reduce the area of the seedling field and the ratio of seedling field area to rice field area may increase to 1:80 from the conventional 1:15. The new method can also save 30-40 kg of rice seed per hectare vis-à-vis the conventional one, and can save 270-280 kg of rice seed per hectare when compared with direct sowing. The second advantage is that the planting of paddy rice is done in the form of throwing seedlings. The seedling falls down into a muddy field, with planting at an appropriate depth, and avoiding too deep planting and damaging seedlings in the course of seedling transplanting. The application of the seedling-throwing technology can produce a greater yield increase, higher production efficiency, and lower labor intensity. This technology has been promoted and used in the whole country.

Harvesting mechanization

Rice harvesting is a key process in paddy rice production. Its mechanization is very important for a timely harvest under high yield. Starting in the 1990s, paddy rice combine harvesters have become popular in developed regions in South China such as Guangdong, Fujian, Zhejiang, Jiangsu, and Shanghai. The whole-feed and head-feed rice combines are now the two major types of rice combine used in the paddy rice area of South China.

The whole-feed rice combine in South China has been mostly developed by the Chinese themselves. It is simple in structure and easy to operate and has a higher working efficiency and lower cost than the head-feed combine. The main examples used in South China are the Zhujiang-1.5 and Huzhou-130, which are manufactured in Guangdong and Jiangsu, respectively. The axial threshing device is used in the two combine harvesters to reduce the size and simplify the structure of the machines. The main problem of these machines is that the performance will be poor when harvesting heavily lodged paddy rice, which often occurs in coastal typhoon areas. The working productivity is 0.2-0.33 ha h^{-1}. Investigation showed that most owners using this machine have received good repayment from it. In general, the Zhujiang-1.5 combine can harvest 27 ha on average in each harvesting season. Total income for one machine per year will be 48,000 yuan (RMB), among which the net income will be 30,000 yuan (RMB). Comparing with imported machines, a combine such as the Zhujiang-1.5 is a kind of machine that needs less investment and has a lower risk and higher return rate. Many farmers welcome it.

In comparison with the whole-feed harvesting technique, the head-feed harvest has three advantages. The first is that it reduces the load of threshing and cleaning and needs less engine power, because it is only the head rice that needs cutting and threshing. The second is that it can keep rice straw unbroken. The third is that it has better adaptability for heavily lodged paddy rice. The main head-feed rice combines used in South China are the Taihu TH-1450 and HL2010. The former is developed and made by the Wuxi combine factory in Jiangsu Province. It was improved in 1998 after the joint venture between Yanmar (Japan) and Jiangsu (China) and was renamed as the Renmin Hao Ce-1. Its nominal horsepower is 25.74 kW and its working productivity is 0.33 ha h^{-1}. Recently, the latest model of the Renmin Hao Ce-2 was developed with wider adaptability and its productivity is 0.4 ha h^{-1}. The HL2010 head-feed rice combine is developed by the Qianjin Agricultural Engineering Company Limited in Hangzhou, Zhejiang Province. It is imported from Japan and is now domestically produced. In South China, imported combines such as the Kubata Pro-601 from Japan usually have an excellent performance in cutting, threshing, and separating of grain, but are too expensive for most villages in China. The performance of the Chinese-made machines is basically the same as that of the imported ones and the price is often only half of that of the imported ones. But the reliability of operation is not as good as that of the imported machines yet.

The conventional combine has played an important role in the harvesting mechanization of paddy rice in South China. Harvesting practices for many years, however, have gradually shown that it is very difficult to adapt paddy rice harvesting in South China for the conventional combine. The whole-feed combine, with a larger and more complex cleaning mechanism, does not adapt well for high-yielding, damp, and fallen-down rice in South China. The head-feed combine made by Japan or Korea has good adaptability, but its complex structure and expensive cost become a large barrier for promotion in South China. In addition, it is also difficult to popularize the head-feed combine made in China in a shorter period because of its poorer reliability and higher operating cost. With this background, since the mid-1990s, research on a new harvesting technique for paddy rice in South China has become a hot topic in the field of agricultural mechanization. During this period, stripper harvesting technology has made great progress and stripper-combine harvesters have been put into batch production. The typical models of stripper combine are the Zhujiang- 130 stripper combine, 4LS-150 stripper combine, and 4ZTL-1800 air-suction stripper rice (wheat) combine.

The Zhujiang- 130 stripper combine was developed by the College of Engineering, South China Agricultural University, and Guangdong Agricultural Machinery Institute together. It took six years and produced five generations of prototypes. Each of them underwent research, design, trial manufacture, experimentation, and improvement. At the end of 2000, the Zhujiang-130 combine was checked and accepted by the Chinese Agricultural Ministry, and was regarded as reaching the advanced level in China. The research mainly involved work on the adaptability and feasibility of stripper harvesting technology for paddy rice in South China, research on the rethreshing-separating characteristics of stripped indica rice, research on the factors influencing stripper loss, and research on the cleaning characteristics of the stripped paddy mixture. This experimental research provided significant references for the structural design, parameter selection, and performance improvement of prototypes. The cutting width is 1.3 m and productivity is 0.134.33 ha h^{-1}. The overall loss rate is less than 3% and engine power is 29.2 kW. This machine has about 30% more power efficiency than the whole-feed combine. Compared with similar machines, the Zhujiang-130 is more suitable for harvesting indica rice in South China, it has better adaptability for damp rice, and it can also keep straw unbroken. The main problem to be solved is its higher impurity content.

The Jiangnan 4LS-150 stripper combine was developed by the Nanjing Agricultural Mechanization Institute of the Ministry of Agriculture and Nanjing Agricultural Machinery Designing Institute and is manufactured by the Zhenjiang thresher manufacturer in Jiangsu Province. Its cutting width is 1.5 m and working productivity is 0.4-0.53 ha h^{-1}. Its overall loss rate is less than 2.5% for rice and less than 1.5% for wheat. Its power is 19.8 kW. The combine is more suitable for harvesting japonica rice and wheat in the Changjiang valley. Its problem to be solved is the stability of the straw-cutting unit.

The 4ZTL-1800 air-suction stripper rice (wheat) combine was developed by the Northeast Agricultural University. To reduce stripper loss effectively and shorten the length of the stripper head, air-suction technology was adapted for conveying the stripped mixture. Therefore, the working mechanism of the air-suction stripper unit was examined in depth with the aid of high-speed photography, a test, and theoretical analysis. As a result, the influence of structural and working parameters on stripper threshing performance, the characteristics of the air-flow field within the stripper head during stripper threshing, and the law of motion for rice granules in the air-flow field were investigated. This research provided an important basis for the optimum design of the combine. Its working width is 1.8 m, with a lower loss rate, and its diesel engine power is 39 kW. The combine is suitable mainly for harvesting rice and wheat in northeastern China. However, because of its too long working width, too large volume and structural complexity, it is unsuitable for paddy rice in South China.

Compared with conventional harvesting technology, stripper harvesting is a technology of threshing before cutting, in which crop straw has no need to be put into the threshing unit, so that it is helpful in simplifying the structure of the equipment and in saving much power and improving working speed and efficiency. At the same time, stripper harvesting can also keep straw unbroken. Therefore, it has the advantages of both the whole-feed and head-feed combine, and is more appropriate for harvesting paddy rice in South China. Implementation of the ancient and advanced harvesting technology, however, needs corresponding equipment and has more requirements for the design and manufacture of equipment. Although the shatter loss of the stripper head has been controlled worldwide, there are still some local problems to be overcome, such as stability of the straw-cutting unit, the higher load of impurities caused by simplifying the cleaning unit, and the structural complexity involving the use of air-suction technology.

Drying mechanization

The paddy rice harvesting season lasts a long time in China. The weather, especially in South China, is frequently cloudy and rainy during the harvest season. In China, losses reach 2.5 million tons every year because the paddy rice cannot be dried in time and it becomes mildewed. The amount can be as high as 10 million tons in a disaster year. Paddy rice drying mechanization is an important process in paddy rice production. Research on and development of paddy rice drying machinery began only in recent years, but much progress has been attained and development accelerated. China now has more than 30 kinds of paddy rice drying machines. The small and medium drying machines are the major types in South China.

The fluid-bed dryer is a higher-temperature dryer with a simple structure and high drying rate. It is suitable for drying paddy rice with high moisture in the summer in South China. It has a high production efficiency and can be moved from one place to another. Normally, coal or oil is used as fuel. It has a temperature control system, an overheating protective device, and an overload protective system. If it is used with circulating tempering equipment, drying quality will be improved. The 5HLY-2.5 model dryer is one of the fluid-bed dryers. The hot-air temperature is 100-120 °C and production efficiency is 2.5 t h^{-1} .

The circulating-type dryer is a popular drying machine. The rice is heated and then tempered. The rice is not taken out from the dryer until the moisture content decreases to the safe range. Drying quality is high and energy consumption is low. There are two kinds of circulating-type dryers: the square shape and cylinder shape. The square circulating-type dryer uses a large airflow and thin grain layer. The rice is heated for a short time and tempered for a long time in the square circulating-type dryer. The hot air temperature is 55-65 ºC and the drying rate is about 1% h^{-1}. The fissure rate is less than 3%. The capacity of the square circulating type is from 1.5 to 6 t. There are two kinds of cylinder circulating-type dryers: innercirculating and outercirculating. The hot-air temperature is 45-50 ºC. The outercirculating dryer combines drying and storage together. The capacity is 6 to 100 t.

In recent years, the Chinese Government has adopted a subsidy policy to encourage farmers to purchase rice-drying machines. The provincial government, local government (county, town), and farmers each provide one-third of the cost. The subsidy policy raises farmers' enthusiasm markedly for buying the dryer and promotes paddy rice drying mechanization. Research on rice-drying theory and technology has also made significant progress in the past 10 years, such as two-stage drying, deep-bed drying, thin-layer drying, tempering, and managing rice with a high moisture content. These research achievements provide an important theoretical basis for optimizing rice-drying processing and developing new rice-drying machines.

Conclusions

This paper has summed up the advances and innovations in some key technologies and equipment that occurred in paddy rice production mechanization in South China after reform. Of these new technologies and equipment, some are the result of technological innovation, such as the paddy rice bowl-form seedling-throwing technology. Some result from innovation in the methods putting technology into effect, such as the air-suction conveying technology (method) and refreshing and separating technology used in stripper-harvesting technology. It is precisely these similar technologies or methods that have gradually improved stripper-harvesting technology and finally made this ancient technology serve in modem harvesting practices. Some of these technologies belong to theoretical advances, for instance, research on the mechanism of air-suction conveying in stripper harvesting and the two-stage falling-rate drying theory and thin-layer drying theory in rice drying. Some of them are more reasonable and suitable in the selection or importing of technology and equipment, for example, the selection and application of circulating-type dryers suitable to South China.

With the efforts in the past 20 years, paddy rice production mechanization in South China has made significant progress and shown great potential for development. On the one hand, there is a long distance between the level of rice mechanization in China and that of the more advanced world. On the other hand, there is the obvious distance between the south and north in China. These distances mean not only difficulty and challenge but also developing potential and opportunity. What's more, the rapid and strong development of high-technology and new-technology industries in the 21st century will bring unprecedented opportunities and very good conditions for innovations in the technology of paddy rice production mechanization. Therefore, we believe that more innovations and faster advances in paddy rice production mechanization technology must come into being in South China through actual economic advantages and capacity building for postharvest management.

Bibliography

Bureau of Chinese Statistics. 2000. Statistical yearbook of China. Beijing (China): Chinese Statistical Press.

Cao Chongwen. 2001. Rice drying and development of rice dryers in China. Trans. CSAE 17(1):5-9:

Cui Shi'an. 2000. Agricultural structure readjustment and agricultural engineering technology. Trans. CSAE. 16(1):1-4.

Editorial Committee of Agricultural Yearbook of China. 2001. Agricultural yearbook of China. Beijing (China): Chinese Agricultural Press.

Gao Huanwen, Hongwen Li, et al. 2000. Prospects of China agricultural mechanization facing 21st century. Trans. CSAE 16(2):9-12.

Jiang Yiyuan. 1999. Farm mechanization in China. Proceedings of International Conference on Agricultural Engineering, Beijing. p 44-49.

Li Changyou. 1999. An analytical solution of the granular product in deep-bed falling rate drying process. Drying Technol. 17(9): 1961-1969.

Luo Xiwen, Ou Yinggang, et al. 2001. Development and contribution of agricultural engineering in South China. Proceedings of 2001 ASAE annual international meeting, California, USA, 30 July-1 August 2001.

Niu Dun. 2000. New situation of agricultural mechanization and the development of paddy production mechanization in China. Trans. CSAE 16(4):7-10.

Xie Xiuxian. 1997. New technologies of the bowl form seedling raising and throwing of paddy rice. Beijing (China): Chinese Agricultural Press.

Yuan Zhaohe, Yang Xinchun. 2000. Development and prospect of paddy rice planting mechanization in China. Proceedings of international symposium on the mechanization of paddy rice production in China. Beijing (China): Chinese Agricultural Press. p 60-65.

Zeng Dechao. 2001. On the agenda of agricultural engineering in China in the 21st century. Trans. Chinese Soc. Agric. Eng. (CSAE) l7(1):1-4.

Zhao Huahai, Zhou Xuecheng, et al. 1995. Experimental research on rethreshing-separating mechanism for stripper harvesting. Trans. CSAE 11(4):73-78.

Zhou Xuecheng, Zhao Huahai, Qiao Ximing. 1998. Research on the threshing and separating characteristics of an axial-flow thresher for stripped paddy rice. Mach. Agric. Food Process. 255(3):4-6.

Notes

Authors' address: South China Agricultural University, Guangzhou, China, 510642.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Developing agricultural mechanization technology in paddy fields in Korea

Lee Dong-Hyeon

Before the 1960s, manual and animal power were used for rice farming operations. In the 1970s and '80s, migration from the rural community to urban centers caused a serious farm labor shortage that in turn led to very high rural wages. These changes required full-scale propagation of the rice transplanter, binder, and combine harvester to relieve seasonal labor shortages in spring and fall. In the 1970s, the power tiller and its attachments were introduced. Propagation of the transplanter and combine harvester started in the latter part of the 1970s. In the '80s, because of the extended dissemination of transplanters and harvesters, about 30% of rice production operations had become mechanized. In the 1990s, almost total mechanization was accomplished in rice cultivation. To implement the agricultural mechanization schemes in the 1960s, the National Agricultural Cooperative Federation (NACF) and the Korean Agricultural Machinery Industry Cooperative were established. These two organizations took a leading role in the nationwide distribution of agricultural machinery, with government subsidies. In the early 1980s, the government established a cooperative use system for farm machinery. The Integrated Farm Mechanization Complex (IFMC) was established in each province. In the late '80s, the government began to supply tax-exempt oils for agricultural use. From 1989 onward, materials such as fertilizers, agricultural machinery, and agricultural chemicals were exempted from value-added tax. For the mechanization of rice postharvest production, 324 units of the RPC (Rice Processing Complex) and 367 units of large-scale rice processing centers were built and operated. In 1962, the Institute of Agricultural Engineering and Utilization was established under the Rural Development Administration (RDA). In the late 1970s, the National Agricultural Mechanization Research Institute was established to conduct overall research on the development and improvement of agricultural machinery, mechanization of postharvest activities, and use of machinery. Through mechanized rice direct-seeding technology and efficient use of the high-performance harvester, labor inputs should decrease from 297 h ha^{-1} in 2001 to 180 h ha^{-1} in 2010. Rice production policy has been directed to produce high-quality rice at a low cost. It is suggested that the production of high-quality rice be increased from 50% in 2002 to 80% in 2005. The application of artificial fertilizer and chemical pesticides will decrease by 30% in 2004. Some biological farming technologies such as the use of natural enemies will also be promoted. Research on labor-saving mechanization has developed a partial plowing/transplanting system to plow while transplanting, fertilizing, and applying herbicide simultaneously to prevent soil movement and loss as well as protect bio-groups in the soil. The technologies of paper mulching, simultaneously done with sowing and direct seeding and a small-size pilotless helicopter for pest control, were developed to prevent weed growth and environmental contamination with herbicides. To overcome competition with other countries, highly labor-intensive farm operations will be changed to automatic operations and will use robots in the future. A study on improving rice quality by improving milling machinery and decreasing the amount of broken rice was conducted. A study has developed a far-infrared and hot-air combine dryer to improve rice taste and decrease by 20% the energy cost and drying time of the existing hot-air dryer. An automated measurement system for rice quality has been developed to quantify rice quality factors and establish objective standards of quality evaluation. For environ ment-friendly agriculture, precise farming mechanization is needed to keep the same amount of harvest and high-quality safe product. Current technologies of automation and remote control of agricultural machinery can be used economically. Research to develop autonomous robots with artificial intelligence should be completed by 2010.

Korea is a peninsula located in the monsoon area, with four distinct seasons, that is known for producing good-quality agricultural products. Its land area is 9.9 million hectares, of which about 65% is mountainous and 20% is cultivation area (Table 1). Of the 20% cultivation area (1.9 million hectares), 61% is rice fields and the rest is upland. Of the total population of 47 million, 8.5% is rural, with one farm household consisting of 2.9 persons. Rice is the major crop in Korea and it occupies 57% of farm holdings among 1.4 million farms. Rice field size per farm is relatively small, 0.83 ha, and most production operations were done manually until the 1960s. After that era, the government began agricultural mechanization programs along with massive planting in the mountainous areas and restructuring lands to increase crop production. The mechanization program in the first stage focused on preventing natural disasters, and machinery dissemination started.

In the 1970s and '80s, the era of large economic growth, by 8.5% per year, led to population migration from the rural community to urban industries, which caused a serious labor shortage in agricultural production, which, in turn, led to large rural wage increases. To solve these problems, of natural disasters and the labor shortage in the rural community, the Korean government began the agricultural mechanization program that centered on small farmholders from the 1970s to the end of the 1990s. With this mechanization project, every farm now owns more than 2.5 power machines that contribute to timely operations and rice yield increasing enough to not

Table 1. Statistics on agricultural status.

Item	1970		1980		1990		2000	
					(000)			
Land (ha)								
Total area	9,848	(100)	9,899	(100)	9,927	(100)	9,946	(100)
Mountainous	6,611	(67.1)	6,568	(66.4)	6,476	(65.2)	6,422	(64.6)
Farm land (A)	2,298	(23.3)	2,196	(22.2)	2,109	(21.2)	1,889	(19.1)
Paddy (B)	1,273	(100)	1,307	(102.7)	1,345	(105.7)	1,149	(90.2)
Upland (C)	1,025		889		764		740	
B/A (%)	55.4		59.5		63.8		60.8	
C/A (%)	44.6		40.5		36.2		39.2	
Land per holder								
Cultivated land	92.5	(100)	101.8	(110.1)	119.4	(129.1)	136.5	(147.6)
Paddy	51.3	(100)	60.6	(118.1)	76.1	(148.3)	83.0	(161.8)
Land per capita	7.31	(100)	5.76	(78.8)	4.92	(67.3)	3.99	(54.6)
Population (thousand)								
Total (D)	32,241	(100)	38,124	(118.2)	42,869	(133.0)	47,275	(146.6)
Farm population (E)	14,432	(100)	10,827	(75.0)	6,661	(46.2)	4,032	(27.9)
E/D (%)	44.8		28.4		15.5		8.5	
Number of farm holders (thousand)	2,488	(100)	2,155	(86.6)	1,767	(71.0)	1,384	(55.6)

import rice from abroad. Now, 98% of rice production operations are performed by various machinery that enables farmers to maintain a good-quality life and liberates them from painful work, thus giving farmers an opportunity to earn extra income from nonagricultural work. In recent years, Korean agriculture has encountered hardships because it has to compete with other countries, especially in the international rice market. The rice production cost in Korea is much higher than in other major rice-producing countries. The Korean rice production cost is US$448 per ha, 2.8-fold more than in the U.S. and 7.5-fold more than in China, and the rice price on the market is five times more than that of the U.S. and China. The reason for this higher price is the excess land price and labor wages.

The Korean government introduced the direct-payment system to reduce excess rice production. This system pays some compensation to farmers who give up rice production. Rice production still occupies a large place in agriculture, turning out 33% of total agricultural production, and a crucial position in food security and public benefit functions.

Development stages of agricultural mechanization

Manufacturing and dissemination of agricultural machinery

Before the 1960s, manual and animal power had conducted farm operations. The means for tillage and land preparation were the iron hoe, animal plow, and puddler. The hand hoe was used for weeding, the "yongdurae" for water pumping, and the sickle and manual thresher for harvesting. With the successful accomplishment of five-year economic development plans in the 1960s, farm labor was siphoned out to other industries that inevitably highlighted the importance of agricultural mechanization in Korea. Because of the labor situation in the rural community and to increase yields, the government had begun a subsidy program for purchasing agricultural machinery, especially for disaster prevention measures, such as the power tiller, water pump, and pest control machine. The power tiller gradually replaced animal power. The farm population peaked in 1967 and then continuously decreased, whereas wages increased 1.8 times in five years after 1965. These changes sped up farm mechanization in Korea and promoted dissemination of the power tiller, pest control machine, and thresher. In 1963, the homemade power tiller gained prominence.

In the 1970s, with much progress made in industrialization and urbanization and greater wage increases for hired labor, the atmosphere for farm mechanization matured faster than ever. These changes in agriculture required full-scale development of the rice transplanter, binder, and combine harvester to offset seasonal labor shortages encountered in the spring and fall. In the 1970s, the power tiller and its attachments began to be disseminated. Diffusion of the transplanter and combine harvester started in the late 1970s; thus, total mechanization was foreseeable. In the 1980s, because of the extended dissemination of the transplanter and harvester, the mechanization rate in rice production increased a lot. About 30% of rice production operations were mechanized at this time. Mechanization was extended to transplanting and harvest operations from tillage, pest control, and water pumping. During this period,

Table 2. Supply ratio of major agricultural machinery. Unit = %.

Machine	1960[a]	1970	1980	1990	2001
Power tiller	–	0.5	13.4	42.5	66.7
Farm tractor	–	0.1	0.1	2.3	14.5
Rice transplanter	–	–	0.5	7.8	24.8
Water pump	0.3	2.2	9.0	19.3	23.5
Power sprayer	1.2 (1.2)	18.8 (17.0)	54.2 (38.9)	39.0	44.3
Binder	–	–	0.6	3.1	5.1
Thresher	8.1 (7.9)	17.8 (6.2)	21.6 (11.4)	15.1	3.9
Combine harvester	–	–	0.1	2.5	6.3
Dryer	–	–	0.1	0.7	4.2
Sum	9.6	39.4	99.6	132.3	193.3

[a] Numbers in parentheses indicate supply ratio of human-powered agricultural machinery.

the combine harvester replaced the power thresher. One hundred thousand units of power tiller were produced in 1985 as well as in 1986, the largest number ever. However, then demand decreased. Some of the demand for power tillers shifted to tractors. In the late 1980s, the mechanization rate in transplanting and harvesting exceeded 50%.

Entering the 1990s, opening domestic commodity markets was unavoidable with the Uruguay round negotiations. So, to improve the competitive power of domestically produced agricultural products, farm-restructuring programs emphasized the development of agricultural machinery and equipment. In particular, small farm machinery, including the power tiller, was sold at half price from 1993 to 1997. Late in the 1990s, almost total mechanization was accomplished in rice cultivation, exceeding 90% of the mechanization rate defined by mechanized cultivation area. To promote rice production mechanization, machinery became larger and could be ridden on. For instance, the two- or four-row walking transplanter was replaced by the six-row riding transplanter; the two- or three-row combine was replaced by the four-row combine, for which traveling speed doubled from 0.6 to 1.2 m s^{-1}. Total mechanization for rice cultivation was promoted (Table 2).

Supporting policies for agricultural mechanization

In the 1960s, to conduct agricultural mechanization schemes, the National Agricultural Cooperative Federation (NACF) and Korean Agricultural Machinery Industry Cooperative were established. These two organizations played a leading role in distributing agricultural machinery nationwide with government subsidies. The major machines distributed were the pump, power tiller, manual or power sprayer, and power thresher. In the first half of the 1970s, the government provided a long-term loan with a low interest rate to both manufacturers and consumers of agricultural machines to accelerate the supply and demand of agricultural machines and to promote farm mechanization (Table 3). In the mid-1970s, the migration of the rural population resulting from urbanization and industrialization became much more serious, which brought about the increased need for farm mechanization, especially in the peak labor-de

Table 3. Loans for agricultural mechanization projects. Unit = US$ million.

Before 1980	1981-85	1986-90	1991-95	1996-2000	Sum
526.9	875.0	1,728.4	2,897.3	2,780.4	8,808.0

manding seasons, spring and fall. To promote the mechanization of rice transplanting and harvesting, the government began to promote the use of the rice transplanter, binder, and combine. These efforts begun by the government in the 1970s contributed greatly to securing food crop production to reach self-sufficiency by solving rural labor shortages.

In the early 1980s, the government established a cooperative use system for farm machinery. The results of this government incentive were the Integrated Farm Mechanization Complex (IFMC) that was established in each province and operated by either the Farmland Improvement Association or the agricultural cooperative. To lessen the economic burden of using agricultural machinery, the government revised the Tax Reduction Regulation Law and began to supply tax-exempt oils for agricultural use in 1986. And, starting in 1989, the value-added tax exempted all agricultural production-related materials such as fertilizer, agricultural machinery, of course, and agricultural chemicals too, which surely helped to mechanize the rice production system.

In the first half of the 1990s, government policies focused on the large-scale integrated rice-farming production system and mechanized postharvest production system. For the large-scale rice-farming system, the agricultural corporation was established, which should possess a 50-ha or larger rice field. In 2000, the number of agricultural corporations reached 1,667 units and more will be set up. Along with the agricultural corporations, an agricultural machinery bank was operated by local agricultural cooperatives that lend agricultural machinery to farmers and receive some fees. It was established in 1992.

Mechanized farm holders who grow rice only and own at least 5 ha of rice fields reached 77,000 in 2000. For the mechanization of rice postharvest production, 324 units of RPC (Rice Processing Complex) were built from 1991 to 2000 and 367 units of large-scale rice processing centers were built from 1995 to 2000 and began operating. In 1994, 44,949 mechanized farming groups were organized for rice production. As agricultural machinery inspection regulations were changed from compulsory to optional, some agricultural machinery was required to have attached safety gears. Some 3,300 after-sales service centers for machine repair work were established throughout the country. Some 130 machine parts were standardized and supplied. The law introduced military service exemptions for repairmen engaged in after-service of agricultural machinery. New technology that employed agricultural machines and their manufacture and development received financial support from the government. The RDA (Rural Development Administration) has been training repairmen for agricultural machinery promotion (Table 4). Policies on mechanization were developed to expand the joint-use system of large agricultural machinery and postharvest

Table 4. Training in agricultural machinery. Unit = one thousand persons.

Item	Before 1980	1981-85	1986-90	1991-95	1996-2000	Total
Skilled workers	26.2	20.3	18.2	22.1	17.3	104.1
Women	51.0	53.4	79.2	25.4	24.8	233.8
Farmers	501.4	725.5	428.7	360.2	964.4	2,980.2
Total	578.6	799.2	526.1	407.7	1,006.5	3,318.1

rice production facilities to reduce rice production costs and produce good-quality rice.

Research on agricultural mechanization

In 1962, the Institute of Agricultural Engineering and Utilization, which specialized in agricultural mechanization and machine inspection, was established in the RDA. Since then, systematic research on agricultural mechanization has continued. During the early 1960s, the animal-powered deep plow, standing hand hoe, human-powered sprayer, and levered atomizers were developed and widely supplied to farms. From the late 1960s to mid-’70s, adaptation tests for rice transplanters and harvesters were carried out (Table 5). In the 1970s, supply standards for the 4-row transplanters, 2-row binders, and how combines were prepared. Also, rice huskers, rice hullers, and rice millers were developed for variety Tongil. Those machines contributed to increased rice quality and reduced processing losses.

In 1970, with the establishment of the National Agricultural Mechanization Research Institute, research on the development and improvement of agricultural machinery, mechanization of postharvesting, and use of machinery was conducted. Also, lime scatterers, nursery media preparers, nursery tray seeders, and tray washers were developed and supplied. Planting devices for young seedlings, fertilizer applicators for the riding transplanter, and herbicide applicators, levee weed mowers, and blade mowers were developed. Blades for the plow and rotary tiller were improved as an energy-saver. Durability of the cutting blades for the binder and combine was increased.

For mechanized farming technology, research on the tractor-cultivating method, combine operational technology, optimal operational ratio of the threshing machine, and rice-drying technology was conducted and disseminated through the rural extension service. For agricultural machinery use, research on software development for optimal usage of machines, establishment of a used farm machinery warehouse, machine durability periods, tax-exempt fuel supply standards, agricultural machinery service equipment, and standards of repair-parts requirements was conducted and used for policy making. Investigative reports on agricultural machinery-related accidents were used for operations to overcome injury and for general aspects of agricultural cooperatives. Also, the reports provided guidelines for designing farm roads, intersections, and field entrances.

Table 5. Development of machines related to transplanting.

Machine	Task	Efficiency
Lime spreader	Lime and silicate spreading	1.5 h ha^{-1}
Nursery machine		
Soil processing	Soil preparing	30 m^3 h^{-1}
Tray seeder	Rice seed sowing	396 boxes h^{-1}
Tray washer	Tray washing	618 boxes h^{-1}
Transplanting machine		
Seedling planter	Modifying for young seedlings	250 boxes ha^{-1}
Fertilizer applicator	Fertilizing	1.0 h ha^{-1}
Herbicide applicator	Herbicide applying	–
Weed mower	Dike weed mowing	235 m^2 h^{-1}
Vertical reaper	Rice plant mowing and spreading	5.8 h ha^{-1}

In the 1990s, to reduce production costs, research on machines for rice direct sowing, high-performance machines for large-scale farming, and the Rice Processing Complex (RPC) was carried out (Table 6). For direct sowing, the ride-on rice transplanter attached to the 6-row puddled-soil drill seeder, 8- and 12-row soil drill seeder on the dry field, partial-width tillage direct seeder, tractor-attachable direct seeder and fertilizer applicator, and herbicide applicator were developed. For high-performance machinery, the tractor harrower and leveler, seedling planter, medium seedling transplanter, young seedling transplanter, paddy- and dry-field direct sower, and optimum machine selections for a given farm size were developed. For the RPC, the continuous grain dryer, dry rice-polishing machine, and automatic milled-rice recovery ratio evaluator were developed. With a purely domestic technique, our own tractor models were designed and manufactured. According to the use of more than 90-hp tractors, the ultra-low-speed speed changer, and magnifying hydraulic outlet port, increasing machine power has been used in various tasks according to their characteristics. For tractor-attached equipment, a variety of sizes of ridge plows and chisel plows was developed. The grain-processing unit of the combine was changed from a bag type to whole type. Also, a lifter for the lodged rice plant, a frame-level controller for preventing combine rolling, and a spin turn unit for a minimum turning curve under sharp turning were developed. Grain dryers equipped with a drying time and moisture-setting unit, a quick discharger, a grain dispersion system, a fire extinguisher, a drum-type feeder, and moisture content measurement system were developed. Also, a room-temperature ventilation-type dryer, which circulates the upper and lower part of grains with an agitator, was developed.

Table 6. Development of machines related to direct sowing.

Machine	Task	Efficiency
Paddy-field leveler	Harrowing and leveling	2.7 h ha^{-1}
Seeder		
Awn remover	Awn removal and sorting	180 kg h^{-1}
Dry-field direct-sow drill seeder	Rice seed sowing on dry field	5.5 h ha^{-1}
Paddy-field direct-sow drill seeder	Rice seed direct sowing on paddy field	3.0 h ha^{-1}
Partial-width tillage direct seeder	Cultivating, sowing, and fertilizer application	3.8 h ha^{-1}
Dry-field direct-sow herbicide applicator	Herbicide spreading on dry field	1.3 h ha^{-1}
Postharvest processing		
Storage dryer	Drying and storage	Dry storing cost, 28% decrease Drying cost, 25% decrease
Continuous grain dryer		Drying rate, 25% h^{-1}
Automatic milled-rice recovery ratio evaluator	Testing the hulling rate of brown rice and whitening rice	–
Dry rice polisher	Remove bran	Polishing rate, 0.7% increase

Table 7. Yearly labor hours for rice farming.

Item	1967	1970	1980	1990	2000
Labor hours (h ha^{-1})	1,367	1,284	928	594	297

Impact on the progress of agricultural mechanization and reconsideration

Impact

Reduced labor input hours for rice farming. During the last three decades, Korea has been developing and improving agricultural machinery technology for rice farming and the technology has been effectively transferred to farmers. Though the rural farming population has decreased continuously during the last three decades, the continuing effort to develop agricultural mechanization technology attempts to improve timeliness in farming. Nevertheless, the labor input per hectare has gradually declined from 1,367 h ha^{-1} in 1967 to 297 h ha^{-1} in 2000 (Table 7); therefore, farm labor has declined by 6.2% per year on average.

Table 8. Yearly labor hours and income per farm household for rice farming. [a]

Items	1970	1980	1990	1999
Labor input (h y^{-1})				
Farming (A)	1,810	1,654	1,535	1,249
Rice production (B)	760	596	475	260
B/A (%)	42.0	36.1	30.9	20.8
Farm income (1,000 won y^{-1})				
Farm income	256	2,693	11,026	20,147
Agricultural income	194	1,755	6,264	9,536
Nonagricultural income	62	938	4,762	10,611

[a] Farm income in 1995: 21.803; agricultural income: 10,469; nonagricultural Income: 11,334 thousand won.

Table 9. Yearly usage area for rice farming machinery (in ha).

Machine	1990			1995			2000		
	Own[a]	Hire	Total	Own	Hire	Total	Own	Hire	Total
Power tiller	2.4	0.9	3.3	1.3	0.3	1.6	0.9	0.1	1.0
Tractor	4.8	14.8	19.6	5.2	11.4	16.6	5.9	7.1	13.0
Rice transplanter	1.6	2.8	4.4	1.5	2.0	3.5	1.5	1.1	2.6
Combine harvester	2.0	9.3	11.3	2.0	7.7	9.7	2.5	6.6	9.1

[a] Own = own farm use, Hire = custom hiring service.

Decrease in labor intensity for farming and income production from outside the agricultural sector. Agricultural mechanization benefited farm households by reducing the annual labor input hours for rice farming per farm household from 760 h in 1970 to 260 h in 1999 (Table 8). In the same time, annual farm labor input hours for total farming activities also declined from 1,810 to 1,249 h during the same period; thus, rice farming labor declined by 65.8% and the total farming labor declined by 31% during the period. The reduced farming labor was allocated instead to work outside the agricultural sector for better income production. Therefore, the reduced farming labor brought about by agricultural mechanization was devoted to increasing farm household nonagricultural income from 24.2% in 1970 to 52.7% in 1999. Nonagricultural income increased by 28.5% during the last three decades.

Establishment of an effective use system of agricultural machinery for small-scale farming. The agricultural mechanization policy and strategy focused on supporting the collaborative use system for agricultural machinery, and it resulted in a larger farm operation area than the break-even point of agricultural machinery. Though the operation area of agricultural machinery has declined according to the increase in number of agricultural machinery in use (Table 9), the operation area of custom-hiring services is high 54.6% for the tractor, 42.3% for the rice transplanter, and 72.5% for the combine harvester in 2000.

Table 10. Comparison of labor hours for rice farming between Korea and Japan (unit: h ha^{-1}).

Country	1980	1985	1990	1995	1999
Korea	9.28	8.55	5.94	3.47	3.10
Japan	6.44	5.51	4.38	3.91	3.51

Table 11. Number of supplied machines according to size.

Machine	1990	1995	2001
Tractor			
Less than 40 HP	12,230	4,349	8,093
40-60 HP	2,114	9,770	6,133
More than 60 HP	470	1,355	1.970
Total	14.814	15,474	16,196
Rice transplanter			
Working-type	34,716	28,293	10,426
Riding-type	2,282	1,935	5,857
Total	36,998	30,228	16,283
Combine harvester			
2-3 rows	13,662	3,284	1,247
More than 4 rows	1,452	3,215	5,246
Total	15,114	6,499	6,493
Dryer			
Less than 4 t	2,865	2,919	1,437
More than 4 t	329	2,481	2,549
Total	3,194	5,400	3,986

The ownership level of agricultural machinery by Korean farmers is still lower than that of Japanese farmers. However, as a measuring stick for agricultural mechanization level, the labor input hours in rice farming were 311 h ha^{-1} in Korea and 351 h ha^{-1} in Japan in 1999 (Table 10).

Reconsideration

The mechanization policy has focused on developing small-scale farming machinery (Table 11); therefore, the policy has been to distribute small-size agricultural machinery (91% of total fund invested). Accordingly, the policy has delayed the low-cost production system more than that of large-scale farming with large-size agricultural machinery.

The mechanization rate of major farm operations for rice farming such as land preparation, transplanting, harvesting, and pest control in Korea has been from 98.1 % to 99.9%, and these operations have been almost completely mechanized (Table 12); however, the mechanization rate of grain drying is 48% (94% in Japan). So, the delay of mechanization in drying operations is a major constraint to the production of high-quality rice.

Table 12. Mechanization ratios of rice-farming tasks. Unit = %.

Land preparation			Transplanting			Harvesting			Drying	Pest control		
Sb[a]	Wo	Ri	Sb	Wo	Ri	Sb	Wo	Ri		Sb	Wo	Ri
99.9	18.0	81.9	98.1	73.2	24.9	99.2	4.1	95.1	48.0	99.6	94.8	4.8

[a] Sb = subtotal, Wo = working-type, Ri = riding-type.

Table 13. Changes in farm population and farm households (in thousands).

Items	2001	2005	2010
Population			
Total population (A)	47,343	50,800	51,600
Farm population (B)	3,933	3,300	2,580
B/A (%)	8.3	6.5	5.0
Farmers more than 60 years old (C)	1,423	1,530	1,730
C/B (%)	36.2	46.4	67.1
Farm households			
Total farm households (D)	1,354	1,145	957
Owner-farmers more than 60 years old (E)	750	649	567
E/D (%)	55.4	56.7	59.2

Prospects for developing agricultural mechanization technology and rice production

Prospects for socioeconomic conditions

Continuous reduction in farm labor force and change in farmers' age. It is predicted that the percentage of the total farm population in the national population will decrease from 8.3% in 2001 to 5% in 2010 (Table 13). Farm households will also decline from 1,354,000 in 2001 to 960,000 in 2010, whereas people more than 60 years old will increase from 36.2% in 2001 to 66.9% in 2010. It is expected that manager-farmers more than 60 years old in farm households will also increase from 55.4% (women 11.8%) in 2001 to 59.2% in 2010.

Development of agricultural technology and increase in the importance of natural resource value. Agricultural technology is changing from traditional industry to bio-industry, which is combined with high-tech, capital-based information technology, which has organized and systematized the production, processing, and marketing sector. Accordingly, young and middle-aged people from the industrial sector will probably be going back to rural areas in the near future.

Traditional agriculture will be developed toward environment-friendly agriculture, for the preservation of the rural environment, control of climate, and provision of ecological space. Eventually, agriculture will serve cultural heritage and provide

Table 14. Farming size of farm households. Unit = 1,000 households.

Year	Total	Less than 1 ha	1-2 ha	2-3 ha	More than 3 ha
1980	1,849	1,525	280	34	10
1990	1,508	1,121	316	53	18
1995	1,205	874	241	56	34
2001	1,054	775	193	46	40

sightseeing, education, and fresh space for the general public. Therefore, visitors from urban areas will also increase farm households' nonagricultural income through "green tourism" every weekend.

Prospects for developing rice farming

Control of rice production. The effects of the good rice harvest during the last six years reduced rice consumption of Koreans and imports of rice from overseas by the MMA (Minimum Market Assessment) regulation of the WTO, so it is expected that the surplus stock of rice at the end of 2002 will reach as much as 1.38 million t, which is twice the quantity of the standard rice stock in the country. To avoid a surplus rice stock, the rice is being used massively in the processing industry and donations of rice are made overseas while the cultivation of substitute crops in rice fields helps to reduce rice cultivation from 1,083,000 ha in 2001 to 953,000 ha in 2005. To reduce the labor input hours of rice production through mechanized direct-seeding technology, the labor input will be reduced by 80-90% in h ha^{-1} and the use of the high-performance harvester can also be reduced by 30 h ha^{-1}. So, it is expected that the labor input will decline from 297 h ha^{-1} in 2001 to 180 h ha^{-1} in 2010.

Though the total economic value of rice produced in the gross domestic product will be comparatively reduced and cultivation area and rice consumption will also decrease, the added value of rice production will be enhanced. In view of the management scale of rice production, the number of small-scale farmers will decrease while large-scale farmers will extend the production of special-brand rice for marketing.

Production of low-cost high-quality rice. The rice production policy has been directed toward producing low-cost high-quality rice. The government envisages reducing the labor input by 67% in nursery rice growing and rice transplanting operations, and it can reduce the labor input by 27% for total rice farm operations. The rice direct-seeding system, which can reduce the direct production cost of rice by 13.1 %, is being suggested to extend cultivation area. In contrast, Korea is rehabilitating the rice production structure to extend rice farm size (Table 14). Larger than 3-ha rice farms with full-time farmers will occupy more than 70% of national rice production in 2011.

In parallel with the above policy, it is suggested that the production of high-quality rice can be extended from 50% in 2002 to 80% in 2005 while a rice-processing facility for wholesome grains can be established in the RPC for the low-temperature and low-pressure processing of rice.

Realization of environment-friendly farming. The rice production policy has been formulated to reduce the application of artificial fertilizer and chemical pesticide on agricultural land by 30% in 2004, and applications of fertilizer and chemicals on agricultural land should decrease by 40% and 50%, respectively, in 2010.

To carry out natural farming activities on rice farms, the government has adopted the direct payment system for applying minimum fertilizer and chemicals. At the same time, some biological protective-farming technology such as the use of natural enemies will also be promoted.

Prospects for developing agricultural mechanization technology

Supply of general agricultural machinery. The prospects for farmer ownership of major agricultural machinery in 2010 were estimated. The power tiller will decrease from 66.7% to 56%; the tractor will increase from 14.5% to 25%, but the size will change to a larger size (30-70 HP); the combine harvester will increase from 6.3% to 12.7%; and the rice transplanter will increase from 24.8% to 35%, but the ride-on type will represent around 50%.

In addition, 360 plants will construct an RPC in 2004 and the Drying and Storing Center (DSC) will extend its plants by 1,117 in 2004. The RPC and DSC plants will be equipped for drying around 40% of the total marketing volume of rice (29% of the nationwide total of rice).

Development of new farm operations and agricultural machinery technology. Agricultural mechanization in the future will be improved and agricultural machinery with a low cost, high efficiency, precision, multipurpose, and easy operation will be developed. In this context, it is proposed that agricultural mechanization be developed with high productivity, better comfort, reinforced safety, and environmental friendliness by a human-computer-machinery combined automatic system.

To overcome competition with other countries that produce low-cost large-scale mechanized farming machinery, this machinery will adopt high-tech electronic and machinery engineering and reduce high labor.

This high-tech machinery and technology such as the global positioning system/geographic information system (GPS/GIS) will be used to monitor crop growth and yield in the field. This system can fertilize and apply agricultural chemicals according to the plant's nutrient requirement in different areas of a field. Accordingly, environment-friendly precision agricultural machinery technology, which can manage minimum inputs and maximize yield of high-quality products, will be developed for farming on small-size agricultural land and the technology will be widely used by 2020.

Developing new agricultural mechanization technology

Technology under development

The 21st-century mechanization of rice production has been designed to reduce the labor burden of rice production, resulting in a decrease in production costs as well as the production of high-quality rice. Research on labor-saving mechanization has developed a partial plowing/transplanting system to plow while transplanting, fertilizing, and applying herbicide simultaneously to prevent soil movement and loss. The area of surface broadcast sowing, which farmers prefer to be 56.6% of the total flooded paddy field, has its operation mostly depending on hysteresis. However, sowing uniformity was not good and pregerminated seeds were also damaged because of the use of a granular pipe attached to a mist and dust blower for the broadcast sowing. Consequently, a flooded broadcast seeder that sprayed the rice 10 m has been developed to precisely and safely solve these problems.

A study has investigated the hole size, shape, and porosity of the nursery chamber to promote the growth and development of rice and help older people and women to easily separate the nursery chamber from the soil. The technologies of paper mulching simultaneously done with sowing and direct seeding and a small-size pilotless helicopter for pest control were developed to prevent weed growing and ecological destruction and environmental contamination from chemical herbicides. To develop mechanization for environmental agriculture, the goal is to apply agricultural materials uniformly to the paddy field in spite of the different requirements of each area. Accordingly, an algorithm has been developed to automatically measure the soil characteristics of the paddy field and space variation of rice growth in real time. Using the measured data, a solution can be found for each case.

The study on improvement of rice quality led to improved milling machinery, which decreased the amount of broken rice. A technology of nonwashable rice processing was also developed to remove rice bran to help cook rice without washing. These new technologies helped develop a head-rice processing system, resulting in a 30% improvement in its value added. Another study has developed a far-infrared and hot-air combined dryer to improve rice taste as well as reduce the energy cost and drying time of the existing hot-air dryer by 20%. Moreover, an automated measurement system for rice quality has been developed to quantify rice quality factors and establish objective standards of quality evaluation. It can contribute to developing delicious rice and improving postharvest processing technology. To effectively use agricultural machinery, the government has promoted an agency for farm operations and diversification of cooperative use methods through the RPC's cooperative use of mechanization, the agricultural machinery bank, and so on.

In addition, some local governments have run rental businesses for agricultural machinery such as agencies for farm operations, the lease of agricultural machinery, and rental, among others, which can decrease the purchasing cost of agricultural machinery and finally help farmers to operate their farms with low initial and maintenance costs. Accordingly, some research has been conducted to develop an effective management program for the businesses mentioned above. Computer programs have also been developed to help farmers easily understand the types of current commercialized agricultural machinery as well as economically available sizes and operating costs of the machines.

Technology to be developed in the future

Use of large-size agricultural machinery and water management. The Korean government has planned to increase the area of land consolidation from 699,000 ha in

2000 to 800,000 ha in 2015, resulting in 69.6% of total paddy field in 2015. Moreover, according to the increase in farm size, each arable land section will gradually increase from 0.3-0.4 ha in 2000 to more than 1 ha in 20 15 because small-size agricultural machines have been replaced by large-size highly efficient machines. This indicates that the 1-ha farm size, 6.4% of the total paddy field, will increase to 8.0% in 2005 and 18% in 2010, and roads for agricultural mechanization will also increase from 9,270 km in 2000 to 35,000 km in 2011. Recently, droughts and floods have frequently occurred because of El Niño and La Niña and other natural disasters. Therefore, an automated water management technology is urgently needed, which links climate and water storage as well as large-size agricultural mechanization, autonomous farm vehicles, the technology of land preparation/leveling using GPS, and so on.

Automation of each operating machine and technology of high-quality production. Agricultural mechanization can improve the efficiency of driving operations and promote automation, robotics, and autonomous operations, resulting in safer and easier farm operations. It will also allow machines to work without drivers day and night, resulting in a large decrease in production costs. For these kinds of circumstances, agricultural mechanization should be developed taking into account precision agriculture, automation, and high-quality multipurpose operations. Accordingly, a highly efficient machine that can be attached to a tractor should be developed to achieve high-speed rotary and automated land preparation and ground leveling. For more efficient interrelated management as well as rice transplanting and direct seeding, a multipurpose machine should be developed to work for transplanting, direct seeding, fertilizing, and weed control simultaneously. To save labor in water management that has completely depended on manpower, an advanced system should be developed for the automated control of water management linked with partial automation and weather information. The current pesticide method is that a machine sends liquid chemical by pressure and then farmers carry the nozzle with a delivery hose. This should be replaced with the dual technology of a small-size pilotless helicopter and weed control using realistic cultivation management. Drying work should be developed from the control of temperature and humidity by a high-quality continuous dryer to an automatic control of temperature and humidity by a dryer with artificial intelligence using far-infrared, micro, and supersonic electric waves. For high-quality rice postprocessing, the rice should be processed under low pressure, a technique of quick rice cooking should be developed, and a functional package should be studied for the MA (Modified Atmosphere) package.

Developing mechanization for environment-friendly precision farming. For environment-friendly agriculture, there has been a large interest internationally in finding a solution to maintain sustainable agriculture while technology for high-quality and safe agricultural production is urgently required. Instead of the conventional farming method of high input and high output, for environment-friendly agriculture, precise farming mechanization has become popular to achieve the same amount of harvest and obtain high-quality and safe agricultural products with lower inputs and energy. Highly developed technology such as GPS, remote sensing, and CIS has already been applied for other industries, and the current technology of automation and remote control of agricultural machinery can also be made economically viable in agriculture. In the advanced countries, the agricultural machinery installed with an agricultural navigating system using GPS, an agricultural database using GIS, mapping software, and other sensors have already been actively used for precision farming. Using machines, the characteristics of soil, the growth process of plants, and the amount of harvest were measured and then analyzed by location in real time while doing plowing, pest control, and harvesting. That information was used by an expert system to make final decisions on the application of agricultural chemicals and fertilizer. The fundamental information for mechanization of precision farming has been accumulated in Korea, such as autonomous control techniques and field information (using GPS and GIS), monitoring of regional field conditions, the measurement of rice's chlorophyll by optical technology, the monitoring technique for the amount of regional harvest during harvesting, analytical technology for space variation of soil, and the influence of different treatments. Accordingly, we urgently need to conduct research to develop an autonomous robot with artificial intelligence, and it should be commercially available by 2010. This robot should continuously operate machines of precision agriculture that collect farming information during agricultural operations, make decisions, and then carry out optimum operations.

Notes

Author's address: Senior researcher, National Agricultural Mechanization Research Institute in the Rural Development Administration, 249, Seodun-dong, Gwonseon-gu, Suwon, Gyeonggi-do, Republic of Korea. E-mail: dhlee@rda.go.kr.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Progress in biomass energy studies in the Ministry of Agriculture, Forestry, and Fisheries of Japan

Y. Mori

The Ministry of Agriculture, Forestry, and Fisheries (MAFF) of Japan has been studying biomass energy development for more than two decades. The major focuses of the studies are biomass production and biomass conversion to energy. The representative results of the biomass energy production studies are (1) a novel steam gasification system for methanol production from biomass, (2) the technologies of converting cellulosic and hemicellulosic materials into ethanol using a naturally occurring bacterial coculture and genetically modified enzymes, (3) the membrane technologies for ethanol separation and concentration, and (4) a semisolid methane fermentation system for swine excreta. Rice husk, straw, and bran are among the major biomass resources in Japan. These rice residues were tested as feedstocks for biomass energy production. Biomass energy studies by MAFF, including the results with rice residues, are presented and future directions for biomass energy development together with the potential of rice as energy and a material resource are discussed.

To achieve sustainable development, we have to improve the quality of life with a minimum use of natural resources and minimum pressure on the environment. Our society depends too much on fossil fuels for energy as well as for industrial raw material. Fossil fuel reserves are limited and, when burned, fossil fuels emit greenhouse gases that cause climate change. Thus, the development of renewable energy is indispensable for sustainable development. Renewable energy includes a wide range of naturally occurring replenishable energy sources, such as sun, wind, water, and biomass resources, all of which generally emit no greenhouse gases. Biomass is regarded as neutral over its life cycle in terms of greenhouse gases.

Biomass, defined as material derived from plants or animal manure, is produced by green plants converting solar energy into plant material through photosynthesis. The annual production of biomass is estimated to be approximately 25–35 billion tons of carbon, which is roughly equal to 10 times the total energy that humankind

Table 1. Biomass energy consumption in 1996.

Countries/region	Biomass ($PJ\ year^{-1}$)	Share of biomass in primary energy (%)
OECD[a]		
Europe	2,340	3.3
North America	3,665	3.5
Pacific	571	1.7
OECD total	6,575	3.1
Non-OECD		
Africa	9,236	49.5
Latin America	3,385	19.1
Asia (excluding China)	14,622	36.3
China	8,628	18.8
Former USSR	803	2.1
Non-OECD Europe	130	2.5
Middle East	40	0.3
Non-OECD total	36,844	20.5
World total	43,419	11.0

[a] OECD = Organisation for Economic Cooperation and Development.
Source: NEDO (2000).

consumes annually (NEDO 2000). There are basically two distinct sources of biomass energy: wastes from agriculture or industries and energy plantations. Global biomass production potential is approximately 301 EJ year^{-1}, with energy crops accounting for 61% and Asia being the most productive region (NEDO 2000). Biomass used to be the predominant energy source for humankind for cooking and heating through combustion. As shown in Table 1, even now, biomass is a major source of energy in the less developed countries, although in the developed countries the majority of energy is supplied by fossil fuels. It is evident that biomass energy will play an important role in the upcoming era when people live on diversified renewable energies. However, to make this happen, biomass should be converted to liquids, gases, or electricity, the forms adapted for the existing energy supply and use systems. The modern biomass energy production system should contain technologies for production, harvesting, pretreatment, and conversion of biomass that do not harm the environment.

The Ministry of Agriculture, Forestry, and Fisheries (MAFF) of Japan has been working for more than two decades on biomass-use technologies aiming at developing efficient biomass energy conversion as well as biomass production. Some of the technologies are regarded as promising and have been under verification using pilot plants. We sincerely hope that our efforts will, in cooperation with other countries, contribute to solving energy and environmental problems that may endanger the sustainable development of humankind.

Table 2. Biomass resources in Japan.

Resource	Amount (million t year^{-1})
Agricultural residues	14
Rice husk	2
Rice straw	10
Forestry	38
Fisheries	4
Animal industries	94
Food industry	10
Waste from household	10
Total	170

Table 3. Biomass use projects of MAFF.

Project	Years
Green Energy Project	197887
Biomass Conversion Project	1981-90
Bio-Renaissance Program	1991-2000
Biomass Energy Project	2001-05
Bio-Recycle Program	2002-06

MAFF activities in biomass energy development in Japan

Biomass resources in Japan

A huge amount of organic wastes or residues is produced by the activities in agriculture, forest product industries, fisheries, and food industries (Table 2). These include rice straw, rice husks, livestock manure, thinned-out trees, and food-processing residues, amounting to 170 million tons year^{-1} in total. Rice straw and rice husks account for the majority of agricultural residues in Japan, with an annual production of 10 million t and 2 million t, respectively. Most of these wastes or residues are now disposed of or incinerated and only fractions are composted or used for litter in the barn. It is thus urgent to develop technologies to use those wastes and residues for energy and material production.

MAFF biomass use projects

MAFF has been working in projects on biomass use since 1978 (Table 3). The focuses of the projects have been changing from biomass production in the Green Energy Project to bioconversion technologies in the Biomass Conversion Project, to the introduction of new plants and crops in the Bio-Renaissance Program, to biomass energy generation systems in the Biomass Energy Project, and then to the recycling system of biomass resources for reducing effects on the environment in the Bio-Recycle Program. Recently, more emphasis has gone to environmental aspects such as the mitigation of greenhouse gas emissions. MAFF is now conducting two projects, the Biomass Energy Project (2001-05) and the Bio-Recycle Program (2002-06), involving researchers from autonomous institutes, universities, and private companies.

Major outcomes in biomass production technologies and the current targets

Major results from MAFF activities in biomass production technologies are as follows:

1. Developing and improving crops for biomass resources

Photosynthesis genes were isolated and characterized. This is the basis for enhancing the photosynthesis activities of C_3 crops such as rice by introducing C_4 plant genes. Potatoes containing 20-30% more starch than ordinary ones were developed. A hybrid that accumulates a large amount of sugar was produced by crossing sugarcane and sweet sorghum. These newly bred crops can be excellent resources for energy and material.

2. Developing cultivation technologies

Cultivating methods for poplar, white birch, and acacia were established. A large-scale cultivation technology for giant kelp was developed. Machines for planting, cultivating, or harvesting bamboo grass and water hyacinth were developed. These trees, seaweed, and plants are good resources for biomass energy because of their fast growth and mass productivity.

Current targets for biomass production are to improve crops for higher sugar content and productivity and to develop efficient cultivation technologies with fewer environmental effects. The plants and crops under study are sugarcane, sweet sorghum, guinea grass, sugar beet, maize, potato, and sweet potato. MAFF has also launched research on the production of gramineous crops for the purpose of nonfood use in the approximately 1 million ha of fallow fields that have resulted from the reduction in rice area to cope with the surplus of rice.

Major outcomes in biomass conversion technologies and current targets

The major results obtained so far are as follows:

1. Synthesis gas (H_2 and CO mixture) production from rice husks by thermal conversion.
2. Methanol production by steam gasification of biomass.
3. Development of semisolid methane fermentation for methane production from swine excreta, kitchen refuse, and combustible municipal wastes.
4. Development of a raw-starch hydrolyzing enzyme.
5. Direct conversion of cellulosic and hemicellulosic materials into ethanol.
6. Membrane technology for ethanol separation and concentration and development of a membrane bioreactor for ethanol production.

The current target of biomass conversion technology is to organize individual technologies into district systems for local energy supply.

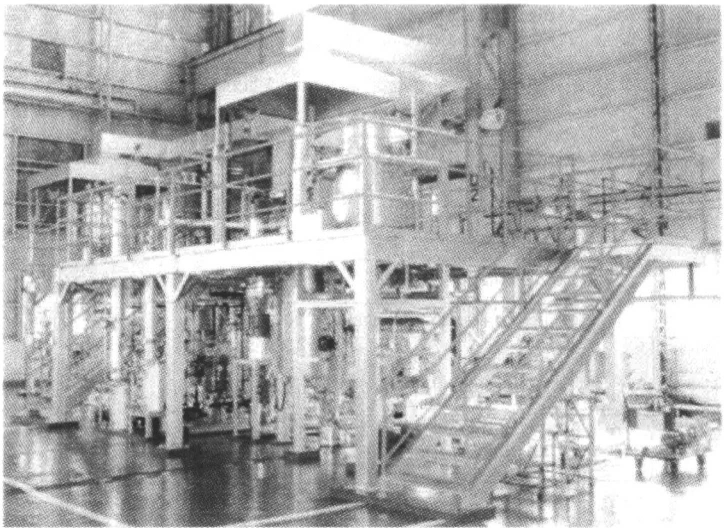


Fig. 1. Pilot plant for methanol production from biomass.

Case study 1 a novel steam gasification system for methanol production from agricultural residues including rice straw and rice husks

Biomass materials contain many volatile compounds, for example, the volatile compound content of wood is 70–90%.These volatile compounds are devolatilized easily at relatively low temperatures (approx. 300 ºC), and organic volatiles are rapidly transformed into gaseous products. When steam is incorporated into gasification, or by using steam gasification, volatile compounds are steam-reformed to produce synthesis gases (mixtures of carbon monoxide and hydrogen) at temperatures above 600 ºC. Currently, the Ni/Co catalyst is used to promote steam reforming. Methanol is synthesized on the Cu/Zn catalyst following the reaction $CO + 2H_2 = CH_3OH +$ 21.7 kcal.

The drawback of steam gasification is tar formation, which results in a low energy recovery. The tar causes clogging of pipes, which eventually stops the whole system. A MAFF team project has overcome the problem by using a low-oxygen-containing gasification agent and pulverized biomass materials. The project team constructed a pilot plant (Fig. 1) and confirmed that a satisfactory amount of methanol was produced from various kinds of biomass feedstocks, including rice bran, rice straw, and rice husks. Typical results are shown in Table 4.

Case study 2: direct conversion of cellulosic and hemicellulosic substances into ethanol (Mori 1990,1995, Mori and Inaba 1995)

Cellulose and hemicellulose are the first and second most abundant biopolymers on Earth and are major components of biomass resources. When ethanol is produced from these polymers, they are first hydrolyzed to glucose and then fermented to

Table 4. Energy recovery in methanol from various biomass resources.

Biomass	Recovery (%)
Rice bran	57
Rice straw	54
Rice husks	55
Sorghum (ear)	57
Sorghum (leaves and stems)	56
Cedar chips	59

Source: Sakal and Nakagawa (2002).

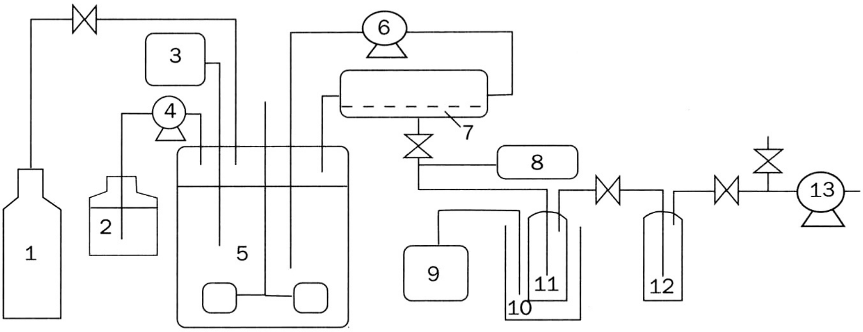


Fig. 2. Schematic diagram of the pervaporation membrane bioreactor. (1) CO_2 cylinder, (2) 4*N* NaOH, (3) pH controller, (4) peristatic pump, (5) jar fermentor, (6) circulation pump, (7) membrane, (8) Pirani gauge, (9) cooler, (10) bath, (11) trap 1 (20 °C), (12) trap 2 (liquid N_2), and (13) vacuum pump. Source: Mori and Inaba (1990).

yield ethanol. The multiple steps of the process result in high costs in both facilities and labor. A MAFF project team succeeded in isolating a symbiotic coculture of cellulolytic and ethanologenic bacteria that efficiently converts cellulose and hemicellulose into ethanol. Exhaustive studies revealed that the cellulolytic bacteria produce the enzyme complexes termed the cellulosome (3.5 MDa) and polycellulosome (50–80 MDa) that exhibit extremely strong cellulose and hemicellulose hydrolyzing activities. These two bacteria form a very stable coculture through nutritional interdependence, which makes the stable and efficient ethanol conversion from cellulosic/hemicellulosic biomass possible. To improve ethanol production using the coculture, a membrane bioreactor was developed. The membrane bioreactor consisted of a fermentor and a pervaporation system (Fig. 2) and the ethanol produced in the fermentor was continuously extracted and recovered as concentrate by the membrane. It was demonstrated that ethanol productivity increased remarkably using the bioreactor.

Table 5. Outline of Biomass Energy Project.

1. Pretreatment methods: drying, destruction of the obstinate structure.
2. Ethanol production technologies: enhancement of enzyme-hydrolyzing activities, improvement of microorganisms by gene engineering, new membranes for ethanol concentrations.
3. Production of fuels for fuel cells: hydrogen and methane production from agricultural residues and dimethylether production from livestock excreta.
4. Demonstration of the key technologies: evaluation of the systems using pilot plants for ethanol production and production of fuels for fuel cells.

The outline of the Biomass Energy Project

MAFF’s ongoing studies on biomass energy are conducted in the Biomass Energy Project. Table 5 shows the outline of the project. The project is composed of four teams: the teams for pretreatment, ethanol production, fuel production for fuel cells, and demonstration. In the pretreatment team, an energy-saving drying method of biomass resources, and physical and enzymatic pretreatments of woody substances to loosen their obstinate structures are being studied. Noteworthy is the effect of the ozone treatment in facilitating enzymatic hydrolysis of woody materials. In the ethanol production team, one main study is the improvement of cellulase and hemicellulases through protein engineering, whereas others are attempts for direct ethanol conversion from cellulose and hemicellulose using a unique mushroom and a genetically modified yeast. In the fuel production for fuel cells team, methane and dimethyl ether production from livestock excreta together with the basic study on hydrogen production by microorganisms from biomass resources are conducted. Finally, in the demonstration team, the systems for ethanol production and fuels for fuel cell production are scheduled to be tested using pilot plants. These systems are to be evaluated on an economic basis and for energy balance and effects on the environment.

Problems and future directions

Since biomass is bulky and scattered in low density, its collection and transportation are difficult and costly. Eventually, biomass energy facilities have to be situated in the vicinity of the region where biomass feedstocks (wastes or energy crops) are produced. Combustion and thermal conversion of biomass produce potentially hazardous emissions. Careful measures should be taken to reduce and remove these emissions. Growing energy crops may have an effect on the environment from the use of agrochemicals and cause changes in water use as well as changes in biodiversity.

It is obvious, however, that biomass energy can make a significant contribution together with other renewable energy to the sustainable security of the energy supply.

It can help mitigate climate change and reduce acid rain and soil erosion. Japan has committed itself to national targets to reduce greenhouse gas emissions to meet the Kyoto Protocol obligation of reducing greenhouse gas emissions by 6% from 1990 levels by 2008-12. To attain this objective and to contribute to maintaining the global environment, studies on biomass energy should be accelerated. The most influential technology in the relatively distant future is probably hydrogen generation from biomass resources.

References

Mori Y. 1990. Characterization of a symbiotic coculture of *Clostridium thermohydrosulfuricum* and *Clostridium thermocellum*. Appl. Environ. Microbiol. 56137-42.

Mori Y, Inaba T. 1990. Ethanol production from starch in a pervaporation membrane bioreactor using *Clostridium thermohydrosulfuricum*. Biotechnol. Bioeng. 36:849-853.

Mori Y. 1995. Nutritional interdependence between *Thermonaerobacter thermohydrosulfuricum* and *Clostridium thermocellum*. Arch. Microbiol. 164: 152-154.

NEDO (New Energy Development Organization). 2000. New energy overseas information. Tokyo (Japan). Vol. 00-2. p 23-166.

Sakai M, Nakagawa H. 2002. Biomass: new liquid energy. Tokyo (Japan): Kagakukougyou Nichihousha. p 57-104.

Notes

Author's address: Japan International Research Center for Agricultural Sciences (JIRCAS), Tsukuba, Ibaraki 305-8686, Japan.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September, 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Producing biomethanol and reducing CO_2 emissions from straw and husk by-products of rice

H. Nakagawa

With a wide array of potentially renewable energy resources, the concept and proposed benefits evolving from the use of biofuels are inspiring. Recently, a new method of gasification of biomass for biomethanol production has been developed and will soon be tested at the Norin Green No. 1 test plant in Nagasaki, Japan. To determine a useful protocol for producing biomethanol, bran, straw, and husks of rice were evaluated for their potential biofuel-use characteristics. From the analysis, rice bran is estimated to produce high methanol yield (55% by weight), whereas rice straw and husks returned 36% and 39%, respectively. Each of these products is a clean material, easily obtained and highly useful for biomethanol production. The potentially positive economic impact of biomethanol production on the farming system and social system is immense. Developing nations that are interested in constructing a national energy policy should pursue a strategy of establishing a biofuel-based economy. The development of a sustainable, agriculture-based biofuel program would reduce the demand for fossil fuels and provide for a more ecologically friendly energy resource. Our research suggests that one possibility for biomethanol production can be found by using rice by-products as raw materials.

More than 10 billion tons of fossil fuels are consumed annually in the world and their combustion is known to produce acid rain, photochemical smog, and an overall increase in atmospheric carbon dioxide (CO_2). Recently, researchers have suggested that the global rise in temperature is a result of increased atmospheric concentrations of CO_2. Predictions relative to these reports suggest that the global temperature will probably increase as much as 4 ºC if CO_2 levels double from the preindustrial levels during the 21st century. A possible result of this global warming is a gradual melting of the polar ice caps and Arctic glaciers, which could result in the world's seas rising approximately 17 cm to 1 m (Brown et al 2000). A second potential problem is the suggestion that, if fossil fuels, such as natural gas and oil, continue to be used at their current levels, known reserves will diminish to critical supply levels in a few decades although we will have coal for a few centuries (Ristinen and Kraushaar 1999). Relative to such dire predictions, it has been recommended that we need to identify and develop alternative sustainable energy resources.

Stabilizing Earth's climate depends on reducing carbon emissions either through reductions in fossil fuel use or through the direct or indirect use of solar energy. A third, and no less important, direction is the potential use of biofuels. Among these possible solutions, (1) the use of biofuels is perhaps the most attainable since plant biomass, produced with solar energy, is the ultimate sustainable energy resource; (2) cleaner-burning biofuels can reduce atmospheric CO_2; and (3) liquid fuels are easily applied as an alternative fuel for factory, automobile, and other engines requiring petroleum to operate.

The use of biomass for energy has been very limited. The most common use is the burning of wood and bioethanol production through fermentation from sugar and starch. Sugar and starch, however, are food products for human beings and, if used in a fermentation process, are not available as a food source in times of famine. In addition, the use of food products to produce energy is repugnant to many who recognize that feeding starving multitudes should be a priority over generating electricity, running factories, or operating automobiles.

Recently, a new technology using a gasification method for converting carbon hydrates into methanol has been developed (Sakai and Kaneko 1996, Sakai 2001). To test this technology, the Norin Green No. 1 test plant for biomethanol production was constructed to evaluate the system. The construction of this plant was funded by the Ecosystem Project of the Ministry of Agriculture, Forestry, and Fisheries of Japan in 2002.

For a sustainable biofuel industry, it will be important to plant fast-growing trees, grasses, and other crops to meet annual needs for biomass. Nakagawa (2001) discussed some promising grasses and their cultivation for biomethanol production. However, the most effective and economical materials will be by-products and residues or wastes of the agricultural and forest industries. Figure 1 depicts the estimated amount of by-product and residue from these industries in Japan. About 40% of this total is derived from rice production, primarily from the straw and husks of rice.

In this report, I provide recent information on the use of biomethanol production by the gasification of straw, husks, and bran of rice and discuss their potential and future use in such an industry.

Estimate of methanol yield from bran, straw, and husks of rice

Straw, husks, and bran of rice were evaluated for various characteristics important to gasification and for methanol yield. The methanol yields of these materials were estimated from a gas composition analysis following gasification of those materials.

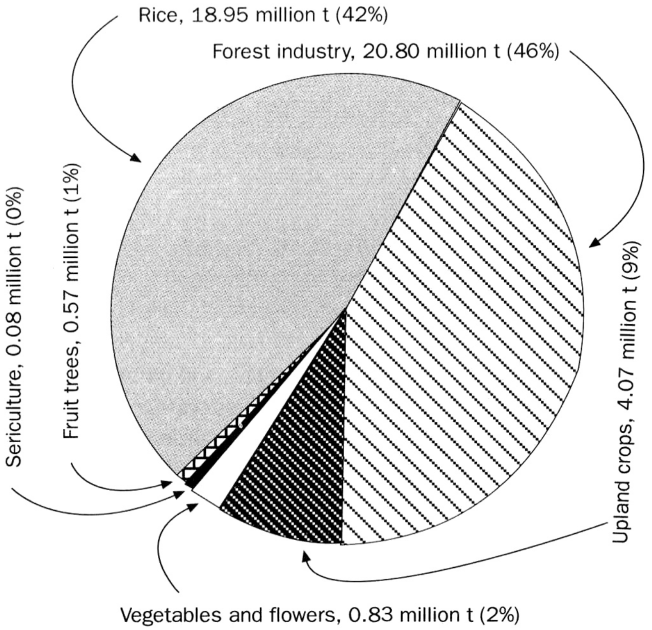


Fig. 1. Estimated annual amounts of by-products and residues from agriculture and the forest industry in Japan.

Materials

Materials used in the study are as follows: (1) Rice straw: cv. Yumehitachi. Seed heads were harvested on 6 September 1999. The straw was left in the field and cut in December 1999. The field-dried clippings were kept in a barn until needed. (2) Husks of rice cv. Koshihikari were obtained on 15 October 1999 following threshing and were immediately placed into plastic bags. (3) Rice bran, cv. Koshihikari, was harvested in 1999 in Ibaraki Prefecture and later polished by Satake NCP-100A (a commercial cereal milling operation) on 20 October 1999. The rice bran constituted 9.2% of the actual waste product of the brown rice. In addition to the rice by-products, sawdust and mature sorghum plants were evaluated as controls: (1) Sawdust: sawdust of Japanese cedar wood, without bark, was isolated and collected by passing the sawdust through a 2-mm mesh sieve; (2) Sorghum: Sudan-type sorghum hybrid cv. Green A was harvested by hand at maturity with both seed and foliage being obtained. The material was then chopped into 5-cm lengths by a standard forage chopper.

Methods

Characteristics important for gasification were evaluated for the above materials as follows: (1) Content of water and ash was measured after drying the materials at 107 ± 10 °C for 1 h and burning them at 815 ± 10 °C for 1 h; (2) Percent carbon (C),

Table 1. Contents of some elements (% by weight without water) in bran, straw, and husks of rice.

Biomass	Element							
	Carbon	Hydrogen	Oxygen	Nitrogen	Sulfur	Chloride	Ash	Others
Bran	48.3	7.0	33.0	2.44	0.21	0.05	8.1	0.90
Straw	36.9	4.7	32.5	0.30	0.06	0.08	22.6	2.86
Husk	40.0	5.2	37.3	0.76	0.22	0.41	14.6	1.51
Sawdust	51.1	5.9	42.5	0.12	0.02	0.01	0.3	0.05
Sorghum	46.1	5.7	40.6	1.16	0.57	0.04	5.5	0.33

hydrogen (H), oxygen (O), nitrogen (N), sulfur (S), and chloride (Cl) were measured by ordinary analytical methods; (3) High heat values were estimated by observing the rise in water temperature produced from the energy liberated by burning. Low heat values were estimated by the following calculation: High heat value - 600 (9 h + w)/100 [h = hydrogen content (%), w = water content (%)]. Typically, the low heat values are similar to that which is actually occurring in the boiler; (4) Chemical composition of the biomass was determined; (5) Size distribution of the particulated materials was measured (diameter, density of materials [g mL^{-1}, etc.); (6) Gas yield and heat generated from the gas were measured. Finally, the potential weight and calories produced as methanol yield were calculated from the gas composition of the materials.

Results and discussion

The contents of C, H, O, N, S, Cl, and ash in the different materials are shown in Table 1. Carbon content was low in straw (37%) and husks of rice (40%) and high in rice bran (48%) and sawdust (51%). Hydrogen content ranged from 4.7% to 7.0%. Rice bran provided the highest hydrogen values, while the other samples were only marginally different. Oxygen content ranged from 32% to 43%, with sawdust showing a higher value than bran, straw, and husks of rice. Nitrogen content was from 0.12% to 2.44%, with rice bran exhibiting the highest value. The content of S and Cl in the samples was low in all materials. These data suggest that bran, straw, and husks of rice are superior materials for biofuel usage and are comparable with sawdust and sorghum in their gasification properties. It should be noted that the ash content in rice straw (23%) and husks (14.6%) was extremely high because of the high silica (Si) content of the rice plant.

The mole ratio of carbon, hydrogen, and oxygen in these materials is shown in Table 2. In general, the mole ratio of C:H:O in carbohydrates is approximately 1:2:1. Our data indicate that the ratio of C:H in rice bran is 1.15:2 and comparable with that of ordinary carbohydrates. The ratio in the other materials ranged from about 1.3 (rice straws and husks) to 1.44 (sawdust). The ratio of H:O in rice bran (2:0.59) was very different from that of the other samples (2:0.9). These results again indicate that rice by-products are suitable raw materials for methanol production. Additional

Table 2. Mole ratio of carbon:hydrogen:oxygen in bran, straw, and husks of rice.

Biomass	Carbon	Hydrogen	Oxygen
Bran	1.15	2	0.59
Straw	1.31	2	0.87
Husk	1.28	2	0.92
Sawdust	1.44	2	0.90
Sorghum	1.35	2	0.90

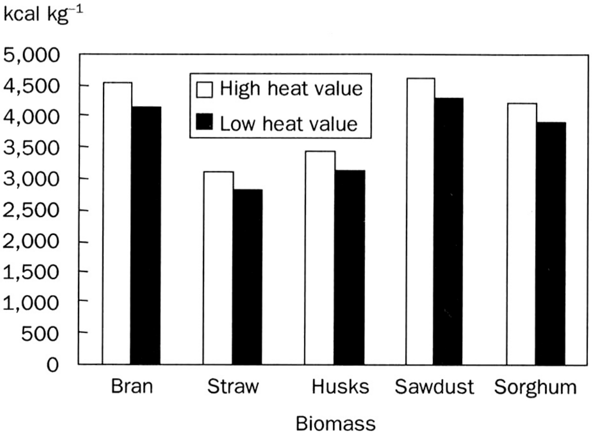


Fig. 2. High and low heat value of bran, straw, and husks of rice.

research is needed to elucidate the optimal ratio for maximizing biomethanol production.

The high and low heat values of the materials are shown in Figure 2. The heat value of rice bran was quite high, similar to that of sawdust, with 4,500 kcal kg^{-1} (high heat value). Rice straw and husks showed very low values, 3,080 and 3,390 kcal kg^{-1}, respectively.

The volume percent of gases, mainly hydrogen (H_2), carbon monoxide (CO), carbon dioxide (CO_2), and vapor (H_2O), produced by gasification of the materials is provided in Figure 3. Although the differences among materials were small, rice bran and sawdust produced a greater percentage of H_2 and CO, whereas rice straw and husks produced a greater percentage of CO_2. The most important gases for methanol production are H_2 and CO and they are directly converted into the methanol synthesis step of our technology. Lastly, the H_2 percentage of the materials was highly correlated with that of the dry-ash-free (daf) methanol yield (Fig. 4).

Figure 4 provides estimated methanol yield following gasification. Rice bran and sawdust indicated potential for high methanol yield at 54.2% and 55.6% on a dry-

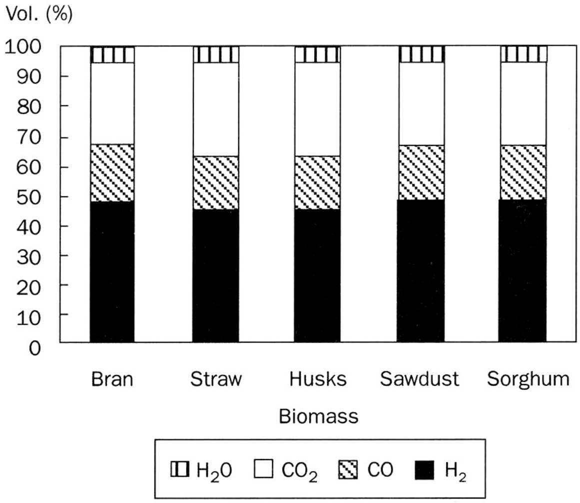


Fig. 3. Gas contents (vol. %) of bran, straw, and husks of rice.

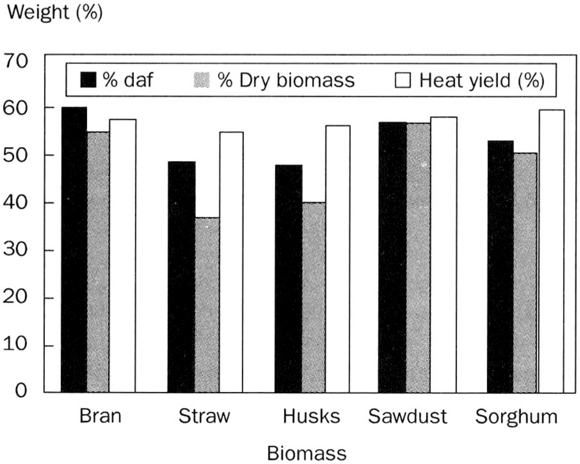


Fig. 4. Methanol yield (weight %) and heat yield of various biomass materials. daf = percentage of methanol weight to dry biomass weight without dry ash.

weight basis, respectively. This indicates that 542 kg of methanol could be produced from 1 t of dry rice bran. The higher ash content of the rice straw that was kept in the field for more than 3 months following the harvesting of grain exhibited a 40% lower yield in methanol production. It is interesting, however, that we can produce more than 350 kg of methanol from 1 t of rice straw and 390 kg from 1 t of husks.

Table 3. Size and handling characteristics of bran, straw, and husks of rice.

Biomass	Size (mm)		Density ($g\ mL^{-1}$)	Handling characteristics
	Diameter	Length		
Bran	0.31	–	0.31	No microcrushing needed
Straw	3.0-4.0	400	–	Micro-crushing needed
Husk	2.05	–	0.11	Micro-crushing needed
Sawdust	0.78	–	0.07	Micro-crushing needed
Sorghum	7.9	50	0.07	Rough and microcrushing needed

The physical characteristics of the raw materials and the handling procedures required to prepare these raw materials for biomethanol production are shown in Table 3. Since rice bran is very fine, there is no need for any prior preparation and it can be used directly for biomethanol production. Although the size of rice husks and sawdust was also small, they required micro-crushing to make them suitable for gasification. Though the rice straw was long, it also required only a single micro-crushing step. Sorghum at the seed harvest stage was cut by a sickle, chopped to a length of 5 cm, and dried in a forced air dryer. This procedure makes the sorghum materials very hard and they require both a rough crushing and a micro-crushing step to prepare them for gasification. Consequently, straw, husks, and bran of rice, as well as the other materials, were identified as being suitable for biomethanol production by gasification, though methanol yield of the materials ranged from 35% to 56%.

Application of this technology to a rice production system

In Japan

The above study suggests that the partial oxidation reaction during gasification of readily available rice bran, straw, and husks can be optimized for methanol production. Among them, rice bran was the superior raw material for gasification and biomethanol production since its material had a fine particle size and its methanol yield was 54%. Rice bran is about 10% of the total composition of brown rice and the total annual volume of rice bran by-product in Japan (1992) was estimated to be 0.92 million t. Rice bran, however, is used as a quality by-product for animal feed and as a raw material for the production of cooking oil in Japan.

One of the most important points for biofuel production is that the raw materials should not compete with our food resource needs. Although rice straw and husks are used as an important animal feed, especially for beef cattle to produce marbling in meat, most are simply burned and the ash is incorporated into farmers' fields to provide additional soil minerals and nutrients. This traditional process can be modified if a mineral by-product results from the waste produced from the ash of a gasification methanol production plant. As has been shown in Figure 1, the total annual weight of rice straw and husks is estimated to be approximately 19 million t in Japan. This will provide a huge amount of raw material for biomethanol production. Its use can lead to a decrease in the consumption of petroleum products and indirectly provide for a reduction in the production of CO_2.

In Japan, we face various difficult problems in our agricultural system. One is the reduction in population and the increasing age of farmers in Japan's mountainous regions and on small islands. This is causing the abandonment of cultivated fields, forests, and grasslands. One remedy to this situation can be the establishment of a new industry that promotes biomethanol production in these regions and the reuse of these abandoned fields. The cultivation of biomass in the form of trees or grass can be a very useful practice in such areas.

We consider our biomethanol technology as a superior system since the raw materials for gasification are abundant and do not use high-starch- or high-sugar-containing food resources. This is the significant point that differentiates this gasification technology from the traditional fermentation process of bioethanol production.

On 18 April 2002, a new test plant, named Norin Green No. 1, became operational and it has a daily capacity to process about 240 kg day^{-1} of dry biomass (Nakagawa 2002). The test plant was developed through cooperation with the National Grassland and Livestock Research Institute, the Nagasaki Institute of Applied Science, and Mitsubishi Heavy Industry Co. in the "Ecosystem Project" and was cosponsored by the Ministry of Agriculture, Forestry, and Fisheries of Japan. This test plant opens the way to accelerated research and practical use of this new technology.

In Asian and African countries

Second only to food production policies, energy policy is among the most important subjects confronting Asian and African nations. The consumption of electricity and petroleum is increasing dramatically and modernization in these developing nations depends on an expansion of their energy-producing capacities. Most of these countries rely on fossil fuels, coal, petroleum, and natural gas. This may be unfortunate. These developing countries should attempt to follow the model of Brazil, which has developed a strong biofuel-based energy economy. The developing countries located in tropical and subtropical regions should attempt to pursue the development of a biofuel-based energy resource with aid from developed countries and perhaps the World Bank.

Soon, I hope that a totally new type of agriculture will include the cultivation of raw material for biofuel production. I believe that grasses and legumes are among the most promising plants that can make a major contribution toward sustainable biomass production. This report has identified that, by using rice by-products and rice crop residues, it is unnecessary to design a plant specifically for biomass production. Rice straw, husks, and bran are an abundant product in Asian nations as well as in Japan and, as a consequence, one need only collect this waste and use it for a productive purpose.

The future of humanity will be directed by the decisions we make today. The development of a sustainable biofuel production technology or adherence to traditional fossil fuel technologies will certainly have consequences for the environment, Earth, and humans.[1]

References

Brown LR et al. 2000. State of the world 2000. New York, N.Y. (USA): W.W. Norton & Company Ltd. 276 p.

Nakagawa H, Sakai M, Harada T, Kitamura Y, Taniwaki K, Hashimoto A. 2000. Biomethanol production and CO_2 emission reduction from various forms of biomass. Proceedings of Fourth International Conference on EcoBalance, 31 October-2 November 2000. Tsukuba (Japan): ECOMATERIAL Forum, JLCA, and Japan LCA Forum. p 405-408.

Nakagawa H. 2001. Development and cultivation of forage grasses and crops for clean biomethanol production to keep global environment. Farming Jpn. 35(2):22-31.

Nakagawa H. 2002. Development of "Norin Green No. 1" test plant for methanol production from biomass and establishment of a new industry. Nourin Keizai 2 September 2002 (No. 9467). p 2-6. (In Japanese.)

Ristinen RA, Kraushaar JJ. 1999. Energy and environment. New York, N.Y. (USA): John Wiley & Sons, Inc. 367 p.

Sakai M. 2001. Technological innovation of production method of liquefied biomass fuels: thermochemical production method of methanol fuels from any types of biomass. Farming Jpn. 35(2):10-15.

Sakai M, Kaneko M. 1996. Biomass fuel for the 21st century. Proceedings of MAFF International Workshop on Versatile Use of Agricultural Products. Tsukuba (Japan): Ministry of Agriculture, Forestry, and Fisheries of Japan. p 13-22.

Notes

Author's address: NARO, National Institute of Livestock and Grassland Science, Nishinasuno, Tochigi 329-2793, Japan. E-mail: ngene@affrc.go.jp.

Acknowledgments: The author expresses his thanks to Dr. M. Sakai, professor at the Nagasaki Institute of Applied Science, Dr. T. Ichinose, manager of the Power System Laboratory, Mitsubishi Heavy Industries Ltd., Dr. T. Harada of the National Forestry and Forest Product Research Institute, Dr. Y. Kitamura of the National Food Research Institute, and Dr. K. Taniwaki of the National Agriculture Research Center for their cooperation in the research. The author expresses sincere thanks to Dr. Bryan Kindiger of USDA-ARS, Grazinglands Research Laboratory, for his helpful comments on the manuscript.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

---

[1] Part of this report was presented at the 4th International Conference on EcoBalance held 31 October to 2 November 2000 in Tsukuba, Japan (see Nakagawa et al 2000).

Economics and policy

Editor: D. Dawe

The role of rice in an agribusiness-led strategy for economic growth and poverty alleviation

B. Saragih

First of all, I would like to thank the International Rice Research Institute (IRRI) and the organizing committee for inviting me to this important and timely International Rice Congress 2002. I should also like to thank my Chinese counterpart, the Minister of Agriculture for the People's Republic of China, as the host of the roundtable discussion.

Rice is by far the most important source of calories and protein in the diet of the people in my country. Food security may not be achieved unless the availability and affordability of rice are secured. Since rice is of such paramount socioeconomic significance to both farmers and consumers, our government rice policy must try to reconcile the often-conflicting goals of ensuring that consumers have access to sufficient supplies of rice at an affordable price while producers enjoy commensurate income and adequate production incentives. For the past 30 years, we have been successful in managing our rice policy to ensure national food security.

To achieve and sustain future food security and agricultural growth, the Government of Indonesia is implementing the agribusiness-led development strategy (ALDS). There are five key ideas behind it. First, agribusiness development is the most effective way to alleviate poverty and assure food security, the twin prime objectives of economic development in Indonesia and in most developing countries as well. The reason is that most of the poor rely on the agribusiness sector for their income and that basic foods of the people are produced by the agribusiness sector. Agribusiness development therefore creates jobs and adds value for the poor, which are necessary for poverty alleviation. At the same time, it also increases the supply of basic foods at affordable prices, which are necessary for assuring food security.

Second, through its roles in poverty alleviation, food security, and inflation reduction, agribusiness development is the key for economic, social, and political stability. This triple stability is the necessary condition for economic development. No economic development can take place in a country plague-stricken with hyperinflation, social disorder, or political unrest. Agribusiness development reduces the country risk factor and hence plays a major role in facilitating a conducive environment for overall economic development.

Third, the agribusiness sector makes a direct contribution to aggregate economic growth. Both the growth rate of the agribusiness sector (gross domestic product, GDP) and its share in aggregate GDP determine its share in economic growth. The higher the sector GDP growth rate and the larger its share, the larger is the agribusiness contribution to aggregate economic growth. In a country where it is the dominant economic sector, as in most developing countries like Indonesia, the agribusiness sector is the major contributor to aggregate economic growth. Agribusiness sector development is the key to achieving high economic growth.

Fourth, the agribusiness sector can have both large and wide multiplier and inducement effects through intersectoral, consumption, investment, and fiscal linkages, which in turn boost overall economic growth and development. These multiplier and inducement effects help accelerate economic growth. If we may say that a large direct growth contribution is the necessary condition, then a large growth-accelerating role is the sufficient condition for the agribusiness sector as the appropriate engine of growth or the leading sector of economic development.

Indeed, the multiplier and inducement effects of primary agricultural enterprises may not be very large. This is why some economists were skeptical, especially in the 1960s, of the capacity of the agricultural sector as the leading sector of economic development. The same argument is also applicable against the ALDS.

But, the multiplier and inducement effects of the agricultural sector can be enlarged by developing agroindustries in both the backward linkages (agrosupplies) and the forward linkages (agroprocessing). That is another reason why we prefer proposing agribusiness-led development, rather than the ALDS. Agroindustrialization is the key to implementing the strategy.

Fifth, if the basis of the agribusiness sector is domestic agriculture, then the economic structure is rooted in domestic resources. The domestic resource-based economic structure is more resilient against external disturbances. The great Asian economic crisis in 1998 should be a good lesson in reminding us of the dangers and perils of high dependency on external resources. The external-oriented economic development could achieve a very high economic growth rate, but the economic structure is very fragile, thus creating a bubble economy vulnerable to external disturbances.

The five logical ideas of the ALDS boil down to one necessary condition—a period (say, ten years) of rapid agricultural growth. Those strategic roles of the agribusiness sector can only be realized through rapid agricultural growth. The most plausible way to achieve rapid agricultural growth is through technological-cum-institutional innovations.

I have outlined the basic tenets of the agribusiness-led development strategy. This framework can be used to assess the roles of any agricultural commodity, including rice, in implementing the strategy for economic growth and poverty alleviation. Any commodity system that contributes to the five basic functions of development that I have enumerated above can be considered as the leading commodity system.

Thus, the rice commodity system is the key or leading agribusiness system in many developing countries because it produces the basic staple of the population, it has a large domestic resource base and production potential, and it is the major contributor to both employment and value-added creation. In such countries, rice could play a major role for national food security, poverty alleviation, economic growth, and overall economic development.

There are two channels through which rice may affect the economy: production expansion and price inducement. The roles of rice can be evaluated through these two channels as if there is exogenous change in either the production or price of rice. Production expansion can be induced through technological change or land expansion, whereas price change can be induced by policy or market forces.

Naturally, if rice is the staple food, domestic rice production is large, and a large number of households depend on the rice agribusiness system for their livelihood, then increasing rice production must be the key factor for both food security and poverty alleviation. Increasing domestic rice production improves the country's self-reliance on food availability, one of the fundamental indicators of national food security. Increasing rice production directly increases rice availability at the farm household level and reduces the rice price at the consumer household level and hence improves food access by households in general. Secure access to adequate food for all households is the necessary condition of food security.

In general, the production expansion effect on food security is positive for both farmers and consumers' households. The price effect, however, is dilemmatic. Increasing the rice price is good for rice production and farmers' income but is bad for consumers, especially the net rice buyer-consumer households. There is a limit to price support policies as an instrument of food security. The best way to achieve food security is by expanding production and enhancing efficiency through technological change, optimal farm management, and marketing improvement.

Food security is interrelated with poverty alleviation. Food security has positive implications for poverty alleviation. First of all, fulfilling basic food needs (food security) is the necessary condition of not being absolutely poor. If rice has a positive role in household food security assurance, then it also has one in poverty alleviation. Many studies have shown that indeed rice production is negatively related, but rice price is positively related, with poverty incidence in Indonesia.

The favorable effects of rice production on poverty alleviation can be explained by its major roles in employment and value-added activities, especially for the poor segment of the rural population. In addition, increasing rice production has negative effects on rice price and some other related "basic need prices and wage rates (rice price as the price leader and wage good), which in turn reduces the cost of living and hence poverty incidence, such as observed in urban areas. It is clear, therefore, that expanding rice production is instrumental for reducing poverty incidence in both rural and urban areas.

Similar to its effect on food security, the effect of pure rice price on poverty incidence is dilemmatic, as trade-offs between the two have to be considered. Increasing the rice price may increase rice farmers' income and hence reduce poverty incidence, especially for those poor rice farmers in rural areas, but at the same time it increases the cost of living and hence poverty incidence of nonrice farmers (including marginal rice farmers with no marketable surplus of rice), especially the poor segment of the population in urban areas.

Based on the same reasoning, a rice production expansion-induced price decline is instrumental in reducing poverty incidence in both rural and urban areas.

The roles of rice in economic growth can be divided into facilitating a direct contribution and being a multiplier of intersectoral linkages. Its facilitating role arises from the role of rice in food security, poverty alleviation, and inflationary control, which are the major determinants of social, political, and economic stability and hence the country risk profile. Stability is the necessary condition for a conducive business environment. An empirical study by Professor Peter Timmer confirms that rice price stabilization has a positive effect on economic growth via investments.

The most obvious role of rice in economic growth is through its direct contribution to GDP. For Indonesia, rice is one of the largest single commodity contributors to GDP. However, its role is evolving and changing over time as the economy improves with rising affluence and changing tastes and preferences even if rice continues to be socioeconomically important.

Another mode through which rice affects economic growth is its intersectoral linkages. The first major one is the input-output impact multiplier through both backward and forward linkages. For Indonesia, empirical studies show that the rice multiplier impact is one of the highest. This higher rice multiplier impact proves that rice has been the leading or key sector for national economic development until now.

The second important linkage is consumption or demand inducement. Most value-added activities created in rice agribusiness go to low-income households, which have a high marginal propensity to consume. Most of this value added is recycled back into the economy through consumption. High domestic consumption (demand) is a pulling factor of economic growth. This is the basic argument of the proponents of the agricultural demand-led industrialization strategy.

Acknowledging the contribution of rice production growth to rural poverty alleviation, the Government of Indonesia sought to diversify and attract farmers out of rice by adopting alternative or complementary policies, among which are rural diversification, agricultural industrialization, and rural nonfarm employment creation.

Rural diversification has come to be viewed as a vehicle for alleviating rural poverty and the strains and distress faced by rice farmers. Ultimately, the process of rural diversification must be consistent with longer-run patterns of structural transformation.

Rural diversification should be treated as a process rather than as a result. The objective, in the near term, is to increase the flexibility of rice-based farming systems so that a variety of activities can be undertaken in response to changing market conditions with relatively low adjustment costs. Creating flexibility at the individual farm level is more costly than creating flexibility for the region.

Regional specialization is possible within an overall pattern of national diversification, thus drawing on differences in resource potentials and economies of scale in marketing that are inherent in well-functioning commodity systems. Unfortunately, regional specialization cannot eliminate the vulnerability of farmers to price changes for the rice commodity they produce.

National diversification through regional specialization is the efficient route to solving the aggregate problems of vulnerability to sharp changes in rice price, but problems of rural poverty and income distribution remain. The rural nonfarm sector is increasingly becoming an important source of employment or jobs for members of farm households. The process of rural diversification has good potential for increasing the role of small and medium rural industry, marketing, construction, and other labor-intensive services. There has been challenging research on the development of rural industry and its requirements in terms of infrastructure, credit, and characteristics of the labor skills it requires.

Government industrial policy has so far been biased toward the urban centers. Governments will need to give more attention to planning for expanded industrialization in rural areas, including policies required to create a favorable environment for private investors to move enterprises to rural areas and communities.

All three approaches have their own problems and solutions, and also successes, but a common lesson is that the diversification process must be market-led in the sense of pointing farmers and rural entrepreneurs toward activities with better market demand and higher potential for income. A market-led diversification process depends on several other factors influenced by government actions, such as

- Infrastructure investments to help reduce marketing costs and thus improve profitability at the farm level. Better roads, communication systems, information access, and public market places enhance agricultural diversification.
- Improved institutional arrangements by strengthening the land tenure system and avoiding excessive concentration of landholdings can improve the willingness of farmers to introduce new systems.
- Improved rural financial markets can broaden participation in the formal and nonformal credit sectors, thus opening up opportunities for traders to receive working capital that will finance short-term investments by farmers in the new systems.
- Improved laws and policies can facilitate a productive role for private firms in seed development and distribution, fertilizer marketing, and processing of products for domestic and foreign markets.

The national government is the key actor in setting all of these factors in motion. No doubt the most important role for the government in fostering a successful agribusiness system and rural enterprise development process is in formulating appropriate policies and creating a conducive policy environment, along with legitimizing their implementation and enforcement.

A more market-oriented approach to agribusiness development with greater reliance on the private sector will help diversify the rural economy, but may do so at the cost of somewhat lower self-sufficiency in the supply of staple foods like rice.

The trade-offs between market-determined diversification and government-directed food security objectives need to be considered in designing such intervention.

Agricultural diversification is not solely an agronomic issue or an economic one. Effective government policy requires an integration of both dimensions and more.

I hope that this brief exposition of mine may be persuasive enough to all of us on the potential roles of rice for further economic growth and poverty alleviation. Hence, we need to pay more attention and allocate more resources for rice development.

Looking to the future, a pragmatic food self-sufficiency policy should be implemented through greater diversification of food production and consumption. Besides rice, other sources of carbohydrates, for example, other grains and cereals such as maize, cassava, sweet potatoes and legumes or pulses, and tuber and root crops must be looked into.

Farm diversification with the agribusiness-led strategy, which I have referred to above, and increasing investments in agricultural research and development to induce higher food crop production are a proper strategy for Indonesia to alleviate poverty and achieve economic growth.

In addition to diversification, the key to the realization of the large potential roles of rice is production expansion through either technological innovations or area expansion.

I think that technological innovations are of the most relevance to our current Congress. I understand that most of you are the leading scientists in rice technology. The leading organizer of this Congress is IRRI, the only specialized international rice research and development institute in the world. IRRI was one of the earliest leaders of the first Green Revolution technology for rice.

Even though we recently implemented a national food diversification policy because of our declining rice production, rice remains an important staple for our people. We definitely need a second Green Revolution for rice. This is our great challenge. In short, only if there is another revolution in rice technology can the potential roles of rice in economic growth and poverty alleviation be realized.

Notes

Author's address: Minister of Agriculture, Republic of Indonesia.

Citation: Mew TW, Bra DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Food security and rice price policy in Indonesia: the economics and politics of the food price dilemma

C.P. Timmer

Food security in Indonesia is intimately connected to rice prices. After more than two decades of stabilizing domestic rice prices around the long-run trend of prices in the world market, Indonesia has emerged from the devastating Asian financial crisis with domestic rice prices much higher than world prices and much higher than long-run trends of real prices in rupiahs. Although the political rhetoric pushing for even higher prices uses food security as the rationale, in fact, few productivity gains are available to rice farmers. More importantly, high rice prices have a major effect on the number of individuals living below the poverty line and on the quality of their diet. This paper reviews research on the effect of rice prices on the poor and on the broader macroeconomic consequences for investments in labor-intensive manufacturing. Discussion then focuses on how political and economic circumstances have changed since price stabilization, implemented by the national food agency (BULOG), balanced the needs of producers and consumers.

Food security is always an emotional issue, as chronic hunger, local food shortages, and sudden spikes in food prices all mobilize public sentiment to "do something." Food security is the vague but still emotionally powerful concept of what people want with respect to these problems. However defined, food security is a clear public good. So, claims that a "time bomb' is ticking for Indonesia's food security if rice imports are not reduced have raised concern among the general population that the country is somehow losing ground in its long-term efforts to keep rice production growing faster than domestic demand.' Understandably, politicians are seeking answers that will reassure the public while gaining support for their parties in the

---

[1] See the story in the Jakarta Post, 4 May 2002. For a discussion of actual production and area harvested trends in Indonesia, see Peter Rosner, "Does Indonesia Face a Food Security Time Bomb?" FPSA Working Paper. 8 May 2002.

run-up to the national elections in 2004. Food security is also, always, a political issue.

Lost in the recent debates has been any clear recognition that food security is primarily an economic issue, one on which a substantial analytical and empirical literature exists, for Indonesia and in general. The universal conclusion from this literature is that only good economic policies can ensure food security on a sustainable basis for both the country as a whole and the millions of households individually. From this economic perspective, the food security time bomb in Indonesia's future is not potential reliance on rice imports ten years from now. Instead, the time bomb is poverty and the failure to restructure Indonesia's economy in a way that stimulates rapid growth of productivity in both rural and urban areas, leading to higher incomes.

The use of price policy to stimulate this growth is fraught with difficulties. Indeed, the current high level of rice prices in Indonesia makes the necessary economic restructuring quite difficult. There is a great deal of confusion in the country about the level of rice prices. Many government spokesmen, private research organizations, and all representatives of farmers complain about low rice prices. Repeated and highly public efforts are made to keep cheap imported rice out of Indonesia. In fact, these efforts have succeeded far beyond their legal intent or mandate. "INPRES 9/2001" requires that rice import policies seek a balance between the needs of rice producers and rice consumers. Figures 1 and 2 show that, despite this presidential instruction, rice prices in Indonesia are near historic high levels, whether compared with long-run trends in real (deflated) rupiahs or with levels in world markets.

Figure 1 shows that real rice prices in Indonesia are at least 30% higher than their stable trend from 1975 to 1996, after the country recovered from the world food crisis and before the Asian financial crisis that saw the country lose control of the entire economy, not just rice prices. During that 21-year period, real domestic rice prices were remarkably stable, although they did respond appropriately to local surpluses and deficits. Rice prices in mid-2002 were down somewhat from the peak during the financial crisis, but they have remained far above the previous level that was regarded as "normal" for more than two decades.

Those "normal" prices sought a balance between the interests of rice producers and consumers. They were adequate to stimulate increases in rice production in the 1980s that brought Indonesia to self-sufficiency at the same time that rice consumption increased dramatically, especially among the poor. This achievement, it should be recognized, was caused by a rice price stabilization policy, not by running up real prices to make rice farming more profitable. Rice profitability came primarily from new technology, massive irrigation investments, and cheap fertilizer. Stable, not high, rice prices gave farmers confidence to make the necessary investments to raise productivity, and allowed consumers access to the rice produced.

The situation now is totally different. Despite very high rice prices by historical standards, farmers do not have much new technology available to raise the productivity of rice cultivation. Even higher rice prices will not produce that technology or raise productivity. Higher rice prices in this environment produce a zero-sum outcome—any increase in rice farmers' incomes will be lost as rice consumers must

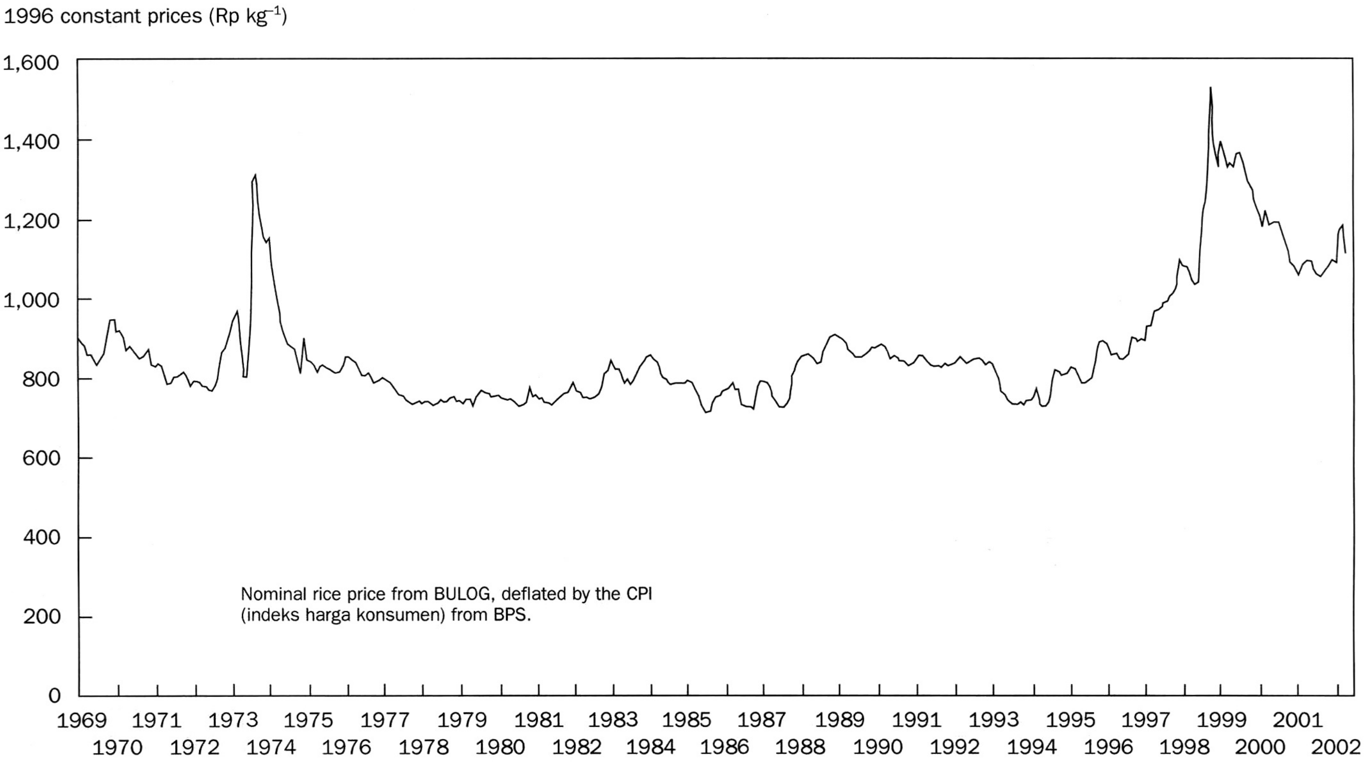


Fig. 1. The real price of rice, January 1969 to May 2002. Source: The nominal price of rice is reported by BULOG (medium quality rice). The consumer price index (CPI) data are from the Central Bureau of Statistics (BPS).

pay higher prices. There is no "spread effect" or multiplier without productivity gains. Consequently, the desirability of using higher rice prices to improve the incomes of rice farmers, and thus win their political allegiance. must be set against the losses to rice consumers, many of whom are quite poor. The available evidence, reviewed below, suggests that the current political environment in Jakarta, which is pushing vigorously for higher rice prices, is heading Indonesian rice policy toward a disaster for the poor, who always bear the brunt of bad economics.

Figure 2 puts the Indonesian rice price in an international perspective. Rice is a tradable commodity and Indonesia has been a substantial importer from world markets for the past half century, except for several years in the mid-1980s when self-sufficiency was temporarily achieved. Especially during the years when BULOG was successful in stabilizing domestic rice prices—from 1975 to 1996—a conscious effort was made to keep domestic rice prices on the long-run trend of world prices. There were two reasons for this policy. First, the world price represents the opportunity cost of rice to the Indonesian economy and economic efficiency requires that domestic

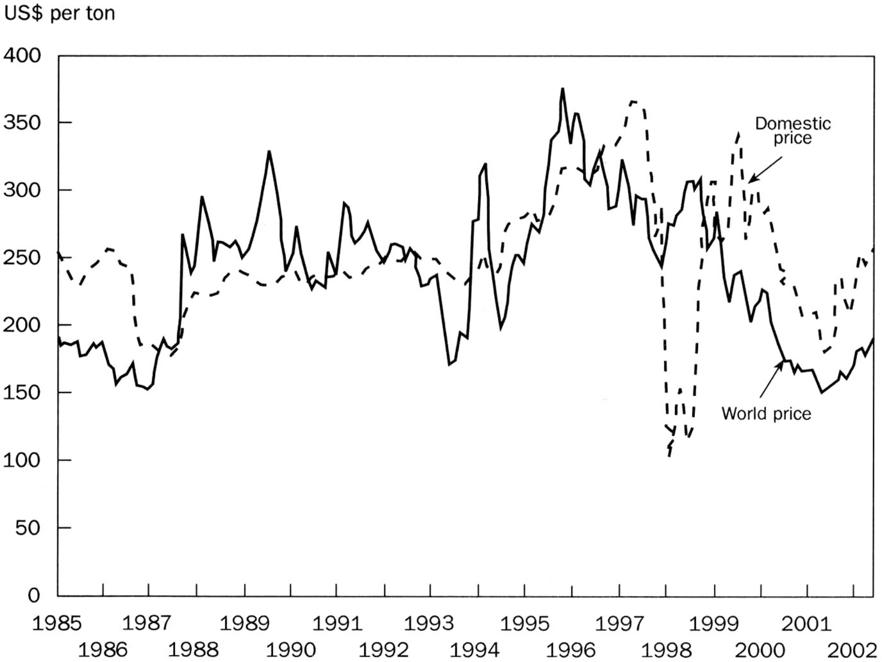


Fig. 2. World rice prices and domestic rice prices, 1985 to 2002. Note: The world price is the price of Thai 15% broken rice, f.o.b. Bangkok. The domestic price is the price of medium-quality rice reported by BULOG. The domestic price is adjusted to the world price using a wholesale-retail markup of 10%, a $20 per ton charge for movement from Bangkok to the Jakarta wholesale market, and the average monthly exchange rate for the rupiah as reported by Bank Indonesia. Source: World price (Thai 15% broken, f.o.b. Bangkok) from The Rice Trader. Domestic price from BULOG.

and world prices track each other over extended periods of time.[2] Second, in the astute words of an early observer of Indonesian economics, "God meant Indonesia for free trade." Because of the country's long and porous coastline, close to several major rice-exporting ports, it is nearly impossible for Indonesia's domestic rice price to be kept substantially above or below prices in those ports for extended periods of time.

In mid-2002, Indonesia's rice prices were at very high levels compared with imports. In the Jakarta market in mid-May 2002, retail prices were twice as high as for comparable qualities of rice imported from India.[3] The trade barriers that produce such substantial price differences are not fully understood. Even if the import duty of Rp 430 kg $^{-1}$ (at recent exchange rates, about US\$0.04 kg $^{-1}$; about 30% ad valorem at recent price levels) were fully enforced, which it is not, less than a third of the price difference would be accounted for. The remainder must come about through trader responses to risks of exchange rate fluctuations, harassment at the port, and confiscatory episodes by local authorities seeking favor with farm supporters (as in East Java in July 2002). A further possibility is that traders are manipulating local prices by restricting supplies to retail outlets, which would be surprising in view of how competitive domestic rice marketing is thought to be.

Whatever the exact set of reasons, Indonesia's domestic rice price is high in real terms and much higher than the world price, and current political rhetoric favors even higher rice prices. Just as in the United States, Europe, and Japan, Indonesia's political parties are competing for farmers' support in the name of food security and higher incomes for family farms. The costs of this competition are horrendous to consumers, taxpayers, or both. The costs in the United States are foregone budget priorities—no prescription drug relief for the elderly, for example. With considerable blame also attributed to farm policies in Europe and Japan, a further result is badly distorted world markets for staple food commodities. Apart from the budget and consumer costs, Europe and Japan also incur a cost for their high farm prices through macroeconomic distortions and somewhat slower economic growth—the farm sector in the United States is not big enough to have much macroeconomic impact. The costs in Indonesia, unfortunately, are more tragic—more people in poverty, more hunger and malnutrition, and significantly slower economic growth with worse distribution.

These are serious arguments against Indonesia's current political determination to force up the already high price of rice in domestic markets. But most economists agree that these will be the results of the policy approach now being recommended by BULOG and its supporters in Parliament. If the economics are so bad, why are higher rice prices so popular, at least in political circles and in the press? Three interconnected arguments are made to support higher prices, each with enough truth

---

[2] There are no similar efficiency arguments for following world prices on a day-to-day basis. See "Food price stabilization:rationale, design, and implementation," in Perkins and Roemer, eds. *Reforming Economic Systems in Developing Countries,* Harvard University Press for HIID, Cambridge, MA, 1991.
[3] See Peter Rosner. "Inpres 9/2001: balancing producer and consumer welfare," FPSA Working Paper, 23 May 2002.

to be deceptively appealing. Upon careful consideration, however, their appeal vanishes.

The three interconnected arguments involve (1) subsidies to United States rice growers and exports, (2) a historically thin and unstable world rice market, and (3) a slowdown in the growth of Indonesian rice production that has returned the country to importer status. The link among the three arguments is the rice price, and this link is established in the following way: U.S. farm subsidies drive down the world price (with the U.S. intending to monopolize the world rice market according to some conspiracy theories, despite selling less than 10% of the rice traded in world markets), forcing Asian rice producers out of business by reducing profitability of growing rice, thus making the world market even more unreliable. In this view, the response by Indonesia to such a strategy should be higher domestic rice prices, encouraging rice self-sufficiency and food security, to be implemented by isolating Indonesia's rice market from the world market.

The political appeal of these arguments is obvious, especially because there will be large profits to be made by BULOG in executing the strategy. But the arguments are wrong on three counts: (1) they do not account for the role of higher rice prices in the level of poverty in the country, (2) they fail to recognize the full macroeconomic impact of high (and higher) rice prices on economic growth, and (3) ironically, they fail to recognize the crucial role of international trade in rice in Indonesia's own food security (and the trivial role that U.S. rice exports play in both). These problems are taken up in turn.

Rice prices and poverty

Rice is the most important commodity in Indonesia, especially for the poorest members of society. It is not surprising that the level of rice prices is the single most important determinant of poverty at the household level in the short run. In the long run, rice prices also exert significant influence on the pace of poverty alleviation by conditioning the rate of economic growth. This growth is the main cause of the structural transformation—the gradual decline of agriculture as a relative share of the economy and the relative growth of industry and modern services. Sectoral contributions to economic growth and to the structural transformation, such as the role of agriculture, must be understood in the context of this long-run process of economic restructuring.

In the short run, the effect of rice prices on the poverty of individual households hinges on the household's status as a net buyer or seller of rice. High prices clearly benefit net sellers of rice, and the larger net sales are, the larger the benefits are. Low prices benefit net buyers of rice, especially those who do not produce any rice at all. This is the classic food price policy dilemma, and it is never a problem that is easily resolved.[4]

---

[4] This dilemma provided the integrating analytical theme for *Food Policy Analysis.* by Timmer, Falcon, and Pearson. 1983. Baltimore, Md. (USA): Johns Hopkins University Press.

Urban dwellers are net buyers of rice. This group includes the wealthiest members of society, but wealthy households are only a small fraction of urban households. In addition to the urban middle class, there are large numbers of urban poor. Rice accounts for a substantial portion of total expenditures of these poor households. In normal times (precrisis), rice constitutes 20% of total expenditures for the poorest quarter of urban households. For the poorest 5%, this share rises to 25% (but it was even higher at the peak of the financial crisis).

The share of the population living in urban areas is also growing over time, another manifestation of the structural transformation. During the 1990s, the level of the rural population was virtually stagnant, but the urban population grew at about 4.5% per year. Because of this differential population growth, the share of the poor that reside in urban areas is growing over time as well. Although the relative importance of the urban poor is growing, the majority of the poor reside in rural areas and will for a long time to come. In rural areas, the most important productive asset is land, and land ownership is a key determinant of both wealth and whether any particular household is a net buyer or seller of rice. On Java, 45% of all rural households do not own any agricultural land. While not all of these households are poor, the great majority of them are in the lower rungs of the income distribution.

Another 20% own less than 0.25 hectare of agricultural land, which is just enough to provide the average per capita consumption of rice for a family of five (if all the land is planted to rice and not to other crops). Together, these two groups account for nearly two-thirds of rural households on Java. By and large, they are much poorer than farmers with larger amounts of land, and they are not likely to be net sellers of rice. For these households, lower rice prices mean higher real incomes and less poverty.

Even Indonesia's larger landowning rice farmers are not wealthy in absolute terms, but in relative terms most of these households fall in the middle (third) quintile of the overall income distribution. On Java, only one-third of rural households own enough land to produce a surplus of rice for a family of five. These are clearly not the poorest of the poor. In fact, the image of abject poverty is of someone without enough food to eat. Almost by definition, this is not a farmer with enough land to sell a surplus of rice to the market.

It is also important to realize that, on average, land-owning, rice-surplus farmers produce only about half of their family income from growing rice. A decline in rice-based income does not lead to a proportional decline in household welfare even for these households. In summary, when urban households are included, only about 20-25% of Indonesia's households are better off from higher rice prices, and very few of these are among Indonesia's truly poor. High rice prices hurt the poor.

Rice prices and economic growth

Rice prices are important for poverty alleviation not only in terms of their short-term direct effects on the poorest segments of the population. In addition, rice prices play a key role in the structural transformation, both within the agricultural sector and for the economy as a whole. Within the agricultural sector, lower rice prices encourage rice farmers to diversify their cropping pattern by making rice less profitable to grow and by making it cheaper to buy rice from the market.

These ex-rice farmers then begin to produce other crops such as fruits and vegetables, allowing consumers to diversify their diets and increase their intake of proteins, vitamins, and minerals, which are crucial for the reduction of malnutrition. This is a slow process under the best of circumstances and must be market-driven. But appropriate government support for research, extension, and marketing initiatives can also speed up the process. Supporting highly protected prices for rice will slow it down.

Crop diversification is occurring to some extent in Indonesia, although not very rapidly. In 1984, when Indonesia temporarily achieved self-sufficiency in rice, 41% of all cropped area was planted to rice. Today, the share is 38%, a relatively small change over a period of 15 years of rapid economic growth. By contrast, rice as a share of total cropped area in Malaysia declined from 25% in 1972 to 13% in 1998. Artificially high (and stable) rice prices have impeded the diversification process unnecessarily. Lower rice prices can speed it along by guaranteeing reliable and affordable supplies of rice in rural markets to farm households that choose to diversify or invest in nonfarm rural activities.

The rural market reforms in China after 1978 provide a lesson in the role of local food availability in supporting decisions by local entrepreneurs to diversify out of grain production. One of the most important policies to support the development of small-scale rural industries in China was the freeing of food-grain markets in rural areas in the early 1980s. This impact has not been lost on the Chinese leadership, which has committed itself to keeping domestic grain prices in line with world prices as part of its entry into the World Trade Organization (WTO). Their argument is that low grain prices will maintain China's competitive advantage in labor-intensive manufactures and encourage Chinese farmers to seek more profitable crop and livestock activities as a way out of the trap of low incomes from grain production.

The lessons for Indonesia from China's WTO commitments are twofold: first, lower rice prices can stimulate small and medium enterprises (SMEs) in Indonesia as well, and also provide reliable food supplies for farmers who wish to diversify. But, second, and far more important for the long run. Indonesia's very competitiveness in international trade will be challenged by the Chinese strategy unless Indonesia also keeps the cost of its main wage good close to international levels.

This potential effect on the profitability of investments in labor-intensive enterprises means that rice prices play a key role in the structural transformation of the broader economy. Low rice prices allow real wages to be higher for employees without any increase in the nominal wages paid by employers in the high-productivity industrial and service sectors of the economy. In conjunction with other factors, this combination of low nominal wages and high real wages stimulates the job creation and economic growth that are necessary for sustainable poverty alleviation. Excessively high rice prices will cause workers to demand higher wages to keep their real incomes from falling, as has happened in the Philippines, where domestic rice prices have been well above world market prices for the past 15 years. These demands on the part of workers are entirely legitimate, but their higher nominal wages discourage investment, both domestic and foreign. The end result is a slowdown in the productivity growth that is essential for poverty alleviation.

If there are so many benefits to low rice prices, why not drive prices well below market levels to create even more of these positive effects? Artificially low food prices have been tried as a development strategy in many countries, for example, in Egypt, China before 1978, and the former Soviet Union, but they have always failed. Such a strategy reduces farmers' incentives to produce, hindering long-term productivity growth in the agricultural sector. Perhaps as important, a strategy of artificially low food prices requires subsidies and results in substantial fiscal costs to the government. These costs then divert scarce government resources from being used to provide the public goods necessary to create a dynamic rural economy, such as roads, education, and agricultural research. There are also efficiency losses to keeping domestic prices substantially below the trend in world prices because of the misallocation of resources.

What is the optimal level of rice prices? In a world of perfect information and competitive markets, the answer is "the world price." In the less-than-perfect world that rice-importing countries live in, research has shown that keeping domestic rice prices above world prices by perhaps 10% may be optimal. This margin ensures that the multiplier effects from increased agricultural incomes are realized, while minimizing the effect on poverty in the short run. However, any large, sustained deviation of domestic prices from world prices in either direction will lead to substantially suboptimal outcomes and slow the rate of economic growth.

Rice prices and food security

Indonesia's rice economy is now midway in a transition from being a sector heavily regulated by a centralized Ministry of Agriculture and stabilized by a well-financed food logistics agency (BULOG) to being a market-oriented sector that depends on farmer and consumer decision making to allocate resources efficiently. The large gap between domestic and world prices that emerged during the financial crisis in 1997 narrowed between late 1998 and mid-2000, but has widened again since then. Thus, Indonesia's rice prices remain substantially above world prices—in contrast to the long-run parity seen from the mid-1970s to the mid-1990s.

The key question at this juncture is how to complete the transition to a market-oriented rice economy while recognizing the constraints on policy initiatives that face the government, primarily the needs (as perceived by policymakers) of rice farmers to receive higher prices to stimulate production, and hence to improve Indonesia's food security. To answer this question, it is worth reviewing briefly how rice prices were set during the New Order government, when they were stabilized and maintained on the long-run trend in world market prices, until the financial crisis. It is also necessary to explain why the policies that achieved that desirable outcome are no longer appropriate.[5]

In summary, BULOG defended a floor price and a ceiling price through a combination of the following policy instruments:

- monopoly control over international trade in rice,
- access to an unlimited line of credit (at heavily subsidized interest rates in the early years; at commercial rates with a Bank Indonesia guarantee in the later years),
- procurement of as much rice as necessary by Dologs (regional branches of BULOG) to lift the price in rural markets to the policy-determined floor price, and
- extensive logistical facilities, including a nationwide complex of warehouses, which permitted seasonal storage of substantial quantities of rice (including the one million tons for the "iron stock" that was considered essential for Indonesia's food security). These rice stocks, accumulated through domestic procurement in defense of the floor price and, when these supplies were inadequate, through imports, were then used to defend a ceiling price in urban markets. In the early years, the ceiling price was explicit and announced publicly; in the later years, it was informal, providing local Dolog officials with more flexibility in maintaining stability of rice prices.

This was a heavily interventionist approach to the formation of rice prices in Indonesia. Still, few observers doubted the need for such intervention in the late 1960s and through the period of instability in the world rice market in the 1970s. An econometric assessment of the 25-year period from 1970 to 1995 concluded that BULOG's stabilization efforts paid very high dividends in fostering faster economic growth during Repelita I and II (the first two five-year plans, from 1969 to 1979), apart from the additional benefits provided by enhanced political stability. But even this positive assessment concluded that benefits from this market intervention were diminishing as rice became a much smaller proportion of the value added in the economy and as a share of consumers' budgets. By the mid-1990s, there was clearly a need to design a much more market-oriented price policy.[6]

This need for reform of rice policy was driven by two forces. First, the price stabilization program was very expensive in budgetary terms because heavy subsidies had to be provided to BULOG to maintain large stocks, subsidize exports when surpluses accumulated, and subsidize imports when domestic supplies were short. The increased corruption in the agency in the mid-1990s further called into question the use of public funds to support the price stabilization role.

Second, successful stabilization of rice prices enhanced the profitability of growing rice and biased farmer decision making toward its cultivation. This bias was desirable

---

[5] The details of this story are contained in "Food Security in an Era of Decentralization: Historical Lessons and Policy Implications for Indonesia" by C. Peter Timmer. This paper is part of the output from FFSA and is available at the project Web site www.macrofoodpolicy.com.

[6] See Timmer. "Does Bulog Stabilize Rice Prices? Should It Try?" *Bulletin of Indonesian Economic Studies.* August 1996.

at the time as new rice technology and extensive investment in rural infrastructure, especially irrigation, meant that farmers had to learn how to manage a radically new way of growing rice. In addition, Indonesia was exposed to a very thin and unstable world rice market in the 1970s and additional domestic rice production enhanced its food security. But, as early as the 1980% the bias toward rice production was causing serious difficulties in diversifying Indonesia's agriculture toward higher-value crop and livestock systems.

A long-run decline in the price of rice in world markets and significantly greater stability in world prices have now sharply lowered the opportunity cost of rice to the Indonesian economy.[7] In 1998, for example, the country was able to import more than 6 million metric tons of rice in the wake of the worst drought in recent history-caused by a historically severe El Niño—with very little effect on the world rice market (see Fig. 2). With Indonesian rice imports returning to the "normal" levels of earlier years after 1998, world prices have continued their long-term decline. In the face of these long-run opportunity costs of growing rice, farmers will need to diversify out of rice to have better income-earning prospects in the future.

The alternatives to the high-cost and inefficient approach to rice price policy in the 1980s and early 1990s were already under discussion in the mid- 1990s.[8] Although various analysts had differing priorities for reform, the core ideas were similar. Indonesia should rely much more heavily on rice imports for its food security, including taking the lead in forming a free trade zone for rice in East and Southeast Asia (possibly to include Bangladesh and India as well). Substantial investments in rural infrastructure to improve the efficiency of rice marketing would be needed so that traders and farmers would buy and store nearly all of the harvest. Continued development of rural capital markets would also be needed to ensure that the financial liquidity traditionally provided by BULOG procurement in defense of the floor price would be available from the formal banking system at reasonable rates to farmers and traders.

Greater variability in seasonal prices would be permitted so that these farmers and traders could earn adequate returns on their investments. Such variability would not be a problem for consumers because rice had declined to a small and manageable share of their budget expenditures. In case of large increases in rice prices in world markets (much less likely with a large Asian free-trade zone) or localized shortages, subsidies to poor consumers could be targeted through special logistical efforts (BULOG had already experimented with such a program during the drought in 1991—the pilot activity was called "Special Market Operations," OPK, which was also the name of a similar program used during the financial crisis to target cheap rice to poor consumers). Variable tariffs on rice imports were also discussed as a mechanism for stabilizing rice prices in Indonesia without the need for a costly logistical agency.

---

[7] See David Dawe, "The Future of the World Rice Market and Policy Options to Counteract Price Instability in Indonesia," FPSA Working Paper No. 3, and Dawe (2002).

[8] See Timmer, "Building Efficiency in Agricultural Marketing: The Long-run Role of Bulog in the Indonesian Food Economy," *Journal of International Development,* 1996.

These discussions about improving the efficiency of the rice economy were put on hold during the financial crisis, although both the International Monetary Fund and the World Bank pushed for liberalization of rice trade and a cutback in BULOG activities as part of their support programs. Indeed, it is these donor efforts that have pushed Indonesia into the transition that is currently under way, and it is clear that the donors would prefer to see the process completed as rapidly as possible.

There is substantial merit to the market-oriented rice economy seen at the end of this transition, and it remains a highly desirable goal. But there are also substantial political barriers in the way of this outcome. One worrisome element of the current policy debate is that there seems to be little understanding of how the previous rice price policy was designed and implemented, what its true costs were, and what the implications might be for price stabilization if BULOG is converted into a commercially oriented state enterprise and given monopoly control over rice imports. Thus, the political discussions are being conducted in a near vacuum of institutional memory and experience with policy design and implementation.

What would a lower tariff on imported rice mean for the balance between domestic rice production and consumption? If domestic prices are kept closer to (but still above) world prices, will Indonesia sacrifice a "satisfactory" degree of self-sufficiency in rice? Self-sufficiency is a worthwhile objective if it is achieved because of high productivity, as happened in 1984. However, self-sufficiency in any commodity is of dubious value if it is caused by higher prices that result in adverse effects on poverty. For Indonesia to be more self-sufficient in rice without hurting the poor, the path is through agricultural research and productivity growth, not from policy-induced higher prices. Because the world rice market is so much more stable now than it was in the 1970s and early 1980s, the justification for self-sufficiency as a defense of Indonesia's food security is far weaker today. Now the justification is based on simple protectionism. Indonesia's food security will come from its economic growth and macro stability, not from its degree of rice self-sufficiency.

Reference

Dawe D. 2002. The changing structure of the world rice market. 1950-2000. Food Policy 27(4):355-370.

Notes

Author's address: Professor of Development Studies, Graduate School of International Relations and Pacific Studies, University of California, San Diego, 9500 Gilman Drive, Mail Drop 0519, La Jolla, CA 92093. ptimmer@ucsd.edu.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Nutrition knowledge, rice prices, and the micronutritional effect of Indonesia's crisis of 1997-98

S.A. Block

This paper analyzes three related questions pertaining to child micronutrient status in Indonesia: (1) What was the nutritional effect of Indonesia's economic and financial crisis of 1997-98? (2) What are the determinants of child micronutrient status? (3) What is the effect of rice price increases on household purchases of micronutrient-rich foods? Analysis of household survey data from rural Central Java reveals that Indonesia's financial crisis had relatively little effect on child caloric intake. Families tended to maintain their rice consumption in the face of a tripling of the rice price, but often did so by sacrificing their consumption of higher-quality micronutrient-rich foods. As a result, child micronutrient malnutrition (e.g., iron-deficiency anemia) increased substantially even while weight-for-age remained constant. This effect was most pronounced among the youngest cohorts of children at the time of the crisis.

More focused analysis of the determinants of child micronutrient status demonstrates that maternal nutrition knowledge is a critical factor. Indeed, specific knowledge of nutrition is more critical than formal schooling as a determinant of child micronutrient status. Other relevant factors include child sex and age, the number of children in the household, household expenditure levels, and access to water. Yet, establishing a reduced-form relationship between maternal nutrition knowledge and child micronutrient outcomes sheds no light on the question of how such knowledge affects outcomes. Understanding the mechanisms through which nutrition knowledge works requires a more structural approach.

A production function for child micronutrient status must include intake of micronutrient-rich foods. Yet, underlying such a specification must also be a demand function for micronutrient-rich foods. Thus, one possible way to understand the mechanisms through which maternal nutrition knowledge affects child micronutrient outcomes is to include nutrition knowledge as an argument in the demand function for micronutrient-rich foods. What is the effect of nutrition knowledge on household budget allocation between food and nonfood, and among foods, between starchy staples and micronutrient-rich foods? Preliminary evidence suggests that households

of mothers with nutrition knowledge allocate substantially greater budget shares to micronutrient-rich foods and smaller budget shares to rice. The cross-price elasticity between micronutrient consumption and the rice price is key, particularly in the Indonesian crisis context in which the baseline rate of child anemia was high and rice prices increased rapidly. Preliminary evidence suggests that the micronutrient consumption of households with nutrition knowledge is substantially less sensitive to changes in rice prices than that of households lacking in nutrition knowledge. This may have been a critical factor in determining the severity with which Indonesia's crisis affected the nutritional welfare of some households relative to others.

Indonesia's economic crisis of 1997-98 provides a relatively unique context in which to study the nutritional effect of dramatic increases in the price of rice and other foods. Rice has long been the mainstay of Indonesian diets. Nearly every family consumes at least some rice, and, in rural Central Java (the focus of this study), an average family obtains more than half of its calories from rice and devotes to it nearly a quarter of household expenditures. Among the very poor, rice expenditures can account for 40% of total household expenditures. Thus, the tripling of rice prices in Indonesia from January 1997 to October 1998 represented a substantial shock to real income. This shock was compounded by substantial increases in the prices of many other food commodities as well, including high-quality foods with high micronutrient content such as meat and dairy products, vegetables, and fruits (Table 1).

What is striking about the effect of the crisis on child nutrition, however, is that families (on average) managed to maintain their children's gross caloric intake. Yet, it appears that this was often accomplished at the expense of children's micronutrient

Table 1. Price changes for selected foods, January 1997 to October 1998.

Food item	Mean price increase (%)	Standard deviation
Rice	195.2	29.2
Other cereals and tubers	137.5	101.8
Fish	89.1	67.4
Meat	97.0	49.3
Dairy and eggs	117.1	31.9
Vegetables	200.3	129.5
Pulses, tofu, and tempeh	95.2	76.0
Fruit	103.7	61.3
Oils	122.0	74.8
Sugar, coffee, and tea	142.9	28.3
Prepared food and beverages	81.4	51.7

Source: Friedman and Levinsohn (2001) based on their analysis of SUSENAS and BPS surveys of urban markets in 27 provinces.

status, as families coped with the crisis-driven increase in the price of rice by substituting high-quality micronutrient-rich foods out of their children’s diets. Indeed, recent research (Block et al 2002) suggests that child micronutrient status declined substantially during the height of Indonesia’s crisis even while caloric intake remained relatively constant.

This finding leads directly to the question of, What characteristics distinguished those households in which the micronutritional effect of the crisis was less severe? The “hidden” nature of the micronutrient content of foods suggests that maternal nutrition knowledge may be critical—mothers have to know that eggs are rich in iron and vitamin A and that those nutrients are important for child development, because they cannot tell simply by looking. Identifying determinants of the demand for child micronutrient status has potentially far-reaching policy implications, particularly if such relatively approachable variables as maternal nutrition knowledge turn out to be important. Yet, if nutrition knowledge is an important determinant of child micronutrient status, why is it so? Through what means might maternal nutrition knowledge lead to improved child micronutrient status? The obvious place to look is at the effect of nutrition knowledge on the demand for micronutrient-rich foods. Yet, in a setting such as rural Central Java, the demand for any food cannot be divorced from the dominant role of rice in household diets and expenditures.

In analyzing the events surrounding Indonesia’s crisis, this study thus analyzes three broadly related questions: (1) What was the effect of Indonesia’s crisis on child nutrition? (2) How important is maternal nutrition knowledge (versus formal schooling) in determining the “demand” for child micronutrient status? (3) What are the mechanisms through which nutrition knowledge operates to condition that demand?

Child nutrition during the crisis

Indonesia’s economic crisis resulted not only in widespread macroeconomic devastation but also in a severe shock to real household income. Friedman and Levinsohn (2001) estimate that the real cost of living approximately doubled for rural families. The consequent effect on poverty, though a subject of ongoing controversy, was also severe. The best estimates suggest that the headcount index of poverty increased from 7% to 20% during the peak of the crisis in 1998 (Suryahadi et al 2000). The effect of these events on child nutrition, however, was more subtle.

Figure 1 tracks changes in mean weight-for-age (WAZ) and weight-for-height (WHZ) z-scores in children under five years old over the course of the crisis.[1] The dates at which these observations occur (along the horizontal axis) reflect the timing of the 14 rounds of household surveys on which the analysis is based. The trend for each of these anthropometric indicators is normalized to zero in the first survey round and each subsequent change is measured relative to that baseline. The period

---

[1] Methodological details for the cohort decomposition underlying the analysis in this section are presented in Block et al (2002).

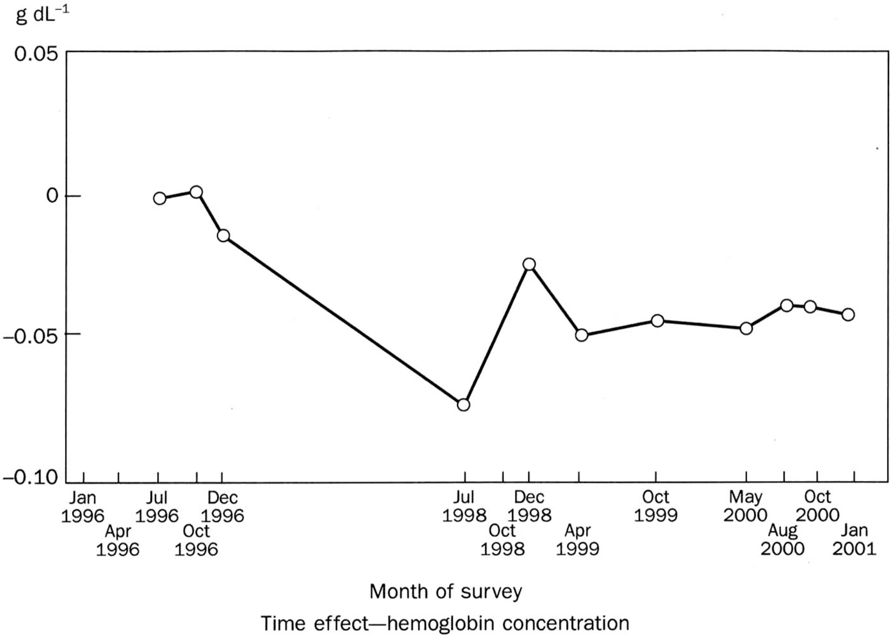


Fig. 1. Relative changes over time in child weight-for-age (WAZ) and weight-for-height (WHZ). Initial (Jan 1996) levels: WAZ = -0.86, WHZ = -0.01.

from December 1996 to July 1998 represents a hiatus in data collection during the period that spans the height of the crisis. The change between those dates thus captures the peak crisis effect on any given indicator.

WAZ is the most commonly used indicator of child nutritional status, and is probably also the least rapidly responsive indicator to changes in diet. It is clear from Figure 1 that child WAZ was essentially unaffected by the crisis. Following a small (though statistically significant) decline in the precrisis year, WAZ remained constant throughout the crisis. This suggests that households on average maintained their children's gross caloric intake, despite rapid increases in food prices.[2]

The picture begins to change, however, when we consider WHZ, which is more responsive than WAZ to changes in diet. Figure 1 superimposes the time trend in mean WHZ over the trend for WAZ. The trend for WHZ reveals a more negative picture of the effect of the crisis on child nutrition. In this case, mean WHZ declined by more than one-third of a standard deviation during the height of the crisis (from December 1996 to July 1998). This change is both statistically and biologically significant, reflecting an increase in the prevalence of wasting, which doubled from 6% to 12% of children during that period.[3]

---

[2] There is anecdotal evidence that this was accomplished, in part, by mothers diverting their own rice consumption to their children during the crisis. See the series of crisis bulletins by Helen Keller International.

[3] Wasting is defined as being beyond two standard deviations below the International mean of weight-for-height.

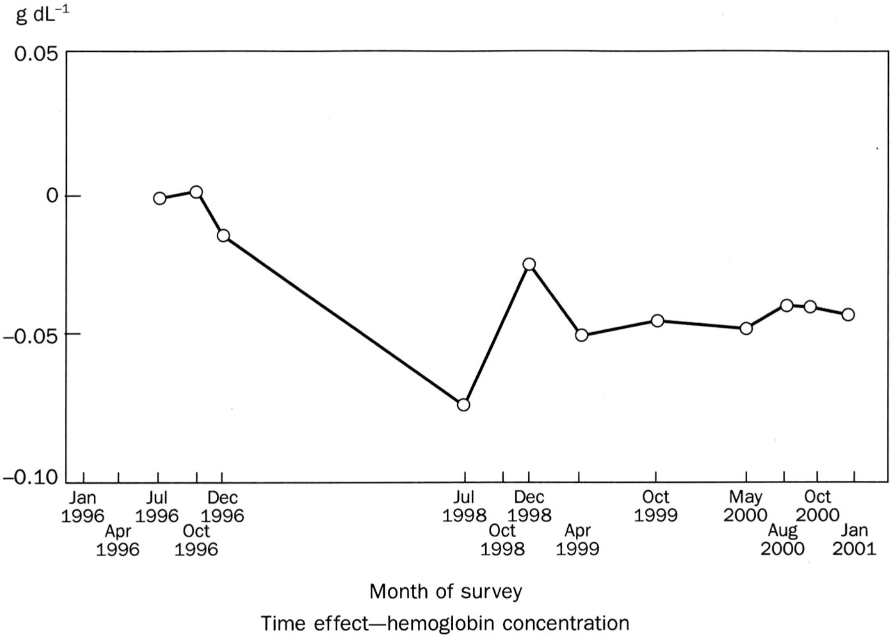


Fig. 2. Relative changes over time in child blood hemoglobin concentration. Initial (Jul 1996) absolute mean Hb = 10.98 g dL^{-1}.

Blood hemoglobin concentration provides a yet more revealing picture of crisis effects-one that reveals effects on dietary qualify in addition to quantity—and serious shortfalls have been associated with heightened mortality and reduced learning capacity. The peak crisis period in Indonesia was accompanied by substantial declines in household consumption of eggs and dark green leafy vegetables—foods that are important sources of iron and other micronutrients. Decomposing the trends in children's hemoglobin concentration reflects the expected consequence for micronutrient status. Indeed, the share of children in rural Java vulnerable to iron-deficiency anemia is substantial. Anemia is characterized by a hemoglobin concentration (Hb) of less than 11 g dL^{-1} of blood (WHO, UNICEF, UNU 1998). Mean Hb in children in rural Central Java was 11.02 g dL^{-1}, and the prevalence of anemia among children over the entire sample period was 47%. [4]

Figure 2 shows the time path of child Hb (in logarithms) over the course of the crisis. The decline in mean child hemoglobin concentration from December 1996 to July 1998 was 6.1% (or 0.32% per month). In absolute terms, this corresponds to a decline of 0.68 g dL^{-1} over the entire period, which is greater than one standard

---

[4] In the absence of other causes of anemia (hookworm, malaria), the main cause of anemia is iron deficiency. Anemia is the final stage in the development of iron deficiency and the prevalence of anemia suggests that a much larger proportion of children, as many as twice, are likely to suffer from iron deficiency (though not with sufficient severity to qualify as anemia).

deviation for the full sample of those cohorts. The time effects (slope) are statistically significant, as are the differences in levels from December 1996 to July 1998. This decline represents an increase in the prevalence of anemia from its baseline of nearly 50% to more than 70% over that period. Although it is difficult to explain the peak in December 1998, average child Hb tended to stabilize at a post-April 1999 average that was 0.5 g dL^{-1} lower than the level in the initial survey round (joint F-score = 16.89). Further analysis reveals that the decline in child Hb was increasingly severe for progressively younger cohorts at the onset of the crisis. Indeed, the most severe reductions in child Hb, measured during the critical developmental age of 6 to 18 months, were found among those cohorts that were conceived during the height of the crisis.[5]

Indonesia's macroeconomic crisis thus had substantial microeconomic (even microscopic) effects. Families sacrificed to maintain their children's caloric intake (e.g., rice consumption); yet, under the circumstances, something had to give, and what gave was the consumption of high-quality micronutrient-rich foods. This choice is reflected in substantial increases in the prevalence of iron-deficiency anemia among children in rural Central Java during the peak crisis months. This finding speaks to a broader issue.

Nutrition knowledge, schooling, and child micronutrient status

The debilitating, pervasive, and potentially fatal consequences of micronutrient malnutrition—or "hidden hunger"—are an increasing priority for public-health officials in developing countries; yet, economists have rarely examined micronutrient demand and the determinants of micronutrient status.[6]

The extent to which micronutrient malnutrition is automatically ameliorated by income growth is unclear. Several studies have asserted that expenditure elasticities for nutrients may be close to zero, despite significantly higher expenditure elasticities for food as a result of consumer preferences for higher-quality calories as income rises.[7] The implications of such substitution, particularly substitution toward red meat, are potentially positive with respect to iron-deficiency anemia. Yet, substitution toward meat typically occurs at relatively high levels of income, and may thus be too remote a solution for those at the lower end of the expenditure distribution.

Thus, the search for other key determinants of child micronutrient status is critical. Maternal education, in particular, has played a central role in empirical studies of the demand for child health (almost universally defined by height-for-age). Many studies have found a strong positive association between maternal education and child height-for-age.[8] Yet, the "hidden" quality of micronutrient content in food

---

[5] See Block et al (2002) for details of the cohort analysis.

[6] Exceptions include Bouis (1991), Bouis and Novenario-Reese (1997), Pitt and Rosenmeig (1985), Behrman and Deolalikar (1987).

[7] Behrman and Deolalikar (1988), Behrman and Wolfe (1984), Pitt and Rosenzweig (1985), Bouis and Haddad (1992), Subramanian and Deaton (1996).

[8] Behrman and Wolfe (1984, 1987), Barrera (1990), Alderman and Garcia (1994), Lavy et al (1996), among others.

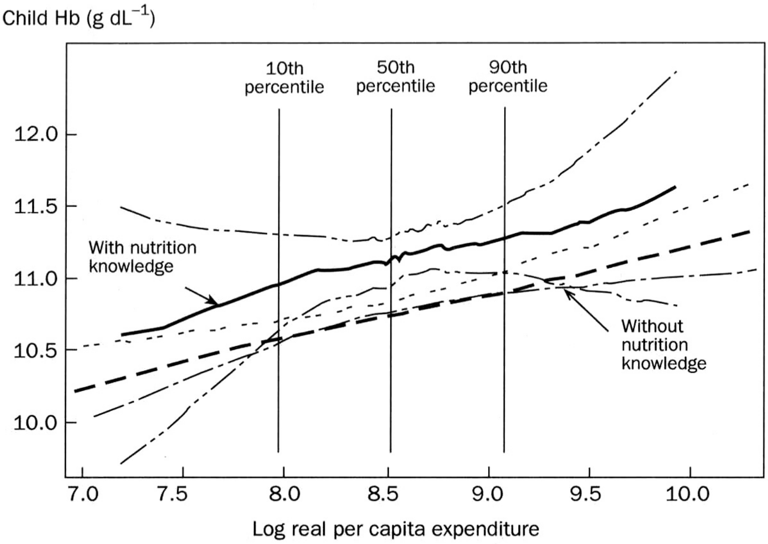


Fig. 3. The effect of nutrition knowledge on child hemoglobin concentration (Hb), conditional on household expenditures.

suggests that improved intake of micronutrient-rich foods may depend importantly on consumers' nutrition knowledge in particular. Indeed, it is especially relevant to know whether maternal nutrition knowledge dominates formal schooling as a determinant of child micronutrient status. Evidence from rural Central Java indicates that it does.[9]

Figures 3 and 4 illustrate this point nonparametrically. Figure 3 traces the relationship between child hemoglobin concentration and real household expenditures per adult equivalent, distinguishing between the children of mothers with and without nutrition knowledge.[10] The results suggest that, at every level of per capita expenditure, mothers with nutrition knowledge demand greater micronutrient status in their children than do mothers without nutrition knowledge. At the sample median, the margin is approximately 0.4 g dL^{-1}— an increase sufficient to raise nearly 25% of anemic children in the sample to the 11.0 g dL^{-1} cutoff for anemia. The difference between outcomes for those with and without nutrition knowledge is not a function of expenditure levels, and the confidence intervals do not overlap for the middle eight deciles of the expenditure distribution. This analysis potentially confounds the

---

[9] This evidence is presented in full detail in Block (2002a).

[10] The definition of nutrition knowledge adopted for this analysis is based on mothers' knowledge of the benefits of vitamin A-rich foods for their children. Mothers were asked to list those benefits of which they were aware. There were nine predetermined correct answers. The survey data include for each respondent whether or not she mentioned each of the nine correct answers. To construct the nutrition knowledge proxy, I count for each respondent the proportion of correct answers given from among the nine possibilities. To split the sample, as in Figure 3, two or more correct answers are required to be said to have nutrition knowledge. This accounts for approximately 13% of the mothers sampled.

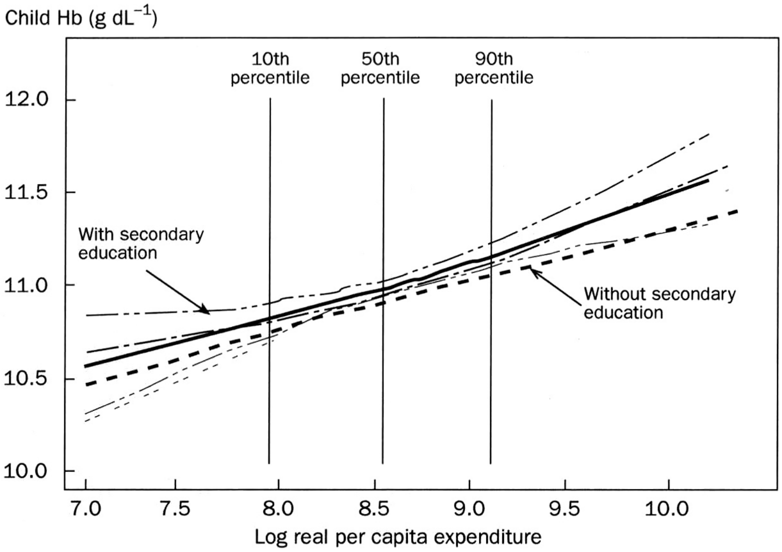


Fig. 4. The effect of maternal schooling on child hemoglobin concentration (Hb), conditional on household expenditures.

effects of nutrition knowledge and formal schooling (which may be related). However, even when this analysis is repeated for a sample limited to mothers with secondary education, the point estimates for the nutrition knowledge group lie above those for the nonknowledge group for all expenditure levels above the 10th percentile. In that case, however, the extent of the difference is reduced and the separation of the 95% confidence intervals is less clear in some portions of the distribution.

In contrast, Figure 4 illustrates that, when the sample is split between children of mothers with and without secondary education, the differences are minimal and not statistically significant even when the analysis is unconditional on nutrition knowledge. Limiting the sample used in Figure 4 to children of mothers with nutrition knowledge eliminates any marginal benefit from formal schooling.

These nonparametric relationships, even with sample splits, are inherently limited in their dimensionality. More traditional regression analysis is still necessary to fill out the picture. The regression results presented in Table 2 clarify and extend this preliminary evidence on the critical role of nutrition knowledge in determining child micronutrient outcomes. The key results pertain to the estimates for maternal schooling and nutrition knowledge (now measured as a continuous variable). The first three specifications include child and household characteristics, but exclude community characteristics. The effect of maternal schooling on child Hb is positive and significant when it enters the specification without nutrition knowledge (column 1). The same is true for nutrition knowledge when it enters the specification without schooling (column 2). When both explanatory variables enter together, both remain significant,

Table 2. Parametric estimation of the conditional demand for child micronutrient status [a] (dependent variable: child hemoglobin concentration).

Explanatory variable Estimator	(1) OLS	(2) OLS	(3) OLS	(4) OLS	(5) 2SLS [d]	(6) 2SLS [f]	(7) 2SLS [d]	(8) 2SLS [g]
Child characteristics								
Sex (1 = male)	-0.116*** (0.039) [c]	-0.116*** (0.039)	-0.115*** (0.039)	-0.113*** (0.039)	-0.119*** (0.040)	-0.110*** (0.038)	-0.120*** (0.040)	-0.118*** (0.039)
Age (months)	-0.034*** (0.019)	-0.035*** (0.012)	-0.035*** (0.012)	-0.033*** (0.012)	-0.033*** (0.012)	-0.035*** (0.012)	-0.033*** (0.012)	-0.035*** (0.012)
Age squared	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)	0.003*** (0.0005)
Age cubed	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)	-0.00003*** (0.000)
Community characteristics								
Tapwater (nslf) [b]				0.113 (0.222)	0.059 (0.229)	0.014 (0.205)	0.083 (0.234)	-0.046 (0.217)
Waste system (nslf)				-0.067 (0.411)	-0.044 (0.412)	-0.109 (0.439)	-0.036 (0.406)	-0.081 (0.436)
Distance to water (nslf)				-0.001** (0.0004)	-0.001** (0.0005)	-0.001** (0.0004)	-0.001** (0.0005)	-0.001** (0.0004)
Log price eggs				-0.391 (0.386)	-0.415 (0.382)	-0.425 (0.398)	-0.407 (0.382)	-0.453 (0.391)
Log price chicken				0.168** (0.083)	0.175** (0.085)	0.116 (0.080)	0.187*** (0.086)	0.126 (0.081)
Log price rice				0.257 (0.320)	0.201 (0.323)	0.440 (0.332)	0.162 (0.326)	0.366 (0.330)
Log price beef				-0.010 (0.029)	-0.013 (0.030)	-0.017 (0.030)	-0.012 (0.030)	-0.020 (0.030)
Log price fish				0.031 (0.044)	0.036 (0.046)	0.049 (0.045)	0.032 (0.046)	0.054 (0.047)

continued on next page

Table 2. continued

Explanatory variable Estimator	(1) OLS	(2) OLS	(3) OLS	(4) OLS	(5) 2SLS^{d}	(6) 2SLS^{f}	(7) 2SLS^{d}	(8) 2SLS^{g}
Household characteristics								
No. children under 6	-0.152***	-0.150***	-0.145***	-0.138***	-0.137***	-0.112**	-0.143***	-0.112**
	(0.049)	(0.049)	(0.049)	(0.039)	(0.040)	(0.044)	(0.040)	(0.045)
Maternal schooling	0.025***		0.018**	0.015*	0.009	-0.012	0.016*	-0.018
	(0.007)		(0.007)	(0.008)	(0.009)	(0.020)	(0.008)	(0.021)
Maternal nutrition knowledge		1.105***	0.872***	0.821***	0.786***	4.331*		4.157*
		(0.280)	(0.296)	(0.281)	(0.276)	(2.443)		(2.317)
Expenditure per adult equivalent	0.066	0.082*	0.062	0.069	0.294**	0.054	0.290**	0.321**
	(0.048)	(0.048)	(0.048)	(0.048)	(0.126)	(0.051)	(0.127)	(0.131)
R^2	0.238	0.239	0.240	0.245	0.240	0.211	0.238	0.207
Observations	3,134	3,134	3,134	3,134	3,134	3,134	3,134	3,134
Sargan test					0.754^{e}	0.264	0.707	0.509

*** = significant at 0.01 level, ** = significant at 0.05 level, * = significant at 0.10 level. OLS = ordinary least squares. 2SLS = two-stage least squares.

[a] All specifications include dummy variables (results omitted) for the six ecological zones included in the sample and for the survey round. [b] "nslf" indicates village average excluding household *i* for each *i*. [c] Robust standard errors, corrected for clustering at the village level. [d] Endogenous variable: expenditures; instruments: number of cows owned, previous year's income from remittances, number of children sleeping in a single room, size of house per adult equivalent (and, for efficiency, all other included exogenous variables). [e] *P* value from Sargan test of overidentifying restrictions. H_0: instruments are valid. Endogenous variable: maternal nutrition knowledge; instruments: nonself village average of proportion of mothers who had heard of vitamin A-rich foods, nonself village average of maternal years of schooling, nonself village average distance in minutes to health center, village proportion of mothers whose source of nutrition knowledge was health worker, village proportion of mothers whose source of nutrition knowledge was school, maternal age, maternal age squared, maternal height. Endogenous variables: expenditures, maternal nutrition knowledge; instruments: combined list from d and f.

though the point estimate and statistical significance of schooling decline. This is consistent with the interpretation that schooling's contribution in part is through its effect on nutrition knowledge.

Adding community characteristics to the remaining specifications, however, undermines the explanatory power of schooling while leaving unchanged the effect of nutrition knowledge. Schooling survives marginally in the fully specified ordinary least squares (OLS) estimate (column 4). Yet, when the potential for endogeneity and measurement error in expenditures and nutrition knowledge are addressed via two-stage least squares in the remaining specifications (columns 5-8), maternal schooling effectively drops out of the model while the estimated effect of nutrition knowledge is robust. [11]

Although these results establish a reasonably strong reduced-form relationship between maternal nutrition knowledge and child micronutrient outcomes (proxied by hemoglobin concentrations), they shed no light on the mechanisms through which nutrition knowledge operates to produce those outcomes.

The consumption of iron-rich foods is clearly critical to hemoglobin concentration (Bhargava et al 2001). Thus, the logical place for an economist to look for a mechanism through which nutrition knowledge contributes to child micronutrient status is in its effect on the allocation of household expenditures and on demand parameters. Does maternal nutrition knowledge condition these parameters?

The effect of nutrition knowledge on food budget allocation and demand

Once again combining nonparametric and traditional regression analysis, we find evidence that maternal nutrition knowledge strongly conditions the allocation of household food expenditures as well as the underlying demand parameters. [12] The household survey data from rural Central Java show that households with and without nutrition knowledge do not differ in their total food budget share (as a function of income). [13] Households at the 10th percentile of per capita expenditure allocate approximately 75% of total expenditures to food; this budget share falls to 60% at the 90th percentile of expenditures. Yet, the allocation of those similar food budgets differs considerably between the "knowledge" and "nonknowledge" households.

Figure 5 traces the share of food budgets allocated to micronutrient-rich foods as a function of real expenditures per adult equivalent, distinguishing between house-

---

[11] Note, as well, that male children have lower Hb concentrations than females, that food prices appear to add little explanatory power, and that child Hb in general declines with greater household distance to water and with each additional child under 6 years old in the household.

[12] Detailed results are provided in Block (2002b).

[13] The criteria used to define nutrition knowledge in this section differ from those used in the previous section. I now define nutrition knowledge by whether or not mothers knew the appropriate age at which to introduce complementary feeding foods to their infants. This is a lower hurdle than applied in the case of knowledge of vitamin A. Approximately 55% of mothers knew the appropriate age (i.e., 4 months).

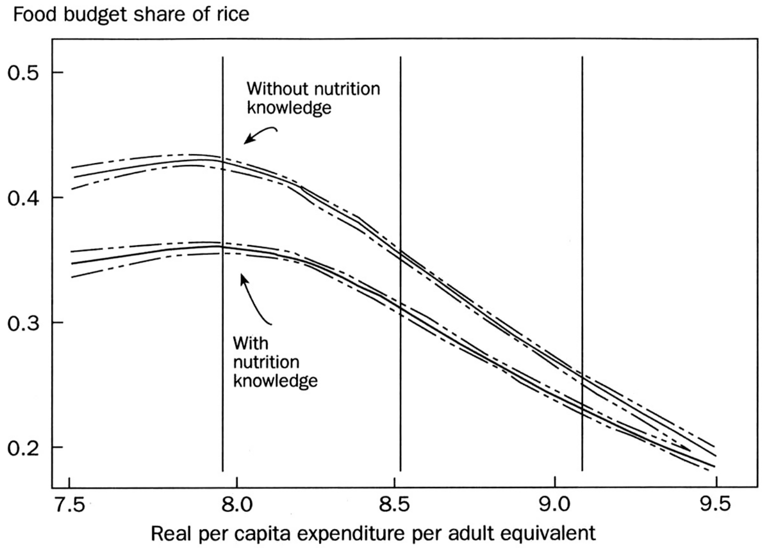


Fig. 5. Share of micronutrient-rich foods in household food budgets, conditional on expenditures. (NB: the nutrition knowledge households are traced in the higher path.)

holds with and without nutrition kowledge.[14] It is clear that households of mothers with nutrition knowledge devote larger shares of their food budget to micronutrient-rich foods. This difference is a declining function of per capita expenditures, but is large at the lower end of the distribution, and remains statistically significant (as indicated by the 95% confidence intervals) throughout the distribution. It is also clear that nutrition knowledge substitutes for income in driving the demand for micronutrient-rich foods: the mean budget share for the knowledge group at the 10th percentile of the expenditure distribution is not attained by the nonknowledge group until it reaches the sample median expenditure level.[15]

A second dimension of demand that is apparent in Figure 5 is its income elasticity. If the budget share was a flat function of log expenditures, the implied income elasticity would equal unity. However, it is well established that the income elasticity of demand for the types of high-quality foods included in the micronutrient aggregate is greater than unity, and this is reflected in the positive slopes of the budget share paths. The positive slopes of these budget share paths thus indicate that micronutrient-rich foods are a luxury for both groups. Yet, the tendency for the budget share paths of these two groups to converge as expenditures increase (e.g., the steeper rate of

---

[14] "Micronutrient-rich foods" are taken here as a composite of beef, chicken, vegetables, milk, eggs, fruit, and fish. Block (2002b) provides a similar analysis for eggs in particular.

[15] As in Figure 3, the apparent effect of nutrition knowledge in Figure 5 may be confounded with the effect of formal schooling. Yet, even more than before, limiting the sample to mothers with secondary education leaves the picture in Figure 5 largely unchanged.

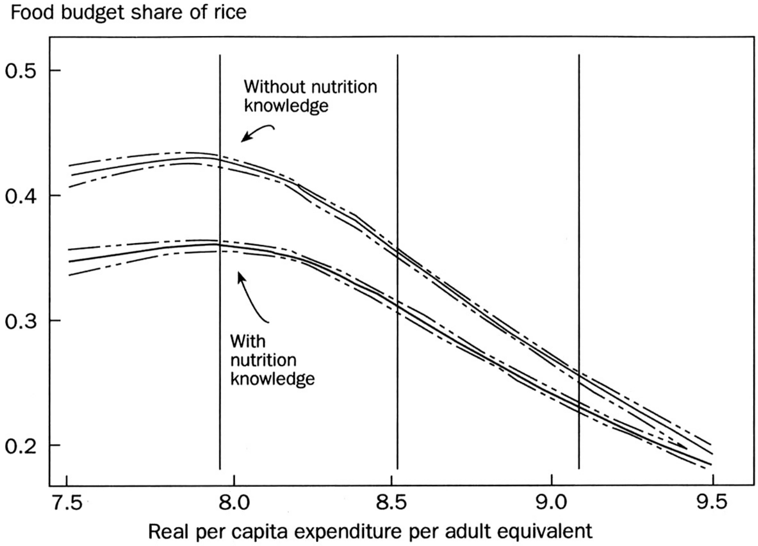


Fig. 6. Share of rice in household food budgets, conditional on expenditures. (NB: the nutrition knowledge households are traced in the lower path.)

incline for the nonknowledge group) implies a higher income elasticity of demand for those households lacking in nutrition knowledge.

If households with nutrition knowledge allocate substantially larger shares of their food budgets to micronutrient-rich foods while their total food budget share is not different from that of nonknowledge households, then what is it that the knowledge households are not buying as intensively? The answer is rice.

Figure 6 traces the share of food budgets for these groups allocated to rice. The result is virtually a mirror image of the micronutrient case. Households lacking in nutrition knowledge allocate substantially larger food budget shares to rice throughout the expenditure distribution. As in the previous case, these statistically and economically significant differences are a declining function of expenditures. This is a particularly striking result in the context of Indonesia's dominant rice economy. The difference in rice shares of the food budget between the knowledge and nonknowledge groups accounts for essentially the entire difference in budget allocations to micronutrient-rich foods. Rice shares of the food budget are a declining function of per capita expenditures for both groups, but, as before, the share for the nonknowledge group at the sample median expenditure is attained by the knowledge group at the 10th percentile of the expenditure distribution.[16]

---

[16] These results, too, are unaffected by limiting the sample to households of mothers with secondary education.

These results have direct implications for understanding the effects of the Indonesian economic crisis on child nutrition. Recall from the section on "Child nutrition during the crisis" that the most severe effect was not on gross caloric (e.g., rice) intake, but rather on the consumption of micronutrient-rich foods. The crisis-driven decline in child hemoglobin concentrations (Fig. 2) reflects changes in mean over time. Yet, this implies that some children were more severely affected than the mean, and others less so. What are the household characteristics associated with different outcomes? The results presented in the section on "Nutrition knowledge, schooling, and child micronutrient status" establish a relationship between maternal nutrition knowledge and child hemoglobin outcomes, and the results of this section suggest that it is through its effect on conditioning food budget allocations and demand parameters that nutrition knowledge works to contribute to improved micronutritional outcomes. These issues are of primary importance in a context in which the poorest families allocate 75% of their total income to food and 40% of their total income to rice, and in which rice prices tripled over a period of 18 months.

The ability to cope with rapidly rising staple food prices may be the central benefit of nutrition knowledge in the context of Indonesia's crisis. The cross-price elasticity of demand between micronutrient-rich foods and rice thus becomes a central concern. Estimation of a demand function for micronutrient-rich food yields point estimates for the income elasticity, along with the own- and cross-price elasticities of demand.[17] Does nutrition knowledge alter these parameters? The results presented in Table 3 indicate the following: knowledge and nonknowledge households do not differ statistically in their own-price elasticity of demand for micronutrient-rich food; yet, as suggested in Figure 5, the income elasticity of demand is greater for the nonknowledge households.

The most striking difference between knowledge and nonknowledge households, however, is precisely in the sensitivity of their micronutrient expenditures to increases in the price of rice. Various approaches to estimating those parameters yield essentially the same result: households without nutrition knowledge significantly reduce their expenditures on micronutrient-rich food when rice prices increase, while households with nutrition knowledge do not change their micronutrient expenditures as a function of rice prices. These differences between household types are statistically significant in three of the four specifications presented in Table 3. Block (2002b) presents similar evidence specifically for eggs (the best single proxy for micronutrient-rich foods).

Conclusions

Additional results from the estimation of demand functions suggest that maternal schooling and having fewer children under 6 also increase households' food budget allocations toward high-quality foods. Yet, these additional findings provide little

---

[17] Full results for the estimation of demand functions, as well as additional nonparametric results, are presented in Block (2002b).

Table 3. Derived elasticities of demand for micronutrient-rich foods.[a]

Dependent variable:	(1) Budget share micronutrient-rich foods[b]	(2)	(3) Log PCE micronutrient-rich foods	(4)
Estimator:	OLS	2SLS	OLS	2SLS
Households with nutrition knowledge				
Own-price	−1.02***	−1.25***	-0.690***	4.751***
Cross-price rice	0.034	0.334	0.014	0.330
Expenditure	0.970***	0.865***	1.076***	0.987***
Households without nutrition knowledge				
Own-price	-1.055***	-0.814***	-0.691***	4.677***
Cross-price rice	0.052	-0.866***	-0.131*	-0.975**
Expenditure	1.058***	1.515***	1.181***	1.572***
Tests for differences between households with and without nutrition knowledge				
Chow test for own-price[c]	0.147	0.009***	0.990	0.752
Chow test for cross-price	0.780	0.021***	0.030**	0.039**
Chow test for expenditure	0.000***	0.0003***	0.000***	0.004***

*** = significant at the 0.01 level, ** = significant at the 0.05 level; * = significant at the 0.10 level.
[a] Based on coefficient estimates from Table 2. OLS = ordinary least squares, 2SLS = two-stage least squares, PCE = per capita expenditure. [b] Elasticities are calculated at the sample mean budget shares. [c] Chow test (*P*-value) of H_0: equal elasticities for knowledge and nonknowledge households.

basis for public policy to promote child micronutrient status. Delivering formal education is difficult and expensive, often more so when targeted toward women, and most countries are already maximizing their efforts in that direction. Similarly, public policies oriented toward reducing fertility are both difficult to implement and highly controversial. However, the findings presented in this study suggest the availability of a relatively simple and powerful approach. Household resource allocation, as conditioned by elasticities of expenditure and price, is a pervasive economic force. The present findings demonstrate that maternal nutrition knowledge shapes household food demand parameters and budget allocations in predictable, positive, and policy-relevant ways. By that means, maternal nutrition knowledge contributes to improved child micronutrient status. This may well explain critical differences across households in the nutritional effect of Indonesia's economic crisis.

Maternal nutrition education may also have a substantial macroeconomic payoff, given the cognitive and labor productivity losses estimated specifically for iron deficiency. The results presented above provide the basis for crude approximations. Using an accounting approach developed by Ross and Horton (1998), the baseline 50% prevalence of child anemia in rural Central Java (if it is broadly representative of Indonesia) costs a $32.52 per capita loss of gross domestic product (GDP) (in 1999 PPP—purchasing power parity—dollars), or approximately $6.73 billion (1.33% of GDP). Increasing real per adult equivalent household expenditures by one standard deviation would (based on the coefficients estimated in Table 2, column 8) reduce the per capita loss to anemia by $1.95, a savings of nearly $404 million. However, a one standard deviation increase in the proportion of mothers having nutrition knowledge (as defined in the section on "Nutrition knowledge, schooling, and child micronutrient status") would save $5.85 per capita, or $1.2 billion in lost national income (nearly 0.0025% of total GDP in 1999 PPP dollars).[18] The prospects for a one standard deviation increase in maternal nutrition knowledge may be low in the short run, but this is surely a more attainable goal than a similar increase in per capita income, and one with three times the benefit in saved GDP. This points strongly toward the importance of public efforts to promote specific nutrition knowledge of mothers.

These figures represent only crude orders of magnitude. Yet, benefits on this order of magnitude suggest that nutrition education programs may provide a relatively cost-effective and tractable vehicle through which governments can promote child micronutrient status. Such benefits are likely to compare favorably with many alternative uses of public investment funds, to say nothing of the resulting improvements in the quality of life and income-earning prospects of the poor.

References

Alderman H, Garcia M. 1994. Food security and health security: explaining the levels of nutrition status in Pakistan. Econ. Dev. Cult. Change 42-43:485-507.

Barrera A. 1990. The role of maternal schooling and its interaction with public health programs in child health production. J. Dev. Econ. 32:69-91.

Behrman J, Deolalikar A. 1988. Health and nutrition. In: Chenery PH, Srinivasan TN, editors. Handbook of development economics. Vol. 1. Amsterdam (Netherlands): North-Holland Press.

Behrman J, Wolfe B. 1984. More evidence on nutrition demand: income seems overrated and women's schooling underemphasized. J. Dev. Econ. 14(1-2):105-128.

---

[18] These calculations are based on the formula of Ross and Horton (1998), who estimate that cognitive loss from iron deficiency = 4% × wage share of GDP × GDP/capita × prevalence of child anemia. Four percent is the empirically derived loss in labor productivity. I make the extremely crude assumptions that the labor share of Indonesia's GDP is 2/3 (a figure in line with recent estimates [not for Indonesia] by Gollin 2002) and that the prevalence of child anemia in rural Central Java is nationally representative. The change in anemia prevalence among children is calculated by shihfting the cumulative distribution function of child hemoglobin concentration by an amount equal to the hypothesized change in the explanatory variable times its point estimate from Table 2, column 8. Calculations are based on a 1999 population of 207 million and a GDP of $505 billion in 1999 PPP dollars.

Behrman J, Wolfe B. 1987. How does mother's schooling affect the family's health, nutrition, medical care usage, and household sanitation? J. Dev. Econ. 27(1-2):395-420.

Bhargava A, Bouis H, Scrimshaw N. 2001. Dietary intakes and socioeconomic factors are associated with the hemoglobin concentration of Bangladeshi women. J. Nutr. 131:758-764.

Block S. 2002a. Nutrition knowledge versus schooling in the demand for child micronutrient status. Working Paper No. 93. Center for International Development, Harvard University, Cambridge, Mass., USA.

Block S. 2002b. Why does maternal nutrition knowledge affect child micronutrient status? Parametric and non-parametric evidence on the demand for micronutrient-rich foods. Fletcher School, Tufts University, Medford, Mass., USA. (In mimeo.)

Block S, Keiss L, Webb P, Kosen S, Moench-Pfanner R, Bloem MW, Timmer CP. 2002. Did Indonesia's crises of 1997/98 affect child nutrition? A cohort decomposition analysis of national nutrition surveillance data. Working Paper No. 90. Center for International Development, Harvard University. Cambridge, Mass., USA.

Bouis H, Haddad L. 1992. Are estimates of calorie-income elasticities too high? A recalibration of the plausible range. J. Dev. Econ. 39:333-364.

Bouis H, Novenario-Reese J. 1997. The demand for micronutrients in Bangladesh. Washington, D.C. (USA): International Food Policy Research Institute. (In mimeo.)

Friedman J, Levinsohn J. 2001. The distributional impact of Indonesia's financial crisis on household welfare: a "rapid response" methodology. NBER Working Paper No. 8564.

Collin D. 2002. Getting income shares right. J. Polit. Econ.110(2).

Lavy V, Strauss J, de Vreyer P. 1996. Quality of health care, survival, and health outcomes in Ghana. J. Health Econ. 15:333-357.

Ross J, Horton S. 1998. The economic consequences of iron deficiency. Ottawa (Canada): The Micronutrient Initiative.

Suryahadi Asep, Sudarno Sumarto, Yusuf Suharso, Lant Pritchett. 2000. The evolution of poverty during the crisis in Indonesia, 1996 to 1999 (using full Susenas sample). Social Monitoring and Early Response Unit, Government of Indonesia, (In mimeo.)

WHO, UNICEF, UNU. 1998. Iron deficiency anemia: prevention, assessment and control. In: Report of a joint WHO/UNICEF/UNU consultation. Geneva, Switzerland.

Notes

Author's address: Tufts University, Medford, Mass., USA, steven.block@tufts.edu.

Acknowledgment: The studies of rural Central Java described in this paper were based on household survey data collected under the direction of Helen Keller International (HKI), the Jakarta-based staff of which generously provided access to the data and collaborated in the analysis. The author is grateful to HKI, as well as to USAID/Indonesia, for its support through the Food Policy Support Project, and to Peter Timmer for collaboration and feedback on all phases of the work.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

National and international agricultural research and rural poverty: the case of rice in India and China

Shenggen Fan, C. Chan-Kang, Kerning Qian, and K. Krishnaiah

Using varietal adoption and performance data, this study calculated the total benefits from rice varietal improvement research in China and India. The study then used genetic or pedigree information to partition the total benefits between these two countries and IRRI. Finally, the study used reported elasticity of poverty reduction with respect to agricultural output growth to assess the effects of national and international research on poverty reduction in rural India and China. The results indicated that rice varietal improvement research has contributed tremendously to the increase in rice production in both countries. In China, research benefits as a share of rice production value range from 14% to 19%. In India, they range from 15% to 23%. The benefits produced just from rice research are on average 10 times higher than the total agricultural research investment in China. In India, the corresponding ratio is 9 to 1. Rice research has also helped reduce large numbers of rural poor. Without research investments in rice, the number of poor would be much higher today. IRRI played a crucial role in these successes. In 1999, for every $1 million invested at IRRI, more than 1,500 and 12,000 rural poor were lifted above the poverty line in China and India, respectively. These poverty reduction effects were even larger in the earlier years. Together with improvements in rural infrastructure, education, and health, agricultural research will play an even larger role in the future in reducing poverty in developing countries. However, increased and stable funding for national and international agricultural research is a must to reduce both rural and urban poverty.

Agricultural research has played an important role in agricultural production and productivity growth in many developing countries. The Green Revolution in the 1960s in Asia is a typical case. High-yielding varieties released by national and international agricultural research centers substantially increased crop production and consequently farmers' income in many Asian countries. As a result, rural poverty was directly reduced. In addition, rapid agricultural growth provided a fundamental base for economic development that led to the regional economic boom of the 1980s and ’90s. Thus, rural poverty also declined through these indirect effects in the region and the food shortage foreseen by many observers disappeared. While there have been many studies on the effects of the Green Revolution on production and productivity growth, there have been few attempts to link agricultural research investments to rural poverty reduction.[1] In addition, what role the CGIAR centers have played as a partner in this process has not been well documented and understood. This study is designed to fill the gap in our knowledge using the case of rice in India and China. Information on poverty effects of agricultural research investments will help national and international policymakers in mobilizing resources and in setting priorities for agricultural research in the future.

India and China are the two most populous countries in the world. Together they account for more than 38% of the total population and for almost 50% of the rural residents in the world. In spite of recent rapid economic growth in both countries, many people are still under the poverty line. It is estimated that India has close to 200 million and China has 30 million rural people under the poverty line. However, if the poverty line of US$1 per day measured in purchasing power parity is used, China would have substantially more poor than the official figure. Using this line, China has more than 100 million rural poor in 1998 (World Bank 2000). These poor people do not have adequate income to maintain a healthy and productive life.

Rice is a major staple food crop for many developing countries, being not only a main source of calories but also an important source of income and employment for many farmers, particularly poor households. For the developing countries as a whole, area planted to rice accounted for 34% of their arable land, while rice production accounted for 47% of their total grain output in 2000. For Asian developing countries, these shares are even larger. China and India are the two leading rice-producing countries worldwide. Of the 112 rice-producing countries, China and India have remained the top two countries of production since 1961, the first year of data available from FAOSTAT. In 2001, they jointly produced 53% of the world’s rice production with 48% of world rice area. In China and India, rice is the most important food crop, accounting for about 30% of their populations’ daily calorie intake (FAO 2002).

The International Rice Research Institute (IRRI) has been collaborating with China and India for the past several decades. The major modes of collaboration have been joint research, exchanges of human resources and scientific information, and exchange of germplasm. Therefore, we select rice in these two countries to evaluate the total benefits from varietal improvement research, to make an attempt to partition these benefits to IRRI, and to estimate the contribution of rice breeding research to poverty reduction.

In contrast to the traditional econometric approach proposed by Griliches (1957), this study uses extensive data on the adoption and performance of the rice varieties

---

[1] Evenson and Gollin (2002) estimated economic returns of varietal improvement of the CG’s research.

used by Chinese and Indian farmers to evaluate the total benefits from rice varietal improvement research. The study then relies on pedigree information to analyze how international agricultural research has contributed to productivity gains in Chinese and Indian rice production. Finally, the study uses the calculated benefits, together with poverty impact parameters reported in recent IFPRI studies, to assess how domestic and international rice research has contributed to poverty reduction.

Rural poverty in China and India

Figure 1 shows the changes in the incidence of rural poverty measured as head-count ratios. The head-count ratio is the percentage of the rural population falling below the poverty line. The poverty line used in India is defined as 49 rupees per month at 1973-74 prices (Datt and Ravillion 1997). This poverty line is equivalent to \$0.965 per person per day measured in 1993 purchasing power parity (PPP), and is only slightly below the \$1 per day widely used for cross-country comparison by the World Bank and others. China adjusts its official poverty line annually (China State Statistics Bureau 1999). In 1990, the official poverty line was 300 yuan per person per year, equivalent to \$0.67 per day measured in 1990 PPP. The poverty line was raised to 635 yuan in 1998, equivalent to \$0.84 per person per day.

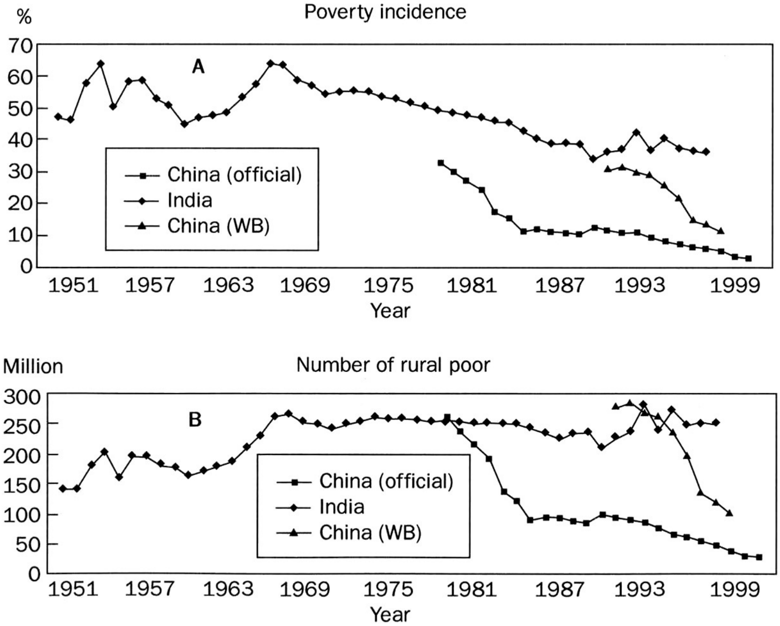


Fig. 1. Rural poverty in China and India. WB = World Bank.

Using these poverty lines, the incidence of poverty declined dramatically over the last several decades in both countries. In India, rural poverty fluctuated from 50% to 65% in the 1950s and early ’60s before beginning a steady decline from about two-thirds of the rural population in the mid-1960s to one-third of the rural population in the late ’80s. Rural poverty increased to about 40% in the early '90s when the policy reforms were implemented. Recent official data show that the poverty rate declined to 27% in 1999.

The long downward trend in poverty in rural India from 1967 to 1999 coincided with several important factors. The rapid adoption of high-yielding varieties (HYVs) together with improved irrigation and the use of fertilizer increased agricultural production and productivity sharply during this period. This change in technology was a direct result of increased government investment in agricultural research and extension, infrastructure, irrigation, and education during the 1960s, ’70s, and ’80s. The increase in government investments also improved nonagricultural employment opportunities and wages, thus contributing to further reductions in rural poverty.

Prior to 1978, per capita income was low in China. In 1978, 33% of the total rural population (260 million residents) lived below the official poverty line without access to sufficient food or income to maintain a healthy and productive life. In the last two decades, however, China achieved remarkable progress in reducing rural poverty. Following the rural reforms begun in China in 1978, per capita income increased from 220 yuan (1990 price) in 1978 to 522 yuan (1990 price) in 1984, averaging a growth of 15% per annum. The income gains were shared widely enough to cut the number of poor, and hence the rate of poverty, by more than half. By 1984, only 11% of the rural population was below the official poverty line. Because of the equitable distribution of land to families, income inequality, measured as the Gini coefficient, increased only slightly despite the sharp income increase observed from 1978 to 1984.

From 1985 to 1989, rural income continued to increase, but at a much slower pace, averaging 3% per annum. This was due mainly to the stagnation of agricultural production after the reforms and, by the end of 1984, the effects of fast agricultural growth on rural poverty were largely exhausted. Rural income distribution became less egalitarian and the Gini coefficient rose from 0.264 in 1985 to 0.301 in 1989 (China State Statistics Bureau 1990). As a result, the number of poor increased from 89 million in 1984 to 103 million in 1989, a net gain of 14 million in five years. Only in 1990 did rural poverty begin to decline again. The number of rural poor dropped from 103 million in 1989 to 34 million in 2000, equivalent to an average rate of 9% per annum.

The above evidence from China and India indicates that, whenever agricultural growth is higher, poverty reduction is greater. This suggests that agricultural growth spurred by agricultural research is critical to reducing rural poverty.

Rice research and rice production[2]

For thousand of years, farmers in Asia have improved their rice yields by selecting high-yielding varieties. Modern national and international rice breeding programs have developed more formal and structured methods in crossing and selecting improved rice varieties. The international exchange of genetic resources in various forms (landraces and advanced lines) has become an important feature of modern rice breeding.

IRRI's rice breeding program began in October 1961 and in the following year 38 crosses were made. Eleven of them involved Dee-Gee-Woo-Gen (DGWG), TN-1, and T-Geo-Tze, three semidwarf varieties from Taiwan Province of China. IR8, released in 1966, was a selection from the eighth cross between Peta, a tall Indonesian variety, and DGWG; IR5 was released in 1967 from a selection of the fifth cross between Peta and Tangkai Rotan, a Malaysian variety of medium height. More varieties were released later. IR20 and IR22 were released in December 1969, IR24 in May 1971, and IR26 in November 1973. All but IR5 were semidwarfs, inheriting their high-yielding and short-statured traits from DGWG. By 1975, 29 IR varieties had been released.

IRRI crosses grew in number and complexity over time. Breeding research gave greater emphasis to insect and disease resistance and to adaptability to unfavorable environments, resulting in greater yield and improved yield grain stability (IR26 and IR42). In addition, newer varieties grew faster, meaning that they use less water, that they are exposed to field hazards for a shorter period of time, and that multiple cropping is facilitated (IR36, IR50, IR58).

Rice research in India has a long history and has been one of the top priorities of the government-supported research program. Although some sort of research is carried out by all universities, which include basic and applied research, about 100 centers and/or locations are prominently involved in the improvement of the crop—varietal development, crop management, and crop protection. Before the introduction of TN-1 and IR8, almost all these centers were functional, with only isolated efforts for rice improvement. The Indian Council of Agricultural Research (ICAR) brought the activities of these centers into one line through the All India Coordinated Rice Improvement Project (AICRIP) in 1965, which is now redesignated as the Directorate of Rice Research (DRR), with the additional mandate of strategic and applied research. The DRR, through AICRP, in partnership with about 60 locations representing all rice-growing ecologies, does work in partnership and produces rice varietal, management, and protection technologies. Most of the activities of all these centers are funded by ICAR. Another 40 centers extend additional cooperation, particularly in testing the newly developed rice cultivars. Core activities of varietal development and related activities are performed by the DRR and its funded centers (about 54)

---

[2] The history of international rice research is heavily drawn from various IRRI publications and Dalrymple (1986), while the evolution of Chinese and Indian rice research programs is drawn from their respective government documents.

located across the country in all the states, and by the Central Rice Research Institute (CRRI) in Cuttack, Orissa, and its substations and a half dozen ICAR institutes. Rice research is also being conducted by the state universities such as in Tamil Nadu, Andhra Pradesh, West Bengal, and Punjab.

The introduction of semidwarf varieties from IRRI to India occurred in 1964 when C. Subramaniam, minister of Food and Agriculture at the time, visited IRRI and was given seeds of new rice varieties that included TN-1. By 1966, IR8 and other IRRI lines were tested in various experimental fields in India. Shortly after their introduction, these IRRI varieties were crossed with local varieties and, by 1998, about three-quarters of the rice area in India was sown to high-yielding rice varieties (Indiastat 2002).

With a history of 7,000 years of rice cultivation, China is one of the origins of cultivated rice in the world. Rice production can be found anywhere in China but more than 90% of Chinese rice production is concentrated south of the Huaihe River and Qin Mountain. Many types of rice are grown in China, including indica, japonica, sweet, and glutinous rice.

Conventional rice breeding began in China in 1906. However, systematic and well-targeted breeding using rigorous methodologies did not start until 1919 when the Nanjing Higher Agricultural School and Guangzhou Agricultural Specialized School set up breeding programs. From 1919 to 1949, about 100 rice varieties were bred and released.

After the establishment of the People's Republic in 1949, the government paid greater attention to rice breeding. The development of the rice breeding program had three stages. During the first stage from 1950 to the beginning of the 1960s, great efforts were made in the selection, evaluation, and use of local rice varieties. During this stage, 121 rice varieties were released. The second stage of rice breeding (from the beginning of the 1960s to the beginning of the '70s) focused on the breeding of dwarf varieties. After a farmer found a dwarf plant (only 70 cm tall) in 1956, Chinese scientists began the breeding program that led to the development of the first high-yielding dwarf variety of rice, Guang Chang Ai, in 1957, a few years before the foundation of IRRI.[3] Guang Chang Ai—an indica variety—and its offspring were quickly adopted in southern China. The first semidwarf japonica variety introduced to China in 1957 was Nongken 58, a selection from a Japanese variety, which was crossed with various local varieties.

With adequate fertilizer and water, farmers produced yields of 5–6 t of rice per hectare. Compared with that of IR8, the Chinese variety had a shorter growing period of 100-115 days, making it possible to expand the double cropping of rice in the south and southeast. In 1965, most rice areas in Guangdong Province were planted with dwarf varieties. By 1977, these varieties were grown on more than 80% of China's total rice area. This wide use of dwarf varieties was 10 years ahead of that of other countries.

---

[3] Scientists at the Guangdong Academy of Agricultural Sciences developed Guang Chang Ai, China's first semidwarf variety (Shen 1980, Dalrymple 1986).

The third stage is characterized by the development of hybrid rice, in which China was a pioneer. Research on hybrid rice in China began in 1964. However, the genetic tools essential for producing F_1 hybrids and cytoplasmic male sterile (CMS), maintainer, and restorer lines were not developed until 1973, and hybrid seed production techniques were not established until 1975. IR8 was used by Chinese scientists as a restorer line. The use of IR8 as a restorer line may have speeded up the development of hybrid rice in China. However, even if IR8 had not been used, Chinese scientists would have found an alternative restorer sooner or later. Since then, the area under hybrid rice has increased steadily. In 1981, hybrid rice accounted for 23%, but two decades later it accounted for 61% of total rice production.[4]

The more formal IRRI involvement in China's rice breeding program began in the 1970s although IR8 was introduced and tested in Guangdong in 1967. In the early 1970s, a delegation of Chinese officials visited the Philippines and was given a bag of rice seeds developed at IRRI. This marked the first formal cooperation between IRRI and China.

As a result of these national and international efforts, rice crop production in both China and India has increased substantially for the last several decades. From 1961 to 2001, rice production grew at an average of 2.6% per year in India and by 2.7% per year in China, much higher than their respective population growth rates of 2.1% and 1.7%. Much of the increase in rice production was a result of a gain in yield. In India, yield increase accounted for 70% of the total increase in rice production, while in China almost all the production increase came solely from yield increase. In India, yield doubled from 1.5 t ha^{-1} in 1961 to 3.0 t ha^{-1} in 2001, while in China yield tripled from 2.1 to 6.3 t ha^{-1} over the same period (Table 1). The development of improved or modern rice varieties in conjunction with irrigation and the greater use of modern inputs (such as fertilizer and pesticide) have been instrumental to the substantial yield increase.

Research benefits and the contribution of international research

In this section, we will first use varietal adoption data to estimate the total research benefits from rice varietal improvement research, and then use genetic or pedigree information on each variety planted in the two countries to assess the contribution of IRRI to these benefits.

To estimate the benefits from rice research we used the following procedure.[5] First, we determined the gain in yield resulting from the development and adoption of high-yielding varieties. To isolate the contribution of improved varieties to yield increase from other factors, we collected experimental yield data of adopted rice varieties in India and China. Next, we chose numeraire varieties specific to each

---

[4] China has never officially published rice output by different type. The shares reported here are calculated by the authors using the area by variety data from the Ministry of Agriculture.

[5] Pardey et al (1996) used a similar procedure.

Table 1. Trends in rice area, production, and yield.

Item	1961	1970	1980	1990	2000	2001	Growth rate (%)
Area harvested (millions of ha)							
India	34.7	37.6	40.2	42.7	44.8	44.5	0.60
China	27.0	33.1	34.5	33.5	30.3	28.6	0.02
World	115.5	133.1	144.6	146.9	154.1	151.5	0.58
Production (millions oft)							
India	53.5	63.3	80.3	111.5	129.4	131.9	2.71
China	56.2	113.1	142.9	191.6	189.8	181.5	2.62
World	215.7	316.4	396.8	518.2	600.6	592.8	2.54
Yield (kg ha^{-1})							
India	1,542	1,685	2,000	2,613	2,890	2,964	2.09
China	2,079	3,416	4,144	5,717	6,264	6,350	2.60
World	1,867	2,377	2,745	3,529	3,897	3,912	1.95

Source: FAO (2002).

country.[6] Ideally, the numeraire should be a variety widely adopted in China and India before the establishment of their respective rice research programs. We then compute the yield premium of newer adopted varieties against the numeraire variety. The benefits for each variety are calculated by multiplying yield gains by price, and again by area sown to the variety. The total benefits are simply the sum of those for all varieties. This approach implicitly assumes that increased rice production from rice research does not affect rice price.[7]

Three major types of rice are planted in China: indica rice, japonica rice, and hybrid rice. Therefore, it is necessary to choose a numeraire variety specific to each type of rice. The numeraire variety we chose for conventional indica rice is Bao Tai Ai, a variety released in 1959 by the Yulin Regional Agricultural Experiment Station in Guangxi. Because of data limitations, we chose Nongken 58, a variety introduced from Japan in the 1950s, as our numeraire for japonica varieties. Since all early hybrid varieties had an IRRI parent, the numeraire we chose for hybrid rice is Zhen Zhu Ai, a conventional indica variety that does not have any IRRI ancestry.[8] These numeraire varieties were all widely adopted and used as breeding materials for subsequent varieties.

For India, we chose a numeraire variety specific to each state. These numeraire varieties were local varieties widely adopted by farmers in the early 1960s before

---

[6] We use the chain rule in estimating the yield premium of various varieties over the numeraire variety. For example, before variety B was released, it was tested against numeraire A. The yield premium of variety B is Yb/Ya. But before variety C was released, variety B was used as a check variety. The yield premium of variety C over B is Yc/Yb'. Note that Yb and Yb' are not equal since they are the yields of the same variety tested at a different time and location. The yield premium of variety C over numeraire variety A is therefore (Yc/Yb') x (Yb/Ya).

[7] Under neutral technical change with fixed factor proportions, the percentage increase in experimental yield translates into an equal, proportional, rightward shift of industry supply in the quantity direction (Alston et al 1995).

[8] This was recommended to us by Professor Yuan Long Ping.

the introduction of IR8 to India. The numeraire varieties used for each state are the following: Andhra Pradesh: HR67; Assam: Latisail; Bihar: N136; Gujarat: Mahsuri; Haryana, Himachal, and Punjab: Jhona349; Karnataka: SR26 B; Kerala: Ptb 10; Madya Pradesh: Safri17; Maharashtra: Ratnagiril; Orissa: T141; Tamil Nadu: CO25; Uttar Pradesh: Sarjoo49; and West Bengal: NC1263.[9]

Figure 2 compares rice farm yield and experimental yield achieved in India and China. Figure 2A shows that farm yield doubled from 1.5 to 3 t ha^{-1} in India from 1961 to 2001. In China, the observed increase in yield was even more significant, tripling from 2.1 t ha^{-1} in 1961 to 6.3 t ha^{-1} in 2001. Compared with farm yield, experimental yield increased substantially less over time in both India and China (see Fig. 2B). This is because the increased use of inputs such as fertilizer also contributed to farm yield while the increased use of inputs has been controlled in the experimental test. On average, experimental yield increased from 3.8 to 4.3 t ha^{-1} from 1967 to 2000 in India, and from 4.5 t ha^{-1} in 1959 to 6.8 t ha^{-1} in 2000 in China.

Figure 2C shows the average yield gain over the numeraire variety. In China, the gain in yield resulting from new varieties accelerated from 1959 to the early 1980s and plateaued afterward. In India, the average gain in yield increased sharply from 1967 to the early 1990s, remained constant in the following years, and increased again in the late 1990s. Overall, the yield gain realized in China was higher than in India. In 2000, the average gain in yield with respect to the numeraire was 31% and 20% in China and India, respectively.

Table 2 presents the estimated benefits from rice research reported in 2000 constant prices. In India, the benefits from rice research were $2.1 billion in 1991, and they increased to $3.6 billion in 2000. In China, the benefits from rice research amounted to $5.2 billion in 2000, a 40% increase from the benefits realized in 1981 ($3.7 billion). The source of these benefits changed significantly over time. In 1981, indica rice accounted for 70% of the total rice research benefits, while japonica rice and hybrid rice accounted for 4% and 26%, respectively. In 2000, 72% of the rice research benefits were attributed to hybrid rice, whereas the share of indica rice declined to only 16% and japonica rice accounted for 12%. India's research benefits as a share of total rice production value increased from 19% in 1991 to 23% in 2000 (Table 3). In China, rice research benefits accounted for a similar share of rice production value, accounting for 18.5% in 1981 and 17.1% in 2000.

The use of IRRI varieties by the national agricultural research system falls within the following categories: (1) direct use of IR varieties under either direct IR names or local names, (2) direct use of IR breeding lines or crosses under either IR numbers or local names, and (3) use of IR varieties or lines as parents in local breeding programs. As mentioned earlier, the impact of IRRI on national rice production occurs through the direct adoption of IRRI varieties (lines) or through the use of these varieties (lines) as breeding materials. To gain some insights into IRRI's impact in China and India, we first examined the share of rice area sown to varieties that have

---

[9] Our source of experimental yield data in India was AICRIP (All India Coordinated Rice Improvement Program).

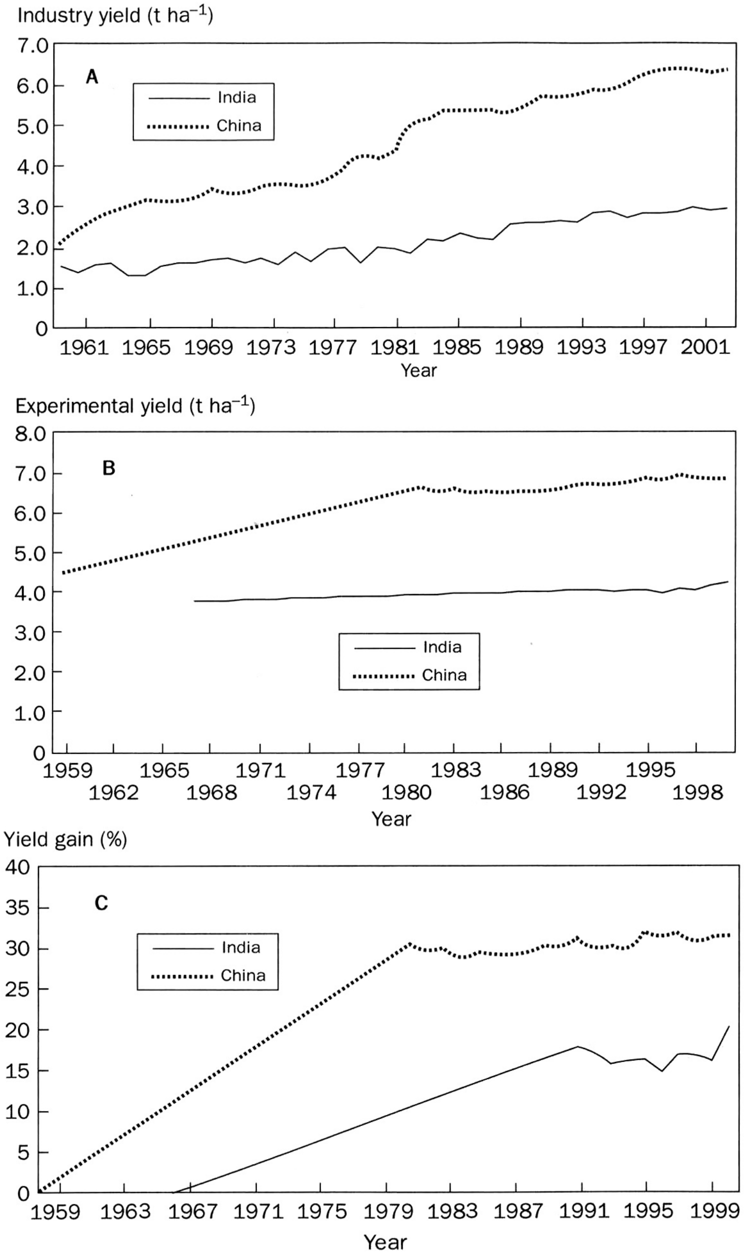


Fig. 2. Farm field yield and experimental yield in India and China. Source: Industry yield was compiled by authors from FAOS (2002); experimental yield and yield gain were compiled by authors from collected experimental yield data.

Table 2. Benefits from rice research.

	China					India	
Year	Indica	Japonica	Hybrid	All rice	Agricultural research expenditures	All rice	Agricultural research expenditures
	(millions of 2000 US$)						
1981	2,592	159	942	3,693	237		
1982	3,078	150	653	3,881	246		
1983	2,697	188	1,006	3,890	306		
1984	1,980	158	1,233	3.370	349		
1985	1,959	181	937	3,077	342		
1986	1,812	214	932	2,958	347		
1987	1,594	209	1,177	2,981	328		
1988	1,749	276	1,761	3,786	384		
1989	2,116	384	2,079	4,579	399		
1990	1,742	314	2,431	4,487	361		
1991	866	342	1,925	3,134	387	2,086	300
1992	1,100	459	2,019	3,578	454	2,354	299
1993	947	510	2,104	3,560	473	2,026	294
1994	1,383	554	2,586	4,523	506	2,125	310
1995	905	526	3,175	4,605	503	2,220	325
1996	1,506	647	4,127	6,281	522	2,065	333
1997	1,341	1,397	4,993	7,731	483	3,837	352
1998	1,379	1,022	5,122	7,522	573	3,764	361
1999	1,151	700	4,417	6,267	660	3,561	455
2000	849	650	3,729	5,228		3,583	

Source: compiled by the authors.

IRRI ancestry (Fig. 3). In China, the share increased from 23% in 1981 to reach a peak of 54% in 1995, then declined to nearly 20% in 2000. Table 4 also reveals that the impact of IRRI in China occurred mostly through the use of IRRI varieties as breeding materials rather than through direct adoption. Moreover, IRRI contributed mostly to hybrid rice, whereas practically none of the japonica varieties were bred with IRRI materials. In 1997, 50% of hybrid, 31% of indica, and only 0.5% of japonica Varieties had an IRRI ancestor in their pedigree. In India, IRRI's impact is found in both the direct adoption of IRRI varieties and the use of breeding materials from IRRI. In 2000, about 14% of the varieties adopted were IRRI-released, whereas the area of varieties with IRRI ancestry (including direct adoption) accounted for nearly 60% of total rice area in India.

To attribute the shares of the rice benefits to IRRI, we followed the method described in Pardey et al (1996), which developed various rules to attribute benefits to a specific research or breeding program, in this case to IRRI research. These rules take into consideration various factors involved in varietal development such as the recent versus the past and breeding efforts versus heritability of traits. The binary-parents rule gives full credit to IRRI if the two parents of a variety or any of its

Table 3. Research benefits as a share of production value.

Year	China				India
	Indica	Japonica	Hybrid	All rice	All rice
			(%)		
1981	24.0	3.3	21.7	18.5	
1982	24.0	2.8	20.0	18.0	
1983	21.1	3.2	17.6	16.0	
1984	21.0	2.8	17.2	15.1	
1985	23.1	3.7	15.9	15.9	
1986	22.9	4.5	14.2	15.4	
1987	21.1	4.3	14.2	14.4	
1988	25.0	6.3	17.0	17.4	
1989	24.6	6.6	16.2	16.8	
1990	25.9	6.0	18.6	18.0	
1991	17.7	7.4	15.5	14.3	19.1
1992	23.8	10.2	17.7	17.4	17.0
1993	22.8	10.3	16.6	16.3	15.2
1994	23.3	9.7	18.3	17.5	15.6
1995	18.1	10.4	16.7	15.9	16.4
1996	21.5	8.0	19.9	17.6	15.1
1997	22.8	13.0	20.5	18.9	21.0
1998	21.5	9.4	21.5	18.3	20.2
1999	19.5	6.8	20.1	16.4	19.9
2000	19.5	7.7	21.1	17.1	22.5

Source: compiled by the authors.

ancestors were IRRI-released. If only one set of parents was IRRI-released or had IRRI ancestry, then the variety was considered to be 50% IRRI. The all-antecedents rule assigns equal weights to the variety and each of its ancestors. Thus, if we trace the pedigree back to the grandparent level, the variety and each of its ancestors is given a weight of 1/7 if released by IRRI. The geometric rule assigns higher weight for the recent generations and lower weight for the early generations. The all-credit-to-last-cross rule takes only the last cross into account, so, if the variety was released by IRRI, it gets all credit, otherwise none. Finally, the any-ancestor rule gives credit to IRRI if a variety or any of its ancestors was released by IRRI. The all-credit-to-last-cross rule and the any-ancestor rule represent polar cases: the former is the most conservative rule and the latter is the least conservative.

Using these various attribution rules, we present in Table 5 the contribution of IRRI to the total benefits from rice varietal improvement research in India and China. IRRI accounted for a sizable share of rice research benefits in India. With the any-ancestor rule, IRRI accounted for 73% of the rice research benefits in 1991 and for 63% in 2000. With the most conservative scenario (all-credit-to-last-cross rule), IRRI's contribution was still important, accounting for 51% of the research benefits in 1991 and for 12% in 2000. According to the binary-parents, all-antecedents, and geometric rule, IRRI's contribution to research benefits ranged from 17% to 66% from 1991 to 2000.

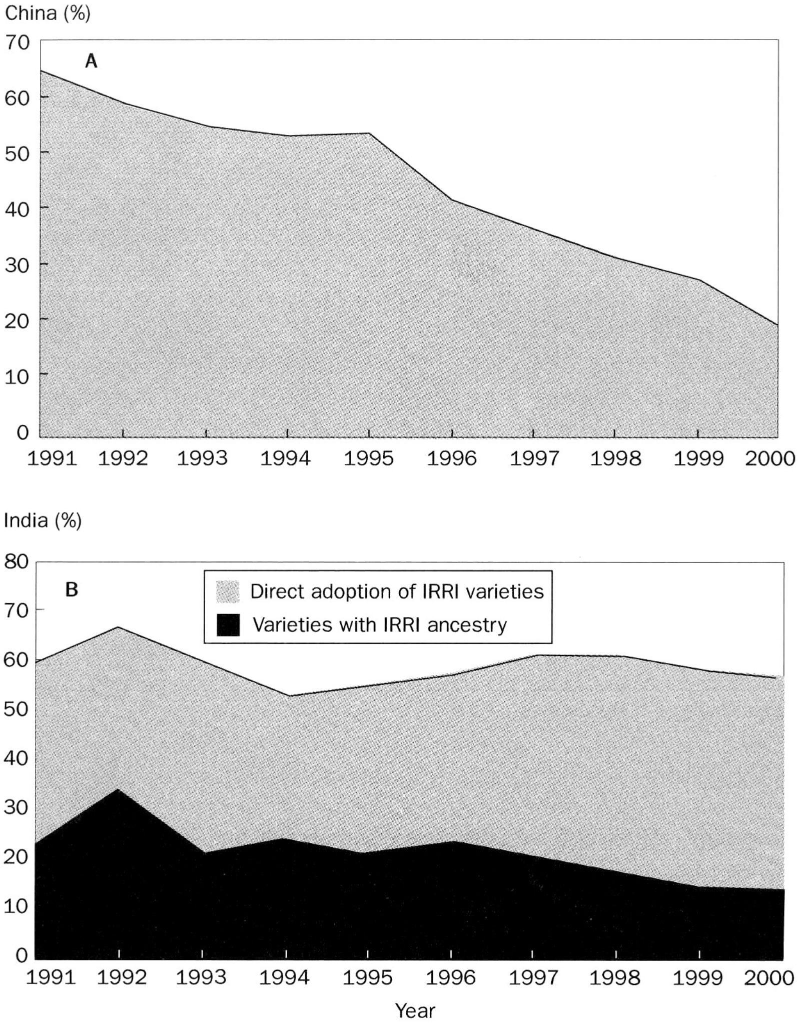


Fig. 3. Area planted to IRRI varieties in China (A) and India (B).

In contrast to India, the share of the rice benefits attributable to IRRI was smaller in China. Furthermore, IRRI's varieties were mostly used as breeding materials in China and not directly adopted by farmers. As a result, the all-credit-to-last-cross rule gives overall 0% of the research benefits to IRRI. With the any-ancestor rule, IRRI's share of research benefits was equal to 25% in 1981 and increased to 68% in 1991, but declined gradually to 22% in 2000. With the geometric rule, IRRI's contribution to total benefits ranged from 1.7% to 8.5% over the 1981-2000 period

Table 4. Area planted with IRRI ancestors.

Year	China			India		
	Direct adoption	With IRRI ancestry	Total IRRI	Direct adoption	With IRRI ancestry	Total IRRI
			(%)			
1981	0	23.0	23.0			
1982	0.2	23.9	24.1			
1983	0.1	29.3	29.4			
1984	0.1	36.0	36.1			
1985	0.0	38.7	38.7			
1986	0.2	45.3	45.5			
1987	0	49.6	49.6			
1988	0	58.8	58.8			
1989	0	56.2	56.2			
1990	0	62.6	62.6			
1991	0	64.9	64.9	23.2	38.8	62.0
1992	0	58.9	58.9	34.7	34.0	68.7
1993	0	54.7	54.7	21.0	41.6	62.6
1994	0	53.0	53.0	25.0	30.3	55.3
1995	0	53.6	53.6	20.8	37.3	58.1
1996	0	41.1	41.1	24.4	35.3	59.8
1997	0	36.8	36.8	21.9	41.7	63.5
1998	0	30.5	30.5	18.7	44.5	63.3
1999	0	27.2	27.2	15.3	44.8	60.1
2000	0	18.7	18.7	14.4	43.9	58.3

Source: compiled by the authors.

compared with 12% to 39% with the binary-parents rule and 4% to 15% with the all-antecedents rule.

Table 6 compares the benefits and costs of IRRI's research. The benefits attributed to IRRI using the geometric-attribution rule are presented next to IRRI's total budget and China's and India's contribution to IRRI. The geometric attribution is one of the most conservative rules. It takes into account not only the recent crosses but also past breeding efforts. More weights assigned to the recent crosses than the earlier ones attribute more benefits to the national agricultural research system than to IRRI. Even using this conservative rule, the benefits from IRRI's research in India and China well exceed both countries' contributions. In 2000, benefits attributed to IRRI are 684 times China's funding contribution to IRRI while they are 4,000 times India's. The benefits from IRRI research in China were nearly 3-fold greater than IRRI's budget, while in India the benefits were 20-fold greater than IRRI's budget. Total benefits attributed to IRRI from China and India were $666 million and $749 million dollars, respectively, in 2000. This amount is twice as large as the entire CGIAR's annual budget.

Table 5. Benefits attributed to IRRI by attribution rules.

Year	China					India				
	Binary parents	All antecedents	Geometric	All credit to last cross	Any ancestry	Binary parents	All antecedents	Geometric	All credit to last cross	Any ancestry
					(%)					
1981	14.9	8.0	5.4	0.0	24.6					
1982	14.6	7.8	5.3	0.2	24.0					
1983	18.2	10.9	7.0	0.2	30.3					
1984	21.6	13.7	8.5	0.1	38.1					
1985	22.4	13.5	7.8	0.1	38.1					
1986	27.2	13.6	7.4	0.2	43.9					
1987	32.8	15.4	7.6	0.0	51.4					
1988	34.3	14.7	7.0	0.0	57.6					
1989	32.3	12.8	6.0	0.0	55.5					
1990	36.7	14.7	6.8	0.0	62.9					
1991	38.9	15.0	6.8	0.0	68.3	64.9	33.7	45.4	50.5	72.5
1992	32.7	12.4	5.7	0.0	59.3	65.9	33.4	44.9	50.2	72.7
1993	31.1	11.2	5.2	0.0	57.6	48.2	23.1	29.8	31.7	60.2
1994	28.7	10.2	4.8	0.0	53.5	49.9	24.2	30.5	32.1	58.0
1995	27.8	9.2	4.1	0.0	50.7	41.6	19.0	20.7	18.2	54.4
1996	22.0	7.3	3.3	0.0	40.8	43.1	21.0	23.7	21.0	56.8
1997	18.9	6.1	2.8	0.0	35.7	40.6	19.7	20.6	16.9	55.6
1998	16.8	5.3	2.4	0.0	31.7	47.7	23.7	24.0	19.2	62.8
1999	16.1	5.0	2.2	0.0	29.7	43.9	19.1	17.8	12.9	62.1
2000	11.9	3.8	1.7	0.0	21.6	46.1	20.6	18.4	11.9	62.8

Source: estimated by the authors.

Table 6. international rice research benefits and costs.

Year	Research benefits contributed by IRRI		IRRI's expenditures		
	China	India	Total	China's contribution	India's contribution
	(thousands of 2000 US$)				
1981	198,032		38,942		
1982	204,655		40,761		187
1983	271,402		38,350		195
1984	285,961		40,429	150	188
1985	238,583		45,592	146	218
1986	217,697		42,435	171	178
1987	225,383		45,243	69	173
1988	266,807		41,395	67	166
1989	274,810		47,010	64	129
1990	303,997		51,668	62	124
1991	213,713	947,936	46,224	60	119
1992	205,043	1,055,909	48,616	93	117
1993	184,082	602,991	50,993	103	114
1994	215,120	647,747	44,631	100	112
1995	190,602	460,699	44,008	98	219
1996	209,050	488,569	42,877	96	187
1997	214,875	790,798	36,736	95	158
1998	181,292	903,169	36,310	na	na
1999	139,089	633,799	35,875	na	na
2000	88,924	660,207	32,600	130	158

Source: Research benefits are compiled by the authors. Only very conservative attribution rule, geometric, was used here. IRRI expenditures from 1981 to 1997 are from the CGIAR secretariat; 1998 to 2000 expenditures are taken from the CGIAR 1999 financial report and the 2000 annual report, respectively. China's and India's contribution to IRRI from 1982 to 1997 are from IRRI's "Facts about Cooperation: People's Republic of China and IRRI" and "Facts about Cooperation: India and IRRI": China's and India's contribution to IRRI in 2000 are from IRRI 2000 annual report. na = not available.

Impact on poverty

We use the following steps to estimate the impact of national and international rice varietal improvement research on poverty reduction. First, we calculate the marginal impact on poverty reduction of an increase in agricultural production value. This measure gives the number of poor reduced per additional unit of agricultural production value. The parameters needed are reported by two recent IFPRI publications (Fan et al 2000, 2002a). Second, we calculate the total number of poor reduced from rice varietal improvement research by considering the estimated research benefits as the additional increase in agricultural production value. Finally, we use IRRI's share of total rice research benefits estimated from the geometric attribution rule to estimate the poverty reduction impact for IRRI. These are lower-bound estimates since the geometric rule is one of the most conservative.

Table 7. Poverty impact of rice research in India.

Year	Rural poor (million)	Poor reduced from rice research (million)	Reduction as a percent of total poor (%)	No. of poor reduced from IRRI's research (million)	No. of poor reduced per million dollars of IRRI spending
1991	233	1.56	0.67	0.63	13,611
1992	237	1.77	0.75	0.79	16,337
1993	242	1.51	0.62	0.48	9,349
1994	274	1.72	0.63	0.61	13,741
1995	252	1.54	0.61	0.41	9,395
1996	251	1.44	0.57	0.48	11,202
1997	249	2.48	1.00	0.77	21,027
1998	212	2.05	0.97	0.84	23,139
1999	169	1.46	0.86	0.46	12,924

Fan et al (2000) estimated a system of econometric equations to identify the relative role of different government spending in agricultural growth and rural poverty reduction in India using state-level data for 1970 to 1993. The model is structured to enable the identification of the various channels through which different types of government expenditures affect the poor. The study distinguishes between direct and indirect effects of agricultural growth due to agricultural research. The direct effects arise in the form of benefits the poor receive from higher income through growth in agricultural production. The indirect effects come from increased rural wages and employment and changed food prices. This approach has two advantages. First, both direct and indirect effects of agricultural growth were estimated. Second, other types of investment such as infrastructure, education, and health were also included to avoid the upward-biased estimates of research investment impact.

Their estimated poverty equation shows that, with every 1% increase in agricultural production or productivity growth, the total number of rural poor in India would be directly reduced by 0.171% as a result of growth in agricultural income. The indirect effects from improved rural wages and employment and changed food prices are 0.07%. Therefore, the total effect is 0.241%. Using this elasticity, we can easily calculate the marginal impact of an additional unit in agricultural production value on poverty reduction. Multiplying this marginal impact by the estimated rice research benefits gives the total number of poor reduced due to rice varietal improvement research. Table 7 shows the estimated results. The number of poor reduced as a result of rice varietal improvement research increases from 1.56 million in 1991 to 2.48 million in 1997 then declines to 1.46 million in 1999. This reduction expressed in percentage of total rural poor ranges from 0.67% in 1991 to 0.83% in 1999. Turning to the impact of IRRI varietal improvement research on rural poverty reduction, Table 7 shows that in 1991, some 0.63 million rural poor were lifted above the poverty line because of IRRI's research. In 1999, the estimated number of rural poor reduced because of IRRI's varietal improvement research was 0.46 million. We also calculated the number of poor reduced per million dollars of IRRI's spending in Table 7. We simply divided the total number of poor reduced due to IRRI's research by IRRI's annual spending. A more rigorous analysis should have been done to calculate the poverty reduction impact based on the research stocks constructed from past investment as Fan et al (2000, 2002a) have done. However, the data limitation prevented us from doing so. But this indicator does give some important indicative information about the impact of IRRI's research on poverty on a per unit investment basis. For India, every million dollar invested by IRRI lifted 13,611 poor above the poverty line in 1991. The number of poor reduced was 12,925 in 1999. There has been no sign of decline in the poverty-reduction effects of rice varietal improvement research, suggesting that rice research will continue to be a factor in promoting rural poverty reduction in the future.

Similar to the India study, Fan et al (2002a) developed and estimated a simultaneous equation model to estimate the effects of different types of government expenditure in China using provincial-level data for 1970-97. From their estimated poverty equation, the elasticity of poverty reduction with respect to agricultural output growth is 1.13. This is the direct impact on poverty through growth in agricultural income. The elasticity of indirect impact from improved rural wages and employment and changes in food prices is 0.79. Therefore, the total elasticity of poverty reduction with respect to agricultural growth is 1.924. As for India, we use this elasticity to calculate the number of poor reduced per unit of increase in agricultural production value, and the number of poor reduced from IRRI rice varietal improvement research.

The total number of rural poor reduced from rice research in China has been much larger than that in India. In 1981, 17 million poor were reduced as a result of rice varietal improvement research. However, in 1999, only 1.4 million rural poor were reduced because of the rapid decline in rural poverty. In relative terms, the number of poor reduced from rice research as a proportion of the total number of rural poor was 9% in 1981 and 4% in 1999. Table 8 also shows that the number of poor reduced from IRRI's varietal improvement research declined from 480,000 in 1981 to 50,000 in 1999. Finally, the number of poor reduced per million dollars of IRRI's spending was 12,427 in 1981. Because of the rapid reduction in rural poverty, the number of poor reduced for every million dollars spent by IRRI declined to 1,532 in 1999.

Conclusions

Using varietal adoption and performance data, this study calculated the total benefits from rice varietal improvement research in China and India. We then used genetic or pedigree information to partition the total benefits between these two countries and IRRI (Fig. 4). Finally, we used reported elasticity of poverty reduction with respect to agricultural output growth to assess the effects of national and international research on poverty reduction in rural India and China.

The results indicated that rice varietal improvement research has contributed tremendously to the increase in rice production in both countries. In China, research

Table 8. Poverty impact of rice research in China.

Year	Rural poor (million)	Poor reduced from rice research (million)	Reduction as a percent of total poor (%)	No. of poor reduced from IRRI's research (million)	No. of poor reduced per million dollars of IRRI spending
1981	194	17.03	8.78	0.48	12,426
1982	140	11.27	8.05	0.32	7,871
1983	123	9.06	7.36	0.35	9,063
1984	89	5.10	5.72	0.24	5,988
1985	96	4.95	5.15	0.23	5,132
1986	97	4.54	4.68	0.22	5,122
1987	91	3.89	4.27	0.20	4,484
1988	86	4.20	4.88	0.24	5,857
1989	103	5.93	5.76	0.35	7,349
1990	97	4.93	5.08	0.33	6,460
1991	95	3.38	3.56	0.24	5,184
1992	90	3.54	3.93	0.22	4,588
1993	80	2.96	3.70	0.19	3,783
1994	70	2.75	3.93	0.21	4,600
1995	65	2.28	3.50	0.17	3,827
1996	58	2.67	4.61	0.17	3,931
1997	50	2.69	5.37	0.14	3,881
1998	42	2.08	4.94	0.09	2,564
1999	34	1.37	4.03	0.05	1,531

benefits as a share of rice production value range from 14% to 19%.[10] In India, they range from 15% to 23%. In both countries, the benefits produced just from rice research are on average 10 times higher than their respective total agricultural research investment.

Rice research has also helped reduce large numbers of rural poor.[11] Without research investments in rice, the number of poor would be much higher today. For every $1 million invested at IRRI in 1999, more than 1,500 and 12,000 rural poor were lifted above the poverty line in China and India, respectively. A similar or even larger poverty impact is observed in Indonesia, Vietnam, and Bangladesh, although formal analyses have not been done yet in these countries.

However, most of these benefits are the results of research conducted in the 1960s, '70s, and '80s. For both China and India, the increase in experimental yield has slowed down in the 1990s. One of the reasons is the lack of agricultural research investment at both the national and international levels. As a percentage of agricultural gross domestic product (AgGDP), agricultural research investment in both countries was relatively low, 0.3% for China and 0.4% for India. For other low-income Asian

---

[10] This is consistent with the findings of Fan and Pardey (1997), who concluded that about 20% of the total production value from 1965 to 1993 is from the increased agricultural research investment.

[11] In separate studies, Fan et al (2002b) and Fan (2002) concluded that the effects of agricultural research on urban poverty are as large as those on rural poverty, and agricultural research may play an even larger role in helping the urban poor in the future as more poor will be concentrated in the urban centers.

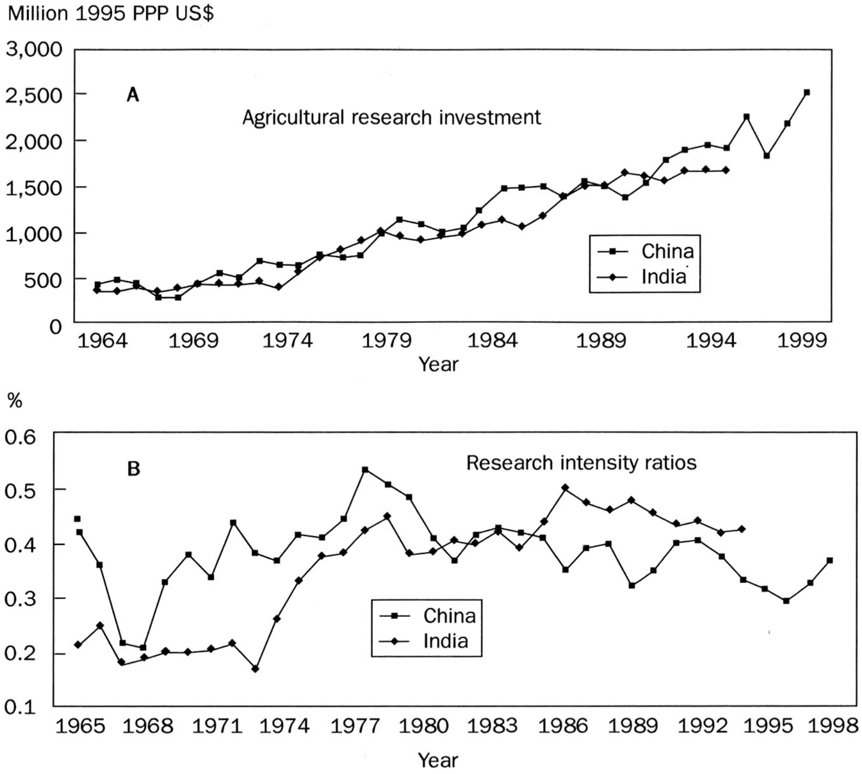


Fig. 4. Agricultural research investment in China and India.

countries, the percentages are in the range of 0.5% to 1%. For developed countries, the percentage is usually as high as 2% to 4%.

The budget of the International Rice Research Institute has also been severely cut in recent years. IRRI's budget of $32.6 million in 2000 was the lowest in 20 years, and was only 63% of its peak of $51.6 million (measured in 2000 prices) in 1990. Today, there are still more than 1 billion poor in the world, and most of them live on agriculture. It has been proved that national and international agricultural research has made a large impact on poverty reduction in the past.

Together with improvements in rural infrastructure, education, and health, agricultural research will play an even larger role in the future in reducing poverty in developing countries. However, increased and stable funding for national and international agricultural research is a must to reduce both rural and urban poverty.

References

Alston JM, Norton GW, Pardey PG. 1995. Science under scarcity: principles and practice for agricultural research evaluation and priority setting. Ithaca, N.Y. (USA): Cornell University Press. 585 p.

Chang TT. 1980. The Rice Genetic Resources Program of IRRI and its impact on rice improvement. In: Rice improvement in China and other Asian countries. Manila (Philippines): International Rice Research Institute and CAAS (Chinese Academy of Agricultural Sciences). p 85-105.

China State Statistics Bureau (SSB). 1990. China development report. Beijing: China Statistical Press.

China State Statistics Bureau (SSB). 1999. China development report. Beijing: China Statistical Press.

Dalrymple DG. 1986. Development and spread of high-yielding rice varieties in developing countries. Washington, D.C. (USA): Bureau for Science and Technology, Agency for International Development.

Datt G, Ravallion M. 1997. Why have some Indian states performed better than others at reducing rural poverty? FCND Discussion Paper No. 26. Washington, D.C. (USA): International Food Policy Research Institute.

Evenson RE, Pray CE, Rosegrant MW. 1998. Agricultural research and productivity growth in India. Research Report 109. Washington D.C. (USA): International Food Policy Research Institute.

Evenson RE, Gollin D. 2002. The Green Revolution: an end of century perspective. Paper presented at the international conference "Why has impact assessment research not made more of a difference?' 4-7 February 2002, San José, Costa Rica.

Fan S, Zhang L, Zhang X. 2002a. Growth and poverty in rural China: the role of public investment. IFPRI Research Report 125. Washington, D.C. (USA): International Food Policy Research Institute.

Fan S, Cheng Fang, Zhang X. 2002b. How agricultural research affects urban poverty in developing countries: the case of China. EPTD Discussion Paper #83. Washington, D.C. (USA): International Food Policy Research Institute.

Fan S. 2002. Agricultural research and urban poverty in India. EPTD Discussion Paper #94. Washington, D.C. (USA): International Food Policy Research Institute.

Fan S, Hazell P, Thorat S. 2000. Government spending, agricultural growth and poverty in rural India. Am. J. Agric. Econ. 82(4):1038-1051.

Fan S. 2000. Research investment and the economic returns to Chinese agricultural research. J. Prod. Anal. 14(2):163-182.

Fan S, Pardey P. 1997. Research, productivity, and output growth in Chinese agriculture. J. Dev. Econ. 53:115-137.

FAO (Food and Agriculture Organization). 2002. FAOSTAT. http://apps.fao.org (accessed 2002).

Griliches Z. 1957. Hybrid corn: an exploration in the economics of technological change. Econometrica 25(4):501-522.

Hayami Y, Ruttan V. 1985. Agricultural development: an international perspective. Baltimore, Md. (USA): Johns Hopkins University Press.

Hazell P, Haddad L. 2001. Agricultural research and poverty reduction. IFPRI 2020 Discussion Paper. Washington, D.C. (USA): International Food Policy Research Institute.

Huang J, Rozelle S, Hu R, Jin S, Pray C. 1999. The creation and spread of technology and total factor productivity in China: an analysis of the contribution of China's research system and CG-supplied genetic materials. Paper presented at the workshop on the Impact of National and International Research Programs on Total Factor Productivity in Developing Countries, 1999.

Indiastat. 2002. Datanet India Private Limited. www.indiastat.com (accessed 2002).

IRRI (International Rice Research Institute). Facts about cooperation: People's Republic of China and IRRI. www.irri.org/VIS/facts/china.pdf.

IRRI (International Rice Research Institute). Facts about cooperation: India and IRRI. www.im.org/VIS/facts/india.pdf.

Lin Shih-Cheng, Yuan Loung-Ping. 1980. Hybrid rice breeding in China. In: Rice improvement in China and other Asian countries. Manila (International Rice Research Institute) and CAAS (Chinese Academy of Agricultural Sciences). p 35-51.

Pardey GP, Alston JM, Christian JE. Fan S. 1996. Summary of a productive partnership: the benefits from U.S. participation in the CGIAR. EPTD Discussion Paper No. 18. Washington, D.C. (USA): International Food Policy Research Institute.

Pardey GP, Alston JM, Christian JE, Fan S. 1996. Hidden harvest: U.S. benefits from international research aid. Food Policy Report. Washington, D.C. (USA): International Food Policy Research Institute.

Pinstrup-Andersen P, Hazell P. 1985. The impact of the Green Revolution and prospects for the future. Food Rev. Int. 1(1):1-2.5.

Shen Jin-Hua. 1980. Rice breeding in China. In: Rice improvement in China and other Asian Countries. Manila: International Rice Research Institute and CAAS (Chinese Academy of Agricultural Sciences). p 9-30.

World Bank. 2000. China: overcoming rural poverty. Washington, D.C. (USA): World Bank.

Notes

Author' addresses: Shenggen Fan is a senior research fellow and C. Chan-Kang is a research analyst, both at the International Food Policy Research Institute, Washington, D.C.; Kerning Qian is the director-general of the Institute of Agricultural Economics, Chinese Academy of Agricultural Sciences; K. Krishnaiah is a former director of the Directorate of Rice Research, Hyderabad, India.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The impact of rice research on food security and poverty alleviation in eastern India

S.C. Modgal

The eastern region of India constitutes the states of Uttar Pradesh, Bihar (including Jharkhand), West Bengal, Assam, Orissa, and Madhya Pradesh (including Chattisgarh). It has been known for floods, food insecurity, and poverty. During the Green Revolution, these states, except for Utter Pradesh and West Bengal, were showing a declining production trend. In the triennium ending in 1994, all these eastern region states were at the bottom of the ladder for rice productivity. Almost 80% of the rice production area in the eastern states is under the rainfed ecosystem, which remains exposed to biotic and abiotic stresses. The rice crop is grown under various unfavorable subecosystems such as flooded and deepwater rice, rainfed uplands, rainfed lowlands, and a relatively smaller area under irrigated conditions cutting across varied seasons. The region is inhabited by the poorest of the rice farmers, who have little access to improved rice production technologies produced through advanced research.

Amazingly, the region has a rich endowment of natural resources such as water and it has some of the most fertile alluvial soils in the Indo-Gangetic Plain and capable human resources. Wherever these resources are managed along the lines of advanced research recommendations, advantages have appeared. The agricultural research network operating in the region with the support of national and international agencies such as the Indian Council of Agricultural Research (ICAR), state agencies, and the International Rice Research Institute (IRRI) has made available to the farmers in the ecosystem high-yielding rice varieties and location-specific improved rice production technologies. These changes, coupled with an improved socioeconomic environment, are now bringing about a steady improvement in rice production. Since rice production in these states is closely linked with the livelihood of the majority of the farm community, this positive trend in rice productivity and production has started altering the food security and poverty scene. The trend, degree, and manner in which rice research has influenced the process of food security and poverty alleviation in eastern India are discussed in this paper.

India's rice production has more than doubled during the last four decades: from 39 million t in 1964-65 (Subbaiah and Balasubramanian 2000) to an estimated 89.5 million t in 1999-2000 (FAI 2001). Since the increase in rice area during these years has been nominal, the production boom is attributed to increased productivity per unit area as a result of improved technology produced through research. Though the major rice area is located in the eastern region of India (63.3%) comprising the states of Assam, West Bengal, Orissa, Madhya Pradesh (including Chattisgarh), Bihar (including Jharkhand), and Uttar Pradesh (Singh and Singh 2000), rice production is now 53% (Subbaiah and Balasubramanian 2000), and this did not match the area figures. Until recently, these states were producing slightly less than 50% of the national rice production.

Poverty and food insecurity were the prominent features of this region, but, because of the availability of modern varieties (MV) of rice for different rice ecosystems, improved rice production technology, and the proper exploitation of the rice ecosystems, the rice production scenario in the six eastern states of India is steadily improving. Since rice production is closely linked with the livelihood of the majority of the farming community in eastern India, this positive trend in rice productivity has started altering the food security and poverty scene.

Rice research initiatives and ecosystems in eastern India

Rice research and the resulting technologies have to maintain a recognizable lead over the surging human population if humanity is to survive in the most populous parts of the world such as eastern India and elsewhere in Asia. A catastrophic situation developed in the past when the reverse happened. The low production of rice coupled with its lack of availability and the outbreak of the devastating epiphytotic brown spot disease of rice in the then Bengal Province of eastern India, areas of which now form West Bengal State in India and Bangladesh, resulted in a serious shortage of rice in 1942, which culminated in the infamous Bengal Famine of 1943. It was in the backdrop of this situation that the Government of India established the Central Rice Research Institute (CRRI) in 1946 at Cuttack in Orissa, another state in eastern India. This was the first serious effort of the Government of India to recognize the role and importance of research on rice to ensure food security, if not alleviate poverty, at that time.

Different states in eastern India had their rice research set up in the form of rice research stations (RRS) at that time or before 1946. CRRI as well as the RRS bred and released tall traditional varieties (TV) of rice that were little responsive to inputs and obviously had low yield potential. Some of these varieties released during the pre-semidwarf era showed yield stability over large areas and periods. Another feature of research during the pre-semidwarf era was that each of these RRSs was sticking to its own area of responsibility without any formal coordination in research activities.

The introduction of a new plant type in rice and for that purpose in food grains (cereals) in the form of Taichung (Native) 1 in 1964 and IR8 in 1965 from Taiwan

Province of China and the International Rice Research Institute (IRRI), Philippines (CRRI 1996), changed the entire perception and character of rice research in South and Southeast Asia. A highly significant development that took place in 1965 was the establishment of the All India Coordinated Rice Improvement Project (AICRIP) under the setup of the Indian Council of Agricultural Research (ICAR). AICRIP's mandate and activities have since then expanded and been reviewed. AICRIP is now renamed the Directorate of Rice Research (DRR), based in Hyderabad. The state agricultural universities (SAUs) network in India works jointly in coordination with the DRR/ICAR and international agencies such as IRRI, the Food and Agriculture Organization (FAO), and International Rice Commission (IRC). The mid- 1960s were when India ushered in the era of plant-type-based modern varieties with a planned strategy between ICAR and IRRI. India thus started its crusade against hunger and poverty. The emphasis in rice breeding in eastern India and other areas in the late 1960s and '70s was to develop varieties with improved grain characteristics and yield equal to or better than that of IR8. Jaya was first identified by AICRIP scientists, and it had a yield range similar to that of IR8 and it was slightly early in maturity. The adoption of both these MVs was fast not only in the traditional rice-growing areas of the eastern and southern states, but also in the areas where rice was not grown earlier, such as Punjab, Haryana, and western Uttar Pradesh. No rice variety could break the yield barriers of IR8 and Jaya up to now at the commercial level.

After reaching a substantially high yield of 6 to 8 t of grain ha^{-1} in these varieties, plant breeders shifted to short-duration rice varieties with resistance to biotic and abiotic stresses. Rice varieties resistant to blast such as Rasi and VL8, resistant to bacterial leaf blight (BLB) such as PR4141 and IR36, and resistant to brown planthopper (BPH) such as Sonasali and others were also released. Some of the rice varieties released had multiple resistance (Suraksha, Shaktiman, Lalat, Ananga, Rasmi, Daya, Kshira, and Bhuban).

The Green Revolution mainly brought about through the introduction of input-responsive MVs took place in the risk-free irrigated environment. Crop response to other commercial inputs such as seed, fertilizer, and pesticide largely depends upon the assured supply of irrigation water. Major research efforts, achievements, and impact on rice production affecting food security and poverty alleviation took place in the irrigated ecosystem. But the irrigated rice ecosystem occupies only about 20% of the total rice cultivated area in eastern India while 80% of the rice crop in this zone is rain-dependent. Under the rainfed system, rice in eastern India is grown under highly variable water regimes from uplands to deepwater conditions (Table 1). Rainfed rice in this large area is subject to biotic and abiotic stresses. No wonder some of India's poorest people reside in this region. The rainfed ecosystem varies widely in its biophysical and socioeconomic requirements and productivity constraints. All these situations increase risk and deter resource-poor farmers from investing in cash inputs such as seed, fertilizer, and pesticide. Consequently, crop yield and its stability are adversely affected.

Table 1. Rice ecosystem area and rice productivity in eastern India.

State	Percentage of net irrigated area to net cultivated area[a]	Rice productivity (kg ha^{-1}) [a]	Irrigated	Area under rice ecosystems (million ha) [b]						
				Rainfed						
				Upland	Lowland (0-30 cm)	Lowland (30-50 cm)	Deepwater (50-100 cm)	Deepwater (>100 cm)	Total	Percent irrigated area of total rainfed area
Assam	20.8	1,497	0.20	0.21	0.89	0.47	0.38	0.10	2.27	8.9
Bihar	48.9	1,540	1.51	0.53	1.69	0.46	0.38	0.67	5.26	28.9
Orissa	34.1	1,127	1.06	0.69	1.74	0.48	0.40	0.15	4.53	23.4
Madhya Pradesh	31.6	1,191	0.61	1.34	2.69	-	-	-	4.65	13.0
Uttar Pradesh	68.6	2,176	0.98	0.71	1.88	0.29	0.23	0.55	4.66	21.0
West Bengal	35.0	2,259	1.32	0.88	1.68	0.47	0.38	0.68	5.42	24.4
Total	-	1.628	5.69	4.38	10.60	2.18	1.78	2.15	26.79	21.2

Source: [a] FAI (2001). [b] Siddiq (1998).

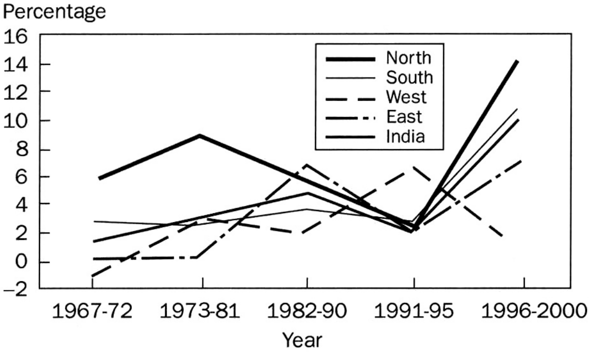


Fig. 1. Annual compound growth rate of rice production in different zones in India.

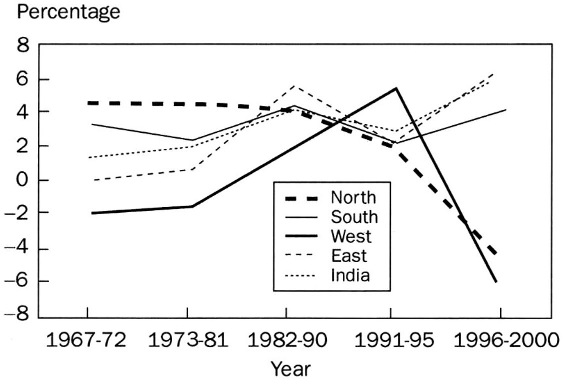


Fig. 2. Annual compound growth rate of rice yield in different zones in India. Sources: Siddiq (1998) and FAI (1998, 2001).

Impact of rice research on production and productivity

Because of inadequate attention given in research and development programs to problems faced by farmers in the highly diversified rainfed rice ecosystem in eastern India, rice yields remained stagnant for a long time. It is only with the change in pattern and approach and making these programs more location-specific and farmer-responsive that an upward swing in the growth rate of rice production and productivity has become visible during the last two decades (Figs. 1 and 2). All three major rice research agencies working in eastern India—CRRI, Cuttack, the AICRIP (DRR) operating in collaboration with the SAUs, and the IRRI-sponsored rainfed rice research consortia—are operating on the basis of different rice ecosystems and are focusing their research activities on catering to the varietal and production technology aspects of rainfed rice. An understanding of coordination and cooperation exists among the ICAR (DRR and CRRI), SAUs, and IRRI (IFAD-funded Rainfed Rice Research Consortia Project, INGER, and other projects).

This shift in focus of rice research strategy from irrigated to rainfed rice ecosystems, which occupy about 80% of the total rice area in the eastern zone, has now started paying dividends in terms of a consistent increase in the productivity and production growth rates of the last two decades (Figs. 1 and 2). Kumar and Rosegrant (1994), quoted by Jha and Kumar (1998), also believe that rice research has paid handsome returns in India and emphatically so in its eastern region. Jha and Kumar (1998) have further supported the contention that greater investment in rice research is required. As per the available information, out of the total spending on agricultural research, rice research is allotted about 10% in Uttar Pradesh, followed by Bihar and Assam, which get a minimum share of 0.73%, followed by West Bengal (Modgal 1998).

As a consequence of these developments in research and the seeds of MVs of rice and their production technologies being available in the eastern states of India, particularly in the major rainfed rice ecologies, yield potential has increased substantially. Frontline demonstrations conducted in eastern India in all the major rainfed rice ecologies have shown clearly that, through the adoption of suitable MVs and use of high-quality seeds and balanced nutrient application, rice yields can increase by 40-60% over those of local varieties grown under poor management (Table 2).

Modern varieties of rice that have been released and have gained popularity among rice growers in different rainfed rice ecologies are listed below.

1. Rainfed shallow lands	
Assam	Laxmi, Biraj, Salivahana, IET-8002, Kaushal, Bahadur, Ranjeet
Bihar	Jayashree, Rajshree, Kanak
Orissa	OR621-6, Mahalaxmi, Manika
Madhya Pradesh	Annada, Kranti, Ruchi, MW-10, IR36, Swarna, Surekha, Mahamaya, RS74-11
Uttar Pradesh	Mahasuri, Jaya, Jayalaxmi
West Bengal	IR42, Biraj, IET-8002, Manasarowar, IET-12515, IET-12690, IET-12130
2. Rainfed semideepwater	
Bihar	Sudaha
Uttar Pradesh	Chakia-59, Jalamagna, Madhukar, Jalapriya
West Bengal	Sabita, Jogen, Nalini, IET-9065, Dinesh
3. Rainfed upland	
Bihar	Chakia, Jalamagna, Birpadhan, Kalma-111, Birpa 101 and 201, Kalinga-3, Tulsi, Vandana

Table 2. Yield advantage of modern rice varieties over locals (L) under rainfed lowland ecosytems In eastern India.

Site/state	Culture	Water regime (cm)	Rice variety	Grain yield (tha-1)	Percentage increase over yield of local variety
Masodha, Uttar Pradesh	Transplanted	15-20	NC492	2.0	33
			Madhukar (L)	1.5	–
Raipur, Madhya Pradesh	Direct-seeded	0-30	R320-300	4.1	21
			Safari (L)	3.4	–
Patna, Bihar	Direct-seeded	0-30	Radha	3.9	117
			Local	1.8	–
Titabar, Assam	Transplanted	0-30	TTB101-7	4.8	41
			Safari17 (L)	3.4	–
	–	30-50	IR43459-81-2	5.5	62
			Manohar Sali (L)	3.4	–
Chinsura, West Bengal	Transplanted	0-30	IR42	4.4	63
			Jhingasali (L)	2.7	–
	–	30-50	NC 492	3.5	40
			Suokalina (L)	2.5	–
Kendrapara, Orissa	Transplanted	0-30	OR60415	4.7	30
			Mochi Banki (L)	3.6	–
	–	30-50	NC492	4.8	55
			Athargadia (L)	3.1	–

Source: Siddiq (1998).

Orissa	Kalinga, Parijat, Patnai, Nilagiri, Gantteswari, Kandagiri
Madhya Pradesh	Aditya, Tulsi, Annada, Kranti, IR36, R28 1-3 1 - 1
Uttar Pradesh	Saket-14, Narendra-18, 80, and 97, NDR-118

Source: Krishnaiah et al (1998)

The spread and adoption of MVs of rice in eastern India have moved at a good pace and are still continuing to move forward. All the states in eastern India have either almost met the target of rice MVs for the 8th Five-Year Plan by the end of its last year, that is, 1996-97, or have exceeded it (Fig. 3). The impact of the spread of MVs on rice productivity in these states is unambiguous. From 1996 to 2000, productivity in Assam increased from 1,336 to 1,479 kg ha^{-1}, in Bihar from 1,427 to 1,540 kg ha^{-1}, in Orissa from 981 to 1,127 kg ha^{-1}, in Madhya Pradesh from 1,172 to 1,191 kg ha^{-1}, in Uttar Pradesh from 2,121 to 2,176 kg ha^{-1}, and in West Bengal from 2,179 to 2,259 kg ha^{-1} (FAI 1998, 2001). The rice productivity growth rate in the eastern states shot up from 0.10 during 1967-72 to an all-time high of 6.62 during 1996-2000 (Fig. 2).

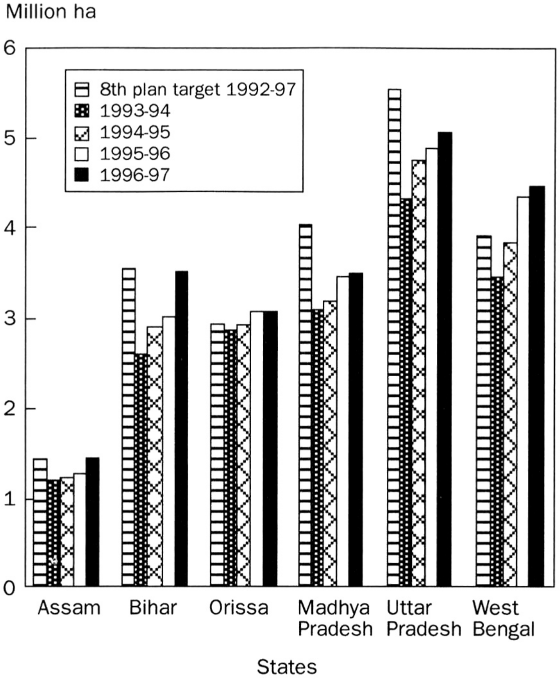


Fig. 3. Statewise coverage of area under modern rice varieties in eastern India. Source: GOI (2000).

To push yield barriers further, hybrid rice research and development programs are important and have begun in eastern India. Efforts on hybrid rice production have been taken up by the public as well as private sector. Public-sector SAUs have already released Pant Sankar Dhan 1 and Narendra Sankar Dhan 2 in Uttar Pradesh and CNRH-3 in West Bengal. Uttar Pradesh has taken the lead in launching a hybrid rice program in the state. Hybrid seed production and training programs are also being taken up in these states. CRRI at Cuttack in Orissa started working on hybrid rice in 1984. This work is in an advanced stage. It may, however, take some time before a sizable impact of rice hybrids is seen at the farm level, though the potential is great and hybrid rice gives hope for the near future. For a viable program, Virmani (2002) favors a close working relationship between the public and private sector in India.

The production of improved crop management technologies in rice aimed at (1) maximizing and stabilizing yield, (2) ensuring cost effectiveness, and (3) sustaining soil health. The improved technology package increased the yield of irrigated rice from 4.5 to 5.5 t ha^{-1}, of upland rice from 1.5 to 2.0 t ha^{-1} more than that of the local check in alluvial soils, and from 1.5 to 3.3 t ha^{-1} more than that of the local check in laterite soils. The lowland package ensured yield of 3.5 to 5.1 t ha^{-1} in states such as Orissa vis-à-vis local practices (Paroda and Siddiq 1993).

A Center-Commissioned External Review was set up by the International Rice Research Institute in October-November 2001 for the Rainfed Lowland Rice Research Consortium (RLRRC) and the Upland Rice Research Consortium (URRC) operating in Bangladesh, India, Indonesia, Lao PDR, Thailand, and the Philippines. These consortia in India are operating in eastern Indian states in close partnership with the states and national agencies (NARES) such as ICAR, SAUs, state departments, and farmers of the area. The consortium approach has not only resulted in some significant research and technology achievements, but, more than that, the conceptual changes brought about in the technology generation process will have far-reaching influence in solving the biophysical and socioeconomic problems of the resource-poor small and marginal rice farmers of rainfed rice ecosystems in eastern India. The research methodology used is basically in the bottom-up mode and is interdisciplinary. It is essentially a farmer-scientist participatory research process. Obviously, the technology produced is farmer-friendly and easy to be adopted. For flood-prone areas, IR67U93-M-2 and IR54112-B2-1-6-2-2-2 have been nominated for release for semideepwater conditions in Orissa, West Bengal, eastern Uttar Pradesh, and Madhya Pradesh. NDR-96005 and NDR-8002 are at an advanced level of release for the rainfed lowland rice ecosystem from Narendra Dev University of Agriculture and Technology (NDUAT) in eastern Uttar Pradesh. Significant advances have been made at NDUAT in characterizing environmental conditions in floodwater and their consequences for rice crop survival during submergence and recovery growth on desubmergence. Excellent strategic research work has been done on physio-biochemical aspects. Seedlings with higher nonstructural carbohydrate contents were found to possess a better capacity to withstand submergence. Scientists from Indira Gandhi Agricultural University (IGAU), Raipur, while analyzing their G × E data, noticed the high and stable yield of certain entries under drought and proposed them for release. Two cultivars from G × E studies are now grown by Chattisgarh farmers (NARES and IRRI 2001).

As a result of consortium activity, research and development institutions, including nongovernmental organizations (NGOs) in the region, such as Holycross at Hazaribagh in eastern India, have begun to operate in a network mode. They exchange information and provide each other with the needed technical support and facilities. They collectively try to solve problems of common concern and share resources and responsibilities (NARES and IRRI 2001).

Rice research has played an important role in expanding boro rice cultivation in eastern India. Boro rice is a system of rice cultivation practiced during the dry season in low-lying areas or even on medium lands. Irrigation is provided from November to May. Boro rice has been cultivated in the riverbed pockets of eastern Uttar Pradesh, Bihar, West Bengal, Assam, and coastal parts of Orissa. When reviewing the rice situation in eastern India, Rao et al (1998) and Singh and Singh (2000) saw great yield potential in boro rice, particularly with the availability of MVs such as Gautam, Prabhat, IR36, Joymati, Vishnu Prasad, Jyoti, Prasad, Richaria, Dhanlaxmi, Chinsura hybrid-3, and a few others. Farmers in West Bengal using MVs and exploiting groundwater along with improved technologies have increased the area under boro rice from nearly 0.1 million to 1 million ha in a short span of 6–7years, resulting in an additional 1 million t of rice (Rao et al 1998), and the area is now estimated to be more than 1 million ha. Encouraged by the West Bengal experience, other states in eastern India have started to expand the boro rice area.

The credit for the improvement in rice productivity and production in eastern India should go to the rice ecosystem-specific MVs, the location-specific technology production process, and provision for the timely availability of inputs such as seed, fertilizer, and pesticide. Because of the bottom-up and farmer participatory research and development process, farmers and the voluntary organizations (NGOs) have themselves started coming forward and thus becoming agents of change. The ICAR-appointed Quinquennial Review Committee for rice in its report covering 1988-96 stated that the low-yielding eastern zone has a better potential for productivity growth, and these states/districts have the most potential for advancing rice yields and production in the immediate future. This group has recommended that both research and development efforts should be directed to these areas for immediate benefits (Rao et al 1998).

Impact on food security and eliminating malnutrition

The years 1964 and 1965 can be termed benchmark years in the history of rice and agriculture in India since this was the time when the modem rice varieties Taichung (Native) 1 and IR8 were introduced in India. This was the difficult period when the country was struggling to feed its fast-growing population and the introduction of these wonder varieties of rice offered the first ray of hope. The food supply was import-dependent as India continued to import food grains to the tune of 15-20% of its needs until 1982-83, when the country attained self-sufficiency in food. The Paddock brothers predicted a serious famine in 1975 and placed India in the category of countries that could not be saved. But nothing of the sort happened and the country prevailed over the difficult times to become self-sufficient in food in 1983 and afterward as the growth rate for food production outpaced the population growth rate. Nonetheless, the food situation before 1983 was grim as the calorie deficit was about 40% since only 1,426 calories per capita per day were available vis-à-vis the normal requirement of 2,400 calories per capita per day.

In eastern India, Assam, Orissa, and West Bengal are the major rice-consuming states and, according to recent food statistics, more than 150 kg of rice per capita are being produced in each of these three eastern states. Per capita production of rice in Assam, Orissa, and West Bengal each is almost double that of the all-India average (Table 3). In three other states, Bihar, Madhya Pradesh, and Uttar Pradesh, where per capita rice production is 70-80 kg, wheat supplements rice as a staple food and, in these three states, wheat is a major crop along with rice, thus ensuring food security.

In addition, food stocks (rice + wheat) nationally are continuously increasing. As of 31 March 2001, the closing stocks for food grains (rice and wheat) in the central pool with the Food Corporation of India (FCI) and state agencies stood at 44.69 million t (provisional) vis-à-vis 28.90 million t (provisional) on the same date

Table 3. Population, rice production, and rice production per capita in eastern India.

State	Population[a] (million) 2001	Rice production[b] (million t) 2001	Rice production (kg per capita) 2001
Assam	26.6	3.86	170.8
Bihar + Jharkhand	109.8	7.74	70.4
Orissa	36.7	5.19	141.4
Madhya Pradesh + Chattisgarh	81.2	6.38	78.6
Uttar Pradesh	166.0	12.91	77.7
West Bengal	80.2	13.95	173.9
All India	1,027.0	89.47	87.1

Sources: [a]GOI (2002). [b]FAI (2001).

in 2000 (GOT 2002). This stock shot up to 58 million t (provisional) by January 2002. This is too high a food stock and it needs to be managed and handled with utmost care. There are serious problems regarding its safe storage, market approach, trade, and distribution. The major problem is how to channel this food to those in eastern India and elsewhere in the country living below the poverty line and who do not have enough purchasing power to buy food at the prevailing market prices. The Government of India is now releasing this stock through the public distribution system at a cheaper rate.

Another problem closely linked to food security that is haunting the eastern states and the country's entire population is undernourishment—what is sometimes called "protein-energy malnutrition." According to the 1998 Nobel Laureate in economics, Dr. Amartya Sen, this type of malnutrition is nearly twice as high in India as in sub-Saharan Africa. The population of undernourished children in India ranges from 40% to 60%. In the predominantly rice-eating eastern states, where many people cannot afford to buy protein-rich foods such as milk and other animal products, rice remains the only major food source to satisfy hunger as well as to get rid of malnutrition, if possible. In eastern India, where rice is a major part of the human diet, this grain contributes from one-third to one-half of the agricultural value added and provides 50-80% of the calories consumed by the people (Hossain and Pingali 1998). Accordingly, scientists have been working to understand the biochemical processes controlling protein synthesis in the rice plant. Rice plant breeders in eastern India and elsewhere have worked out the basics and are now engaged in breeding and releasing protein-rich rice varieties. These efforts, however, need increased focus and better coordination. Besides protein deficiency, vitamin-A deficiency commonly occurs among the people of eastern India. Fortunately, rice grain naturally contains an early precursor for beta-carotene. Using biotechnological tools, Ingo Potrykus and Peter Beyer and a researcher in Dr. Potrykus's laboratory, Dr. Xudong Ye, successfully bred "Golden Rice." IRRI has obtained the gene construct and the transgenic rice from Dr. Potrykus. We now hope that Asian varieties of Golden Rice rich in vitamin A will soon be available (BIS 2001). Possibly within the next three to four years, rice varieties rich in vitamin A will be available in eastern India. Anemia caused by iron deficiency is common for countless millions of the world's poor, including those in eastern India. Efforts made by IRRI scientists in evolving a rice variety such as IR68144 that increases the serum ferrite in the blood are noteworthy (IRRI 2000).

Poverty analysis and economic access to rice in eastern India

As per the 2001 census, India's population surpassed one billion (1,027 million) and, according to expert projections, India will overtake China by 2035 as the world's most populous nation. Assam, Bihar, Orissa, Madhya Pradesh, Uttar Pradesh, and West Bengal—the six eastern states—account for half (500.5 million) of the country's population. This is a frightening situation and should give alarm to Indian policy-makers and public officials alike. At the dawn of independence in 1947, almost half of India's population lived below the poverty line and this situation continued till the early 1970s. After the mid-'70s, when Indian farmers obtained access to the seeds of modern varieties of rice and wheat and used chemical fertilizers and irrigation water, growth picked up and resulted in the Green Revolution. Poverty started declining in the rural sector since most of the poor there depend on agriculture (IFPRI 1999). Hossain (1995) has established a direct relationship between food grain yield and the poverty ratio, citing the example of the Indian states. In the eastern states of Bihar, Orissa, West Bengal, Madhya Pradesh, and Assam, where food grain yield was less than 2 t ha^{-1}, the poverty ratio was 20-45%, and, in Haryana and Punjab, where yield averaged 2.5 t ha^{-1} or higher, the poverty ratio was 5-15%. This is a good example of the impact of research-oriented technology on production for poverty alleviation. But now, because of the adoption of modern rice varieties and production technology by farmers, an improving trend is visible in the eastern zone of India. Quoting the Planning Commission and National Sample Survey Organisation of India (NSSO) estimates on poverty, Pandey (2001) reported a substantial decline in the percentage of the population living below the poverty line in eastern India from 54.7% in 1983-84 to 45.6% in 1993-94 and down to 36.9% in 2000.

In comparison to 1947, when about 50% of the population lived below the poverty line, at present, according to the Planning Commission of India's estimates, 26.1% of the Indian population lives in poverty. This is a significant achievement and agriculture's contribution to this performance is commendable (mostly because of rice and wheat). But even this record is not good enough when compared to the achievements made in other Southeast Asian countries such as Indonesia, where poverty declined from 58% in 1970 to only 8% by 1993. China has also done a remarkable job in poverty alleviation, where, from 270 million poor in 1978, the number by 1996 declined to a low of 65 million poor (IFPRI 1999).

Suffering from poverty in India is highly uneven. The eastern states have been the most poverty stricken and had the least human development (Table 4). But now, according to a Hindustan Times (a leading national daily newspaper) report dated Lucknow, 24 April 2002, "The human development index (HDI) of India improved by over 3% a year from 1993 to 2001. Urban-rural disparities declined. Among

Table 4. Poverty and human development profile of major Indian states (rural areas).

State	Per capita income (US$) (Rs. 49 = US$1)	Persons below absolute povert) line (%)[a]	Health subsidy (US$)[b]	Literacy rate age 7+ (%)[a]
Punjab	130.0	32	1.14	60
Haryana	129.9	27	0.84	55
Kerala	117.9	30	0.97	90
Maharashtra	112.7	34	0.91	58
Gujarat	107.9	39	0.75	59
Andhra Pradesh	100.3	21	0.76	50
Rajasthan	86.3	40	0.66	41
Uttar Pradesh	85.4	40	0.60	47
Himachal Pradesh	85.1	45	-	68
Bihar	75.3	42	0.44	44
West Bengal	64.4	51	0.78	59
Orissa	61.8	55	0.66	55
Average for rural India	91.5	39	-	54

Sources: [a]Swaminathan and Balaji (1997). [b]NCAER (1996, original source), published in Hindustan Times, Lucknow, 28 April 2002.

eastern states, West Bengal and Bihar improved significantly in HDI. Poverty in the eastern states of Bihar and Uttar Pradesh declined moderately."

It is significant to note in a study reported from Bihar that the adoption of modern rice varieties had a substantial impact on household income in areas with a developed infrastructure, that is, assured irrigation, transportation, and marketing facilities. Income inequality is mostly on account of nonagricultural income. Rice and/or agricultural income are relatively uniformly distributed compared with income from nonagricultural sources. Poverty incidence was substantially lower in technologically progressive villages (Thakur et al 2000).

In another study conducted in Chattisgarh villages, a tribal region in eastern India, rice was found to be the basic source for household income, accounting for about 46% of total income. The distribution of total income was relatively less equal in the irrigated ecosystem than in the rainfed ecosystem (Janaiah et a1 2000).

One of the important factors responsible for the slow growth rate in agriculture and in rice production and productivity along with other biophysical factors related to rural income has been the declining public-sector investment in agriculture. Such an investment is crucial for the development of much-needed infrastructure such as agricultural education and research, electricity, irrigation, rural linking roads, markets, and the communication network. The fall in national public-sector investment remained unchecked from 1993-94 (US$911.6 million) to 1998-99 ($789.6 million). Public-sector investment in agriculture started picking up in 1999-2000.

The introduction of modem rice varieties and production technology developed through research has undisputedly increased production and productivity and thus improved the rural economy in eastern India, but a sluggish growth of rice-based modern industry and agribusiness has denied farmers the much-needed value addition of their produce for fetching high prices. This region has enormous potential in rice agribusiness and to create wealth in the rural sector in the entire chain from the farm gate to food plate. At both the farm level and industry level, the size and scale of operations will have to be increased manyfold and brought to a global competitive platform to match the WTO regime requirements. The rice industry has started modernizing itself and this could be the first step in this direction.

Jha and Kumar (1998) have shown the impact of rice research in terms of changes in real production costs across some selected Indian states. According to these projections, in the eastern states of Assam, Uttar Pradesh, and West Bengal, the cost of rice production during 1971-80 declined by two or more percentage points per annum. But, during the same period, a rise in the cost of rice production was noticed in Bihar, Madhya Pradesh, and Orissa. In the next decade, a declining trend in the cost of rice production was noticed in Bihar, Madhya Pradesh, Orissa, Uttar Pradesh, and West Bengal. This could be seen as a positive effect of the adoption of improved technology produced through research, giving increased leeway to rice farmers to enhance their income and thus reduce poverty.

Another aspect related to poverty alleviation and rice is the dynamics of the "issue" prices of rice. The price of common, fine, and superfine rice on 1 February 1986 was US$4.71, $4.96, and $5.16 per 100 kg, respectively. These prices by 20 January 1999 rose to $14.30 and $18.47 per 100 kg for the common and fine categories of rice (GOI 2000). But the point for consideration here is the proportion of this price shared by the farmers who produce this rice. Because of the faulty marketing process, the overhead charges going from producers to consumers are quite high and these reduce the margin of poor farmers' profit. On the other hand, the price paid by low-income consumers is unbearable. Hence, there is a need for substantial improvement in the marketing of rice to achieve the desirable benefits at both ends.

The World Trade Organization (WTO) agreements that concluded in 1995 have broadened the horizons for marketing of food grains, including rice, by making rice trade global, liberal, rule-oriented, and transparent. Through a free flow of grains globally as envisaged under the WTO regime, it was expected that the prices of food grains, including rice, would increase and the Asian rice farmers, including those in eastern India, Bangladesh, and other countries, would benefit economically. But, to the dismay of poor farmers, the prices of food grains worldwide have been declining at 2-3% annually. For this situation, both developed and developing countries are responsible. The developed countries did not adhere strictly to the Uruguay round of agreements and also did not permit access to imports from the developing countries as per expectations of the WTO agreements, They also continued protection policies at home. Developing countries, on the other hand, lacked preparation to enter the WTO regime and take full advantage of the new economic situation. These countries could not switch over smoothly from a deficit to a surplus food management situation. Also, they did not fare well in lowering production costs and matching the quality of their produce with the international market demand. Awareness is now developing and it is hoped they will be able to obtain advantages.

In the rice-producing countries of Asia, particularly in India, women's contribution to rice production and the postharvest process is substantial. Hence, the level of women's activity, their level of participation, and their empowerment are directly related to poverty alleviation in a society linked to rice and its economy. Compared with other countries in South and Southeast Asia such as Nepal, Bangladesh, Indonesia, Thailand, and the Philippines, the contribution of women to the production process and harvest and postharvest process of rice in India is maximum. Quoting Paris and Luis (1990), Adalla et al (1993) have indicated that farm women in India constitute 80% of the work force in transplanting rice, 80% in weeding operations, 60% in harvesting and threshing rice, and 100% in postharvest operations. Despite their significant contribution to rice in particular and the rural economy in a broader sense, they lag behind men in terms of the level and quality of employment. To obtain the full social and economic benefits to the farm household and farming society out of the rice research and development process, it will be necessary to ensure that farm women get their rightful remuneration for both their labor and their managerial contribution.

Sustainability concerns and rice research

Soon after independence in 1947 till the end of the 20th century, initially, physical access followed by economic access to food were major concerns for India. Physical access to food has by and large been met through a more than fourfold increase in food production, mostly in rice and wheat in the era of the Green Revolution and thereafter, but the economic and ecological access to food continues to haunt the Indian population and, more specifically, the people of eastern India in the 21st century. While economic aspects have been discussed earlier in this paper, the ecological or environmental situation vis-à-vis rice production will be emphasized briefly.

The use of modem varieties along with their high demand for plant nutrients, pesticides, and water and the resulting Green Revolution are often questioned by environmentalists for disturbing the ecological balance. But the reality is, and India can be cited as an example, where, with almost one-third of the human population in the late 1940s and '50s, there was not enough food. But, today at least, in physical terms, India has no problem supplying enough food to a population triple in number. This colossal feat has been possible largely as a result of cutting-edge research to evolve modern rice and wheat varieties and their production technology. The contribution made by farmers, policymakers, and extension agencies cannot be overlooked. What ecological devastation would have occurred had there been no modem varieties and their production technology available to farmers? The green forests we see today would not have survived the axe of food seekers looking to grow more food for the fast-multiplying human population, and, more than that, probably the prophecies made by Malthus in 1798, followed by Ehrlich in 1968 and the Paddock brothers, about a serious famine in India would have come true. Hence, maintenance of the growth rate of food production at a rate superior to the population growth rate is essential. An unplanned increase in population presents the greatest threat to the environment and disturbs the ecological balance most. The eastern states are the most densely populated ones in India, where, according to the 2001 census, the population density per square kilometer in Bihar is 880, in Uttar Pradesh is 689, and in West Bengal is 904. Since rice is one of the major sources of livelihood in this region, a planned development of the rice crop and rice-based farming systems with the proper use of natural resources, modern varieties, and technology to take care of the ecological and social carrying capacities can be a sustainable approach. Maintenance of sustainable production of the system at a higher level has been emphasized by Modgal (1999). To achieve this goal, an uninterrupted use of modern scientific technology such as modern varieties, balanced fertilizer use, natural resource management, geographic information systems (GIS), biotechnology, information technology, simulated modeling, and the like will be necessary.

Conclusions

The threat of the population growth rate exceeding the food production growth rate, even in the near future, has not receded globally, more so for South Asia and specifically for eastern India. But, there are also definite indications of a positive impact of rice research producing a viable technology capable of ensuring food security, reducing malnutrition, and alleviating poverty in eastern India. Since the rural economy of the region revolves around the rice crop, which continues to be the major source of livelihood to millions of farmers, the improving trends in this crop brought about by using modern technology have started bringing social and economic change by making possible the equitable distribution of income and simultaneously increasing the purchasing power of the rural poor. There is a need to look at environmental problems more pragmatically and in a new perspective to keep the growth rate of food production ahead of population growth to save humanity from hunger. This is only a beginning. We must continue with this course of action and sustain the growth rate through an increased investment in rice research with an enhanced partnership between national and international organizations. An active involvement of farmers of the region in the process will make it more realistic and purposeful.

References

Adalla CB, Thelma RP, Hoque MM. 1993. Women in Asian rice farming families: research agenda and strategies for the year 2000. In: Muralidharan K, Siddiq EA, editors. New frontiers in rice research. Hyderabad (India). p 347-353.

BIS (Biotechnology Information Service, Monsanto). 2001. Biotechnology: global update. 3(4):2.

CRRI (Central Rice Research Institute). 1996. Fifty years of rice research at CRRI. Sridhar R, editor. Cuttack (India): CRRI.

FAI (The Fertiliser Association of India). 1998. Fertiliser statistics, 1997-98. New Delhi (India): FAI.

FAI (The Fertiliser Association of India). 2001. Fertiliser statistics, 2000-2001. New Delhi (India): FAI.

GOI (Government of India). 2000. Indian agriculture in brief. 27th edition. Ministry of Agriculture, Government of India.

GOI (Government of India). 2002. INDIA 2002. A reference annual. Publications Division, Ministry of Information and Broadcasting, Government of India.

Hossain M. 1995. Sustaining food security for fragile environments in Asia: achievements, challenges, and implications for rice research. In: Fragile lives in fragile ecosystems. Proceedings of the International Rice Research Conference, 13-17 February 1995. Los Baños (Philippines): International Rice Research Institute. p 3-23.

Hossain M, Pingali PL. 1998. Rice research, technological progress, and impact on productivity and poverty: an overview. In: Pingali P, Hossain M, editors. Impact of rice research. Proceedings of the International Conference on the Impact of Rice Research, 3-5 June 1996, Bangkok, Thailand. Bangkok (Thailand): Thailand Development Research Institute and Los Baños (Philippines): International Rice Research Institute. p 1-2.5.

IFPRI (International Food Policy Research Institute). 1999. Pushing back poverty in India: news and views. Washington, D.C. (USA): International Food Policy Research Institute. p 1-8.

IRRI (International Rice Research Institute). 2000. The rewards of rice research. Annual report: 1999-2000. Los Baños (Philippines): IRRI. p 8-9.

Janaiah A, Bose ML, Aganval AG. 2000. Poverty and income distribution in rainfed and irrigated ecosystems: village studies in Chattisgarh. In: Income distribution and poverty in rural Asia. Papers presented at the Third Conference of the Asian Society of Agricultural Economics at Jaipur, India, 18-20 October 2000. p 103-118. Reprinted from Economic and Political Weekly, Mumbai 35(52 and 53). Review of Agriculture, 30 December 2000.

Jha D, Kumar P, 1998. Rice production and impact of rice research in India. In: Pingali PL, Hossain M, editors. Impact of rice research. Proceedings of the International Conference on the Impact of Rice Research, 3-5 June 1996, Bangkok, Thailand. Thailand Development Research Institute and Los Baños (Philippines): International Rice Research Institute. p 279-291.

Kumar P, Rosegrant MW. 1994. Productivity and source of growth for rice in India. Econ. Polit. Weekly. Dec. 31.

Krishnaiah K, Reddy MN, Das SR, Pathak AK. 1998. Promotion of rainfed rice production technologies through frontline demonstrations for increasing rice productivity in eastern India. In: Proceedings of the International Symposium on Rainfed Rice for Sustainable Food Security, 23-25 September 1996, Central Rice Research Institute and Association of Rice Research Workers, Cuttack, India. p 472-482.

Modgal SC. 1998. Investment in rice research in eastern India. Paper presented at the National Symposium on Farming Rice in Eastern India, jointly organized by the U.P. Council of Agricultural Research and International Rice Research Institute, 19-21 March 1998, Lucknow, India.

Modgal SC. 1999. Rice-wheat cropping system: an ecological approach. In: Kushwaha KS, editor. Changing scenario in farming practices, policies, and management. Udaipur (India): Kushwaha Farm—Book Series. p 127-146.

NARES (National Agricultural Research and Extension Systems), IRRI (International Rice Research Institute). 2001. Group discussion with rice scientists at Narendra Dev University of Agriculture and Technology at Kumar Ganj and then a group of eastern India rice scientists at the Central Rice Research Institute, Cuttack, in the 3rd and 4th week of

October 2001, and thereafter with the scientists of the International Rice Research Institute at Los Baños in the 1st and 2nd week of November 2001 as a member of the Rainfed Lowland and Rainfed Upland Rice Research Consortium Review Team.

Pandey S. 2001. The unfavorable rice ecosystems: an overview. A group review presentation at the International Rice Research Institute, Los Baños, Philippines, November 2001.

Paris IR, Luis J. 1990. Gender analysis in Asian farming systems research. Paper presented at the AFSRE symposium, 11-17 October 1990, Michigan State University, East Lansing, Michigan, USA.

Paroda RS, Siddiq EA. 1993. Accomplishments of the coordinated rice research: an overview. In: Muralidharan K, Siddiq EA, editors. New frontiers in rice research. Hyderabad (India): Directorate of Rice Research. p 15-24.

Rao NGP, Singh A, Sivasubramanian V, Murthy KS, Mukhopadhyay AN, Abraham CC. 1998. Rice research and production in India: present status and a future perspective. Quinquennial Review Committee Report, 1988-96. Hyderabad (India): Directorate of Rice Research (Indian Council of Agricultural Research).

Siddiq EA. 1998. Constraints to rice production in eastern India. In: Proceedings of the International Symposium on Rainfed Rice for Sustainable Food Security, 23-25 September 1996. Central Rice Research Institute and Association of Rice Research Workers, Cuttack, India. p 34-52.

Singh VP, Singh RK, editors. 2000. Rainfed rice: a sourcebook of best practices and strategies in eastern India. Los Baños (Philippines): International Rice Research Institute. 292 p.

Subbaiah SV, Balasubramanian V. 2000. Wet seeding of rice in India. DRR-(ICAR)-CREMNET (IRRI) Project. Directorate of Rice Research, Hyderabad, India, and International Rice Research Institute, Los Baños, Philippines.

Swaminathan MS, Balaji V. 1997. Food security for the poor: What does it take? IASSI Quart. 16(1):17-35.

Thakur J, Bose ML, Hossain M, Janaiah A. 2000. Rural income distribution and poverty in Bihar. In: Income distribution and poverty in rural Asia. Papers presented at the Third Conference of the Asian Society of Agricultural Economics at Jaipur, India, 18-20 October 2000. p 81-102. Reprinted from Economic and Political Weekly, Mumbai 35 (52 and 53). Review of Agriculture, 30 December 2000.

Virmani SS. 2002. Development and large-scale seed adoption of hybrid rice in India. India Grains 4(2):15-16.

Notes

Author's address: International agriculture consultant, 13/579. Indira Nagar, Lucknow 226 016, India, Tel. 0091-522-712351, E-mail: modgalsc@rediffmail.com. Former vice-chancellor, G.B. Pant University of Agriculture and Technology, Pantnagar, India, and former director general, U.P. Council of Agricultural Research, Lucknow, India.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Natural resource management

Market adaptations to increased water prices in China: the effects on water demand and rice production

M.W. Rosegrant and X. Cai

China faces rapidly growing water scarcity in many important river basins, particularly in the north. New supplies of water for both the agricultural and nonagricultural sectors are increasingly expensive. Rapid growth in domestic and industrial demand is likely to draw water from irrigation, putting downward pressure on rice and other irrigated crops. However, despite growing scarcity, in much of China, water is not treated as a scarce resource. Irrigation water is generally provided at little or no cost and in urban areas the price of water often does not cover the cost of delivery. With little incentive for water managers, farmer-irrigators, and urban water consumers to conserve, water is overused and wasted. Water price policy reform could provide incentives to use water more efficiently. In this paper, we examine the effects of increased water prices on demand for water for irrigation and for the domestic and industrial sectors, and on the availability of water for environmental purposes. The effect of the change in rice and other cereal production because of water price changes in China on food demand and trade status for China will also be analyzed. The analysis uses the IMPACT-WATER model, a global integrated water and food supply and demand model. The model allows assessment of the effect of water prices in nine major river basins in China. The results show that significant but reasonable water price increases will lead to considerable water savings for environmental uses, especially in dry basins in North and Northwest China, while irrigated food production will not be affected much if water prices induce the improvement of irrigation water-use efficiency.

Rice is of utmost importance in food production in both China and the world. China has slightly more than one-fifth of the global harvested rice area and produces one-third of the world's rice. Within China, nearly half of the total harvested irrigated area is cropped with rice and rice accounts for nearly half of the production of irrigated cereals and one-third of the total cereal production. However, rice production in China, almost all from irrigated land, is challenged by rapidly growing water scarcity in many important river basins, particularly in the north. New supplies of water for both the agricultural and nonagricultural sectors are increasingly expensive. The diversion of water to rapidly growing domestic and industrial demand, the depletion of underground supplies in aquifers, and the increasing pollution caused by rapid industrialization put downward pressure on the water available for rice and other irrigated crops.

However, despite growing scarcity, in much of China, water is not treated as a scarce resource. Irrigation water is generally provided at little or no cost and in urban areas the price of water often does not cover the cost of delivery. With little incentive for water managers, farmer-irrigators, and urban water consumers to conserve, water is overused and wasted. Water price policy reform could provide incentives to use water more efficiently. China plans to raise water prices over the next five years as an economic incentive to conserve scarce water resources (People's Daily 2001). However, in China, where rural incomes are low, any water price increase is fraught with political risks.

In this paper, we examine the effects of increased water prices on demand for water for irrigation and for domestic and industrial sectors, and on the availability of water for environmental purposes. The effect of the change in rice and other cereal production because of water price changes in China on demand and trade status for China will also be analyzed. We first briefly describe the methodology; present alternative scenarios for water and food in China, including business as usual and alternative water price scenarios; and then summarize the results and present policy conclusions.

Methodology

The analysis uses the IMPACT-WATER model, a global integrated water and food supply and demand model (Rosegrant et al 2002). The model divides the world into 69 spatial units, including nine major river basins in China, including the Changjiang, Huanghe, Huaihe, Haihe, Songliaohe, Zhujiang, river basins in southwestern and southeastern China, and inland basins in northwestern China. The model simulates water demand and supply in domestic, industrial, livestock, and irrigation sectors and food production in the nine basins.

Industrial water demand depends on income (gross domestic product, GDP, per capita), industrial water demand intensity (m^3 of water per $1,000 GDP), a technology variable that varies with time, and water prices. The effect of water prices is captured through the elasticity of industrial demand with respect to water price. Domestic water demand includes municipal water demand and rural domestic water demand. Domestic water demand is estimated based on projections of population, income growth, and water prices. Livestock water demand is projected as a function of livestock production and water prices.

Irrigation water demand is assessed in two steps. The first step is to estimate the physical demand, which is based on crop irrigation water requirement (crop evapotranspiration minus rainfall used by crops) and irrigation water-use efficiency at the basin scale, which is defined as the ratio of beneficial water consumption to total consumption. The second step is to adjust the physical water demand with respect to water prices using price elasticities of demand for water in irrigation. Committed flow for the environment is defined as the quantity of water that is reserved for environmental and instream uses and is thus unavailable for other uses.

The model calculates water supply based on both hydrologic processes and anthropogenic effects as described below. Committed environmental and ecological flows are treated as a predetermined hard constraint to water supply, and off-stream water supply for the domestic, industrial, livestock, and irrigation sectors is determined through two steps. The first step is to determine total water that could be depleted in each time period (month) for various off-stream uses and the second is to determine the water supply for different sectors. Assuming that domestic water demand is satisfied first, followed in priority by industrial and livestock water demand, irrigation water supply is the residual claimant. Moreover, irrigation water supply is further allocated to different crops in the basin based on crop water requirements and profitability.

Food demand and production are calculated in a partial equilibrium agricultural sector model representing a competitive agricultural market for crops and livestock. Demand is a function of prices, income, and population growth. Growth in crop production in each country is determined by crop and input prices and the rate of productivity growth. World agricultural commodity prices are determined annually at levels that clear international markets. The model produces projections for crop area, yield, production, demand for food, feed, and other uses, prices, and trade; and, for livestock numbers, yield, production, demand, prices, and trade. Water supply is incorporated as a variable in the crop yield and area functions for each of eight major food crops—wheat, rice, maize, other coarse grains, soybean, potato, yam and sweet potato, and cassava and other roots and tubers. Irrigated and rainfed area and yield are calculated separately for these crops.

Assumptions and projection–business as usual (BAU)

The starting point for the analysis is a business as usual (BAU) scenario that incorporates our best estimates of the policy, investment, technological, and behavioral parameters driving the food and water sectors. In the water component, the model uses hydrologic data (precipitation, evapotranspiration, and runoff) that recreate the hydrologic regime of 1961-91 (Alcamo 2000). Results for the BAU in this section are based on the mean of 30 hydrologic samples specified based on various year sequences of the hydrologic regime from 1961 to 1990.

Moderate increases are projected for water withdrawal capacity, reservoir storage, and water management efficiency, based on estimates of current investment plans and the pace of water management reform. Total water withdrawals in China are projected to increase by 25% from 1995 to 2025, from 680 km^3 (groundwater pumping 138 km^3) in 1995 to 845 km^3 (groundwater pumping 171 km^3) in 2025. Reservoir storage for water supply increases by 157 km^3 (nearly 30%) in the Changjiang, Zhujiang, and Songliaohe basins) over the next 25 years. Basin efficiencies are higher in the Haihe, Huaihe, and Huanghe basins (0.60-0.70 in 1995 and 0.70-0.80 in 2025) than in others (0.50-0.55 in 1995 and 0.55-0.60 in 2025) and the countrywide average basin efficiency increases from 0.55 in 1995 to 0.60 in 2025.

Nonirrigation water uses, including domestic, industrial, and livestock water uses, are projected to grow rapidly (Table 1). Total nonirrigation water consumption in China is projected to increase from 47 km^3 in 1995 to 98 km^3 in 2025, an increase of 110%. Potential nonirrigation was almost 100% supplied in 1995. However, in 2025, the water deficit will be 3-6% of the potential demand in Haihe, Huanghe, Songliaohe, and Huaihe basins (Table 2)

Potential harvested irrigated area for cereal crops in China is projected to increase by 8% from 64.1 to 69.3 million hectares in 2025, while rice irrigated harvested area will decline by 11% from 30.5 to 27.2 million ha in 2025. Irrigated areas of noncereal crops will have a relatively large increase by 40% from 27.4 to 38.4 million ha. The total irrigated area (harvested) will increase by 17.6% or 16.1 million ha (Table 3). As a result, potential irrigation water demand will increase by 8%—a lower percentage increase than potential irrigated area because of improved water-use efficiency, and because of the decline in proportion of area in rice. However, as shown in Table 1, realized (actual) irrigation water consumption in China will decline by 6% from 244 km^3 in 1995 to 231 km^3 in 2025 because of the very rapid increase in nonirrigation demand and relatively slow growth in water supply. As a result, total actual irrigated crop area increases by only 15.4%, from 90.1 million to 104 million ha; actual cereal irrigated area increases by 7.5% from 62.4 million to 67.1 million ha; and rice irrigated area declines by 12.4%, from 30.5 million to 26.7 million ha (see additional discussion below).

To show water scarcity for irrigation, we define a term, irrigation water supply reliability (IWSR), which is the ratio of the realized water demand over the potential demand. The potential demand is the irrigation water requirement to meet the full evapotranspiration demand of all crops included in the model over the full potential irrigated area. Potential demand is thus the demand for irrigation water in the absence of any water supply constraints. In terms of IWSR, river basins in northern China display different water supply trends than those in the south (Table 4). The IWSR in northern China is projected to remain below 0.8 in most years, and will fall as low as 0.5 in some dry years. Southern China will have an IWSR above 0.85 in most years, although this ratio falls as low as 0.5 in some particularly dry years. Figure 1 shows the IWSR in the Haihe Basin (as an example of basins in northern China) and in the Changjiang Basin (as an example of basins in southern China) from 1995 to 2025 under a single climate regime of 1961 to 1990.

Water scarcity in the north and the south has different causes. Serious source shortages could occur in the Haihe Basin, inland basins of Northwest China, the Yellow River Basin, and the Huaihe Basin. The Huaihe Basin and the Yellow River Basin will also have infrastructure constraints in some dry years (when the water requirement from irrigation is large to make up for lack of rainfall) because of reaching the limits of withdrawal capacity. Although it is seemingly paradoxical that withdrawal

Table 1. Water consumption by sector in nine major basins in China, 1995 and 2025 (km^3).

Basin	Domestic		Industry		Livestock		Irrigation		Total	
	1995	2025	1995	2025	1995	2025	1995	2025	1995	2025
Huaihe	4.0	7.9	1.2	5.2	0.5	1.0	24.4	22.4	30.2	36.6
Haihe	1.9	3.6	1.1	1.8	0.3	0.6	22.1	17.9	25.4	23.9
Huanghe	2.4	4.0	1.0	1.8	0.3	0.7	21.3	22.3	25.0	28.7
Changjiang	12.3	24.3	5.7	11.3	1.2	2.8	82.5	77.4	101.7	115.8
Songliaohe	2.2	3.5	2.0	4.1	0.4	0.8	18.9	20.2	23.4	28.6
Inland basins	0.7	1.5	0.1	0.4	0.1	0.2	31.8	32.7	32.7	34.9
Southwest basins	0.4	0.8	0.1	0.7	0.0	0.1	2.3	2.2	2.8	3.8
Zhujiang	4.3	10.3	1.6	3.5	0.4	1.0	26.6	23.3	32.9	38.1
Southeast basins	1.9	3.5	0.3	2.2	0.1	0.3	14.4	12.4	16.6	18.4
China basins	30.1	59.4	13.1	31.0	3.3	7.5	244.0	230.8	290.7	328.8

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Table 2. Nonirrigation water supply reliability in nine major basins in China, 1995 and 2025.

Basin	1995	2025
Huaihe	0.99	0.94
Haihe	1	0.97
Huanghe	0.99	0.95
Changjiang	1	0.99
Songliaohe	0.98	0.93
Inland basins	1	1
Southwest basins	1	0.99
Zhujiang	1	0.99
Southeast basins	1	0.98
China	0.98	0.97

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

capacity would be a constraint when water supply is low, low rainfall also increases the proportion of crop water demand that must be met from irrigation. Basins in South and Southeast China will experience a dramatic drop (as much as 50%) in water supply in some years because of a lack of storage capacity that can deliver water during the dry season.

The effects of water withdrawal on the environment can be shown by the ratio of water withdrawal to runoff at the basin scale. This *criticality ratio* is an indicator of water scarcity stress at the basin level (Alcamo et a1 2000, Raskin 1997). The higher the criticality ratio, the more intensive the use of river basin water and the lower the water quality for downstream users. Hence, at high criticality ratios, water usage by downstream users can be impaired, and, during low flow periods, the chance of absolute water shortages increases. Criticality ratios equal to or greater than 0.4 are considered "high water stress" and 0.8 "very high water stress" (Alcamo et al 2000).

Many basins in China have very high and increasing water stress. Although minimum environmental committed flow has been assumed as 25-30% in the Huanghe, Huaihe, and Haihe basins, 45% in the Changjiang Basin, 15% in inland basins, and 30-35% in other basins, water withdrawal in some basins is greater than the amount of runoff because of a high degree of reuse of return flows. Even in 1995, the ratio of water withdrawal to runoff is more than 2.0 in the inland basins, 1.4 in the Haihe Basin, 0.83 in the Huaihe Basin, and 0.89 in the Huanghe Basin, and the countrywide average is 0.26. These already high intensity levels increase significantly by 2025, when the ratio in inland, Haihe, Huanghe, and Huaihe basins will be 3.5, 1.49, 1.11, and 1.15, respectively, and the countrywide average ratio will be 0.33. This shows that, by 2025, the environmental system in some major basins will be highly affected by off-stream water uses (Table 5).

To assess the relation between water and food production, we first examine water productivity, which is defined as crop yield per cubic meter of water consumption,

Table 3. Potential harvested irrigated areas in nine major basins in China, rice, other cereals, other crops, and total, 1995 and 2025 (000 ha).

Basin	1995				2025			
	Rice	Other cereals	Noncereal crops	Total	Rice	Other cereals	Noncereal crops	Total
Huaihe	1,869	9,921	4,638	16,428	1,707	12,153	7,110	20,970
Haihe	252	5,162	1,747	7,162	230	5,782	2,258	8,269
Huanghe	296	4,271	2,257	6,825	268	5,534	2,571	8,374
Changjiang	15,941	8,296	8,380	32,617	,13,619	11,010	12,255	36,883
Songliaohe	1,073	2,004	1,809	4,885	1,528	3,010	2,325	6,863
Inland basins	96	2,264	1,858	4,217	110	2,351	2,578	5.039
Southwest basins	314	373	867	1,554	284	501	927	1,712
Zhujiang	7,706	884	3,304	11,894	6,863	1,189	4,651	12,703
Southeast basins	2,960	428	2,560	5,948	2,632	506	3,721	6,859
China	30,508	33,603	27,419	91,529	27,243	42,034	38,396	107.673

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998). and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Table 4. irrigation water supply reliability in nine major basins in China, 1995 and 2025.

Basin	1995	2025
Huaihe	0.83	0.66
Haihe	0.78	0.62
Huanghe	0.80	0.75
Changjiang	0.92	0.90
Songliaohe	0.85	0.71
Inland basins	0.81	0.79
Southwest basins	0.99	0.96
Zhujiang	0.98	0.91
Southeast basins	1.00	0.84
China	0.87	0.80

Sources: 1995: authors' estimation based on HPDGI(1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

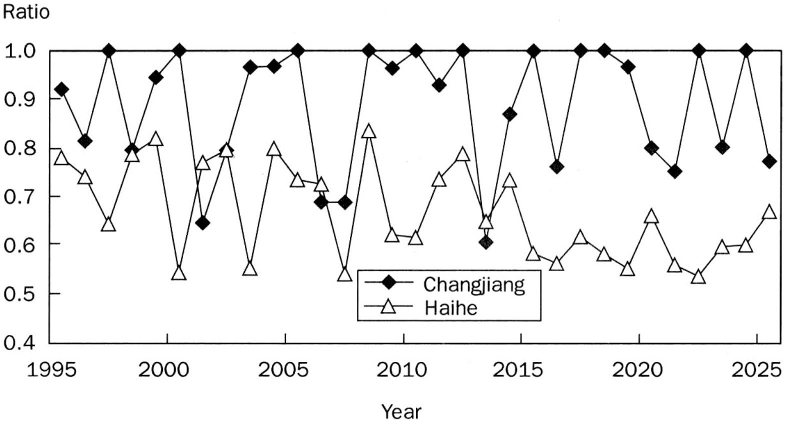


Fig. 1. Irrigation water supply reliability in the Haihe and Changjiang basins during 1995-2025 under a single climate regime of 1961-90.

including "green" water (effective rainfall) for rainfed areas and both green and "blue" water (diverted water from water systems) for irrigated areas. Because rice usually consumes more water than other crops, the water productivity of rice is significantly lower than that of other cereals. The water productivity of irrigated rice ranges from 0.15 to 0.70 kg m^{-3} in the world in 1995, and China's value is in the upper range from 0.4 to 0.7 kg m^{-3}, with an average of 0.67 kg m^{-3}. The average water productivity of irrigated other cereals in China ranges from 0.4 to 1.4 kg m^{-3}, with an average of 1.0 kg m^{-3}, which is higher than the average in developing countries—0.56 kg m^{-3}—and close to the average of developed countries. In 2025, water productivity for irrigated rice and nonrice cereals will increase to 0.85 and

Table 5. Water withdrawal and ratio of withdrawal to renewable water in nine major basins in China, 1995 and 2025.

Basin	Water withdrawal (km^3)		Ratio of withdrawal to renewable water	
	1995	2025	1995	2025
Huaihe	77.9	108.3	0.83	1.15
Haihe	59.2	62.9	1.40	1.49
Huanghe	64.0	79.5	0.89	1.11
Changjiang	212.6	259.1	0.23	0.29
Songliaohe	51.5	67.6	0.26	0.34
Inland basins	89.5	111.2	2.99	3.71
Southwest basins	8.3	12.3	0.01	0.02
Zhujiang	77.1	96.9	0.19	0.24
Southeast basins	38.8	47.7	0.27	0.33
China	678.9	845.5	0.26	0.33

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

1.53 kg m^{-3}, respectively, which will both be higher than the global average, 0.53 and 1.10 kg m^{-3}. The increase in water productivity is driven mainly by increases in irrigated crop yield per hectare because of improved crop varieties, together with an increase in water-use efficiency over time.

The effect of water stress on crop yield can be represented by relative crop yield, which is the ratio of actual crop yield over the maximum without water constraint. Yield deficits existed for both rice and nonrice cereals even in 1995, and significant drops occur from 1995 to 2025 in relative yields for both rice and nonrice cereals, especially in North China, including the Huanghe, Huaihe, Haihe, and Songliaohe basins, and inland basins in northwestern China. Relative rice yields decline from 0.82-0.93 in 1995 to 0.65-0.89 in 2025; nonrice cereal yields decline from 0.78-0.99 in 1995 to 0.67-0.91 in 2025 (Table 6). The fall in the relative crop yield index because of water deficits is a significant drag on future yield growth.

From 1995 to 2025, irrigated rice production will increase by 19.1 million metric t or 16% in China (Table 7), which will be mainly produced in the Changjiang and Zhujiang river basins. Rainfed rice contributes less than 2% to the total in both 1995 and 2025. Irrigated nonrice cereals will increase by 121.4 million metric t or 86% and rainfed nonrice cereals will increase by 43.4 million metric t or 47%, which will be produced mainly in the Huaihe, Changjiang, Songliaohe, Huanghe, and Haihe basins (Tables 8 and 9). Irrigated agriculture will dominate cereal production growth in China, 87% of the production increase of all cereals during 1995 to 2025 (355.9 million metric t), compared to a contribution to future cereal production in the world as a whole of 50% (Rosegrant et al 2002).

Growth of yield will contribute more than expansion in area to future production growth in China. For rice, irrigated area even decreases by 3.8 million ha or 12%

Table 6. Relative irrigated rice and nonrice cereal yields.

Basin	Rice		Other cereals	
	1995	2025	1995	2025
Huaihe	0.90	0.82	0.91	0.77
Haihe	0.83	0.65	0.80	0.70
Huanghe	0.82	0.74	0.91	0.71
Changjiang	0.92	0.88	0.88	0.84
Songliaohe	0.85	0.66	0.91	0.67
Inland basins	0.82	0.65	0.78	0.67
Southwest basins	0.93	0.89	0.94	0.91
Zhujiang	0.93	0.89	0.94	0.88
Southeast basins	0.93	0.87	0.99	0.86
China	0.91	0.86	0.87	0.75

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATERprojections(June2002).

Table 7. Irrigated area (AI), yield (Yi), and production (PI) for rice in nine major basins in China, 1995 and 2025.

Basin	1995			2025		
	AI (000 ha)	YI (kg ha^{-1})	PI (million t)	AI (000 ha)	YI (kg ha^{-1})	PI (million t)
Huaihe	1,869	5,104	9.5	1,675	6,308	10.6
Haihe	252	4,499	1.1	226	4,694	1.1
Huanghe	296	3,930	1.2	263	4,624	1.2
Changjiang	15,941	4,153	66.2	13,359	5,536	74.0
Songliaohe	1,073	4,816	5.2	1,499	4,858	7.3
Inland basins	96	4,097	0.4	108	4,535	0.5
Southwest basins	314	3,609	1.1	279	5,025	1.4
Zhujiang	7,706	3,525	27.2	6,732	4,923	33.2
Southeast basins	2,960	3,680	10.9	2,582	4,960	12.8
China	30,507	4,025	122.8	26,723	5,311	141.9

Sources: 1995: authors' estimation based on: HPDGI (1989). Qian (1991). NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

from 1995 to 2025 in the whole country, with a major decline in the Changjiang, Zhujiang, and Southeast basins. Irrigated rice yield will increase by 10% to 40% over the nine basins and by 1.3 t ha^{-1} or 31% in the whole country. For nonrice cereals, irrigated area has a significant increase by 8.5 million ha or 26% from 1995 to 2025 in the whole country, with declines only in the Haihe Basin. However, the irrigated yield increase for nonrice cereals will still be more significant than area, by 2.1 t ha^{-1} or 47% for the whole country. For rainfed nonrice cereals, area increases by 2.7 million ha or 11%, while yield increases by 1.2 t ha^{-1} or 33% for the whole country from 1995 to 2025.

Table 8. Irrigated area (AI), yield (YI), and production (PI) for nonrice cereals in nine major basins in China, 1995 and 2025.

Basin	1995			2025		
	AI (000 ha)	YI (kg ha^{-1})	PI (million t)	AI (000 ha)	YI (kg ha^{-1})	PI (million t)
Huaihe	9,671	5,131	49.6	11,846	7,521	89.1
Haihe	4,912	4,829	23.7	4,798	7,297	35.0
Huanghe	4,081	3,578	14.6	5,472	4,566	25.0
Changjiang	7,944	3,510	27.9	11,000	5,476	60.2
Songliaohe	1,625	7,224	11.7	2,860	11,431	32.7
Inland basins	1,965	4,310	8.5	2,215	5,223	11.6
Southwest basins	373	3,015	1.1	499	4,143	2.1
Zhujiang	884	2,669	2.4	1,165	3,871	4.5
Southeast basins	428	3,054	1.3	486	4,314	2.1
China	31,883	4,417	140.8	40,341	6,501	262.3

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991). NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Table 9. Rainfed area (AR), yield (YR), and production (PR) for nonrice cereals in nine major basins in China, 1995 and 2025.

Basin	1995			2025		
	AR (000 ha)	YR (kg ha^{-1})	PR (million t)	AR (000 ha)	YR (kg ha^{-1})	PR (million t)
Huaihe	4,456	3,827	17.1	5,191	5,192	27.0
Haihe	3,971	3,289	13.1	4,239	4,731	20.1
Huanghe	4,338	2,614	11.3	3,730	3,540	13.2
Changjiang	3,542	3,671	13.0	4,003	4,705	18.8
Songliaohe	6,817	4,411	30.1	8,624	5,292	45.6
Inland basins	847	2,428	2.1	810	4,205	3.4
Southwest basins	399	3,406	1.4	429	3,353	1.4
Zhujiang	1,226	3,108	3.8	1,305	4.290	5.6
Southeast basins	0	0	0.0	11	1,700	0.0
China	25,596	3,585	91.8	28,342	4,769	135.2

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990 98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

The ongoing transformation in the structure of cereal demand in China is projected to continue. Strong growth in income, rapidly increasing urbanization, and changing tastes and preferences cause a shift to more diversified diets with higher per capita consumption of meat, milk and milk products, fruits, and vegetables, and a relative shift in food demand from rice to wheat (Rosegrant et a1 2001). Increasing meat demand will lead to a strong increase in demand for maize and other coarse grains for animal feeds. As a consequence, rice demand will increase by only 16.8 million metric t, while nonrice cereal demand will increase by 169.6 million metric t from 1995 to 2025 (Figs. 2 and 3). As a result, per capita annual rice demand will decline

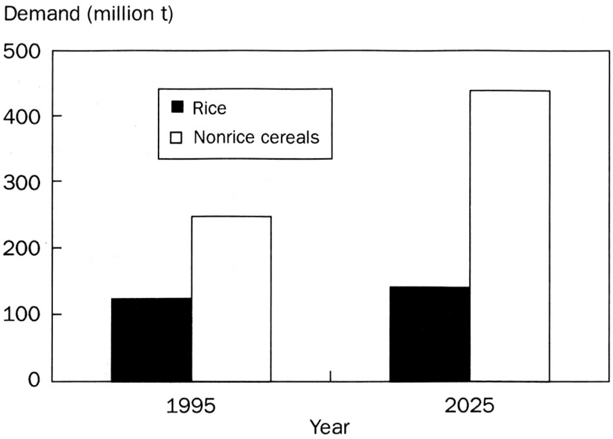


Fig. 2. Rice and other cereal demand for China in 1995 and 2025.

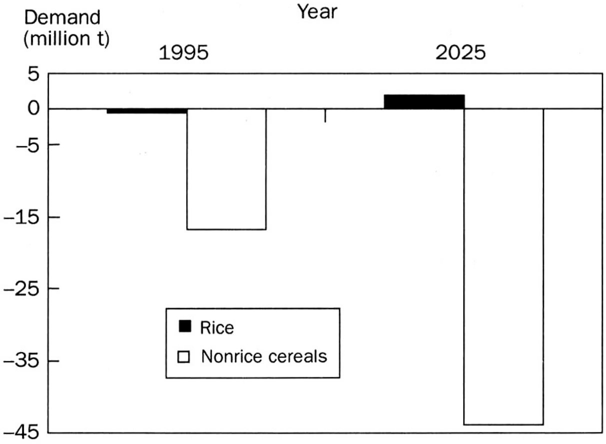


Fig. 3. Rice and other cereal trade for China in 1995 and 2025.

from 102 kg in 1995 to 96 kg in 2025, while per capita annual nonrice cereal demand will increase from 203 kg in 1995 to 297 kg in 2025. For water conservation, the changes in demand are favorable, with rice, the most water-consuming crop, being replaced by other cereals.

Because of the relatively slow growth in rice demand, there are projected to be small exports of rice, 1.9 million metric t by 2025. But, for nonrice cereals, although their production will increase more than rice as described above, imports of nonrice cereals will increase by 27.1 million metric t, to 43.9 million metric t in 2025 with the rapid growth in demand for these commodities outpacing production growth.

High water price scenarios: assumptions and analysis

Data and assumptions

Next, we examine two scenarios in which water prices are higher than those under BAU. Our analysis focuses on the effects on food security and environmental water flows, based on available data and various policy assumptions, because the irrigation sector will continue to be the major water user in China and the conflict between irrigation demand and environmental requirements is growing. Under the high-price scenarios, water prices for agriculture, industry, and connected households are assumed to increase gradually from 2000 to 2025. By 2025, the water prices for industrial water use are 2.25 times higher than the prices under the BAU scenario, 2.0 times higher for domestic water use in connected households, the same as those of the BAU for unconnected households, and 3.0 times higher than BAU prices for agricultural water uses.

Values for water price elasticity vary based upon many factors, including the sector for which they are estimated, season, region, whether they are calculated for rural or urban areas, and indoor versus outdoor use (for domestic demand). The available evidence shows that the elasticity of water demand with respect to water prices is relatively low, particularly in the agricultural sector. Gracia et al (2001) present a survey of the main problems involved in the estimation of residential water demand and Dalhuisen et al (2002) and Espey et al (1997) provide meta-analyses of price elasticities of residential water demand. We assessed water price elasticities for domestic, industrial, and agricultural water demand based on a review of relevant literature and compiled the results of many empirical studies that estimated price elasticities of demand for water in the relevant sectors mentioned above. The elasticities used in the model for China are -0.09 - -4.16 for irrigated agriculture and livestock, -0.55 - -0.80 for the industrial sector, and -0.35 - -4.55 for the domestic sector.

These industrial, household, and livestock water demand elasticities with respect to water prices are long-term elasticities reflecting full adjustment in water demand to changes in water prices. However, the irrigation water demand elasticities are short-term elasticities that reflect the changes in water withdrawal and total water consumption in response to changes in water prices, including substitution of variable inputs such as labor and fertilizer for water. The longer-term response of beneficial irrigation water demand to water prices is also determined by the response of water-use efficiency to water prices.

Farmers can respond to higher water prices not only by a direct reduction in water withdrawals and consumption but also by improving the efficiency of use of that water so that a greater portion of it is used beneficially for crop production (Varela-Ortega et al 1998, Zilberman et al 1997, Shah et al 1995, Caswell and Zilberman 1985,1986). Water-use efficiency can be increased by investment in water-conserving irrigation technology, such as drip and sprinkler irrigation, or by improving the on-farm management of the water to reduce losses to nonbeneficial consumption. In the context of the water-food model, the longer-term efficiency response to water

Table 10. Basin efficiency (ratio) for the two higher-water-price scenarios. [a]

Basin	HP	HP-HE
Huaihe	0.67	0.74
Haihe	0.78	0.90
Huanghe	0.64	0.73
Changjiang	0.58	0.64
Songliaohe	0.61	0.70
Inland basins	0.52	0.62
Southwest basins	0.53	0.63
Zhujiang	0.53	0.64
Southeast basins	0.53	0.63
China	0.60	0.68

[a] HP = higher-price, HP-HE = higher-price-higher-efficiency. Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

prices is represented by an elasticity of basin water-use efficiency (BE) with respect to water prices. The literature cited immediately above shows that higher water prices induce improvements in irrigation technology and reductions in water use. But there is little direct evidence on the quantitative response of basin efficiency in the literature. Two alternative efficiency responses are therefore examined. The higher-price (HP) scenario is a "worst-case" scenario that assumes a basin efficiency response to water prices of 0.0. Under the higher-price, higher-efficiency scenario, HP-HE, the basin efficiency elasticities with respect to water prices are set at a moderate level of 0.067 in China, with slightly lower values in high-scarcity, high-efficiency river basins and lower values in other basins.

The resulting values for the BE for each scenario for each of the nine major river basins are shown in Table 10. Under both higher-water-price scenarios, we assume that a large portion of the conserved water is allocated to environmental uses, and that the minimum fraction of the conserved water for environmental uses will be 60-80% in all the basins.

The BAU and the two high-price scenarios presented here use the climate regime of 1961-90 as opposed to the 30 climate-scenario simulations used in the BAU presented above. Because of climate variability, specific projection results in this section are the annual average values in the period of 2021-25.

Results for higher-water-pricing scenarios compared with the BAU

Water results. Under all the higher-price scenarios, nonirrigation consumptive water use in 2025 decreases from the BAU levels for all regions (Table 11). Compared with BAU, total nonirrigation consumptive water use decreases by 26.1 km^3 or 27% nationwide. Higher water prices lead to a decline in irrigation water demand also. Irrigation water consumption declines by 25.6 km^3 or 11 %. Total water consumption,

Table 11. Consumptive water use (km^3) for nonirrigated sectors under "business as usual" (BAU) and higher-price (HP) scenarios, 2021-25.

Basin	Domestic		Industrial		Livestock		Total nonirrigation	
	BAU	HP	BAU	HP	BAU	HP	BAU	HP
Huaihe	8.0	6.3	5.1	3.0		0.9	14.1	10.2
Haihe	3.5	2.5	2.0	1.1	0.5	0.5	6.0	4.1
Huanghe	4.0	3.1	1.8	1.1	0.6	0.6	6.4	4.8
Changiiang	23.7	19.3	11.8	7.6	2.6	2.4	38.1	29.3
Songliaohe	3.5	2.8	4.0	2.3	0.8	0.7	8.3	5.8
Inland basins	1.5	1.1	0.4	0.2	0.2	0.2	2.1	1.5
Southwest basins	0.7	0.5	0.7	0.4	0.1	0.1	1.5	1.0
Zhujiang	9.6	6.9	3.7	2.0	0.9	0.8	14.2	9.7
Southeast basins	3.3	2.5	2.2	1.2	0.3	0.3	5.8	4.0
China	57.8	45.0	31.7	18.9	7.0	6.5	96.5	70.4

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990 98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Table 12. Irrigation and total water consumptions (km^3) under "business as usual" (BAU) and two higher-price (HP) scenarios, 2021-25.

Basin	Irrigation		Total	
	BAU	HP	BAU	HP
Huaihe	22.0	20.1	36.1	30.3
Haihe	17.9	15.6	23.9	19.7
Huanghe	22.0	19.7	28.4	24.5
Changiiang	78.4	71.9	116.5	101.2
Songliaohe	19.8	17.5	28.1	23.3
Inland basins	32.1	27.9	34.2	29.4
Southwest basins	2.2	1.9	3.7	2.9
Zhujiang	25.5	21.8	39.7	31.5
Southeast basins	12.7	10.6	18.5	14.6
China	232.6	207.0	329.1	277.4

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

including irrigation and nonirrigation under the higher-water-pricing scenarios, is lower than the BAU by 52 km^3 or 16% (Table 12).

These numbers correspond to water withdrawal decreases—and increases in environmental flows—of 167.9 km^3 nationally under HP and HP-HE. These are very large reductions in withdrawals, equivalent to a water savings for the environment of 20% of total BAU withdrawals in 2025 (Table 13).

Increases in water price significantly reduce water stress at the basin level. The criticality ratio of water withdrawal to total renewable water for the whole country under the high-price scenarios is 27%, compared with 33% under BAU. For the

Table 13. Water withdrawals and the ratio of water withdrawal to total renewable water under "business as usual" (BAU) and two higher-price (HP) scenarios, 2021-25.

Basin	Withdrawal (km^3)		Withdrawal/total renewable water	
	BAU	HP	BAU	HP
Huaihe	106.8	84.4	1.17	0.93
Haihe	62.7	48.3	1.58	1.22
Huanghe	78.7	64.2	1.24	1.01
Changjiang	260.4	219.0	0.30	0.25
Songliaohe	66.4	51.9	0.33	0.25
Inland basins	108.6	87.4	3.39	2.73
Southwest basins	12.0	8.8	0.02	0.01
Zhujiang	100.2	75.7	0.28	0.21
Southeast basins	47.7	35.9	0.32	0.24
China	843.5	675.6	0.33	0.27

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Huanghe, Huaihe, and Haihe basins and inland basins in northwestern China, the criticality ratio in 2025 falls to 0.9, 1.2, 1.0, and 2.7 under the two high-price scenarios compared with 1.2, 1.6, 1.2, and 3.4 under the BAU, respectively (Table 13). With higher water prices, the criticality ratio drops dramatically in the severely water-scarce basins compared with BAU, indicative of the decline in water withdrawals for human uses, causing increased environmental flows and reduced reuse of water, ultimately improving the quality of water in the river basin.

Total water consumption and water withdrawal are the same for HP and HP-HE, while the IWSR index varies across these two scenarios because of the difference in BE that results in higher beneficial use of water for crop production (Table 14). The values of IWSR under HP are significantly lower than the BAU levels because of the reduction in irrigation water use, while the values of IWSR under HP-HE are very close to the BAU levels. Total irrigation consumption in the country is 207 km^3 under HP-HE, which is lower than the 233 km^3 under BAU. But, the basin efficiency for the country is 0.68 under HP-HE and 0.60 under the BAU, so the beneficial irrigation water consumption (total consumption multiplied by basin efficiency) is close for HP-HE (141 km^3) and BAU (140 km^3), which leads to the close values of IWSR.

Food results. How will the assumed higher water prices affect food production, demand, and trade in China? Table 15 shows the change in irrigated cereal production relative to BAU by basin as an annual average during 2021-25. Larger reductions will occur with the HP, where total irrigated cereal production declines by 4% or 16.7 million metric t in the country, with a large reduction in some dry basins, such as 19% in inland basins, 12% in the Haihe River Basin, 9% in the Songliaohe River Basin, and 6% in the Yellow River Basin. Under HP-HE, the change in irrigated

Table 14. Irrigation water supply reliability under "business as usual" (MU) and two higher-price (HP) scenarios, 2021-25.

Basin	BAU	HP	HP-HE
Huaihe	0.66	0.61	0.66
Haihe	0.61	0.53	0.59
Huanghe	0.74	0.66	0.74
Changiiang	0.84	0.77	0.83
Songiiaohe	0.72	0.63	0.72
Inland basins	0.79	0.68	0.80
Southwest basins	0.84	0.72	0.83
Zhujiang	0.85	0.73	0.86
Southeast basins	0.81	0.68	0.79
China	0.77	0.69	0.77

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991). NIHWR (1998). and CMWR (199C98): 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Table 15. Change in irrigated cereal production (million t) relative to the "business as usual" level for four higher-price (HP) scenarios, 2021-25.

Basin	HP	HP-HE
Huaihe	-3.4	0.1
Haihe	-4.0	-0.9
Huanghe	-1.5	0.1
Changiiang	-1.6	0.0
Songiiaohe	-3.4	0.1
Inland basins	-2.3	0.2
Southwest basins	-0.2	0.0
Zhujiang	-0.2	0.2
Southeast basins	-0.1	-0.1
China	-16.7	4.2

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991). NIHWR (1998). and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

cereal production from the BAU is virtually zero except for the Haihe Basin, where a 3% reduction still exists. Since the Haihe Basin has a high BE under the BAU (0.78), irrigation loss will not be able to be replenished even when the BE increases to 0.9 under the high-price scenarios.

Food demand will be only slightly affected in 2021-25, as shown in Table 16, with about a 1% decline in cereals under HP and almost no change under the HP-HE compared with the BAU, respectively. Cereal imports will increase by 9.2 million metric t under HP and by only 0.9 million metric t under HP-HE compared with the BAU.

Table 16. Net rice and other cereal demand and trade (million t) under "business as usual" (BAU) and four higher-price (HP) scenarios, 1995 and 2021-25.

Crop	Demand		Trade	
	1995	2021-25	1995	2021-25
Rice				
BAU	125.7	143.6	-0.6	-0.1
HP	125.7	141.5	-0.6	0.5
HP-HE	125.7	143.6	-0.6	-0.2
Other cereals				
BAU	249.4	428.3	-16.8	-47.2
HP	249.4	424.4	-16.8	-56.9
HP-HE	249.4	428.0	-16.8	-46.3

Sources: 1995: authors' estimation based on HPDGI (1989), Qian (1991), NIHWR (1998), and CMWR (1990-98); 2025 (or 2021-25): IMPACT-WATER projections (June 2002).

Summary and conclusions

Water scarcity in all nine major river basins, especially those in North China, will grow in the next 25 years because of the rapid growth of domestic and industrial water demand as well as the modest growth of agricultural water demand. The increasing water scarcity will reduce crop area and yield growth. At the same time, the increasing water withdrawal will deplete more environmental flow and make the environment more fragile.

Our projections show that per capita rice demand will decline and some irrigated rice area will shift to other crops. In the next 25 years, the growth of cereal production will mainly depend on irrigated cereal crops and will depend on the growth of crop yield more than the growth of crop area.

The results for the higher-water-price scenarios show that industrial water prices of 2.25 times BAU prices, domestic water prices of 2.0 times BAU prices, and agricultural water prices of 3.0 times BAU prices result in about 168 km^3 less water withdrawal in China by 2025, which is about 80% of the sum of the water withdrawal in the Huanghe, Huaihe, and Haihe basins in 1995. If no improvement of irrigation water-use efficiency occurs, irrigated cereal production will decline by 4% in the country in 2021-25 compared with the BAU level, cereal demand will decline by only 1%, and cereal imports will increase by 9.3 million metric t.

Results demonstrate that reasonable increases in BE in response to a price increase can maintain the IWSR and food production at the BAU levels except for the Haihe Basin, where the BE values are already high. The higher prices combined with improved water-use efficiency will result in almost the same agricultural production in the country, while a large increase in flows (168 km^3) will remain in-stream for environmental purposes.

The alternative scenarios for water prices show that even very large percentage changes in water prices have relatively modest effects on food production, primarily because the water price response is low in agriculture and because the resulting crop price increases induce partially compensating increases in rainfed and irrigated production. Another important reason for relatively small effects is that, in some water-scarce regions, irrigation water demand is constrained primarily by water availability, not by water prices. In these water-scarce regions, the water released from nonagricultural uses because of price increases for those uses will increase the availability of water for agriculture, thus easing water scarcity constraints and counterbalancing the effect of higher prices.

For China's water management in the next 25 years, the largest effect from increased water prices will likely be reduced water consumption for domestic, industrial, and agricultural uses, and corresponding increased water allocation for the environment, while the negative effect on agricultural production can be nearly eliminated, particularly if water prices induce significant efficiency gains in irrigation.

While this paper shows great potential of water-pricing policy to achieve water conservation and balance irrigation and environmental water uses, the problems of implementing water-pricing policy reform in developing countries, including China, should be noted. Most obviously, equity issues must be examined so as to provide water to low-income households. Second, measuring and monitoring water use are costly activities, constraining water pricing where institutions and infrastructure are weak. Nevertheless, innovative water-pricing systems can be designed and implemented that have reasonable administrative costs and provide increased incentives for water conservation without reducing income, and possibly even enhancing the income of the poor. In the domestic and industrial water sectors, water price increases could be made directly, replacing existing generalized subsidies with subsidies targeted to the poor.

Designing a water-pricing system for agriculture to protect farm income is more challenging. Direct water price increases are likely to be punitive to farmers because water is such a significant input to production. Nevertheless, pricing schemes could be designed that, rather than charging farmers for using water, pay them for reducing water use (Pezzey 1992, Rosegrant and Cline 2002). Higher water prices establishing incentives for more efficient use could also be established through the development of water markets and water trading (Easter et al 1998). The results presented here show that higher water prices could be a powerful tool for reducing water demand in domestic, industrial, and agricultural sectors while maintaining food production growth and dramatically increasing the availability of water for the environment. Innovative solutions should be sought for implementing incentives for water conservation through water pricing.

References

Alcamo JP. 2000. Personal communications on global change and global scenarios of water use and availability: an application of water GAP. Kassel (Germany): Center for Environmental Systems Research (CESR), University of Kassel.

Alcamo J, Henrichs T, Rosch T. 2000. World water in 2025: global modeling and scenario analysis for the world commission on water for the 21st century. Kassel World Water Series Report No. 2. Kassel (Germany): Center for Environmental Systems Research, University of Kassel.

Caswell M, Zilberman D. 1985. The choices of irrigation technologies in California. Am. J. Agric. Econ. 67:224-234.

Caswell M, Zilberman D. 1986. The effects of well depth and land quality on the choice of irrigation technology. Am. J. Agric. Econ. 68:798-811.

CMWR (Chinese Ministry of Water Resources). 1990 to 1998. China's water resources annual book. Beijing (China): China Water Resources and Hydropower Press.

Dalhuisen JM, Florax RJGM, de Groot HLF, Nijkamp P. 2002. Price and income elasticities of water demand: why empirical estimates differ. Tinbergen Institute Discussion Paper TI 2001-057/3. Amsterdam (Netherlands): Tinbergen Institute.

Easter KW, Rosegrant MW, Dinar A, editors. 1998. Markets for water: potential and performance. Boston, Mass. (USA): Kluwer Academic Publishers.

Espey M, Espey J, Shaw WD. 1997. Price elasticity of residential demand for water: a meta-analysis. Water Resources Res. 33(6): 1369-1374.

Gracia FA, Garcia Valinas MA, Martinez-Espineira R. 2001. The literature on the estimation of residential water demand. St. Francis University, Department of Economics Working Paper Series. www.stfx.ca/people/rmespi/department/-RoberMarian21NOV.pdf, accessed in June 2002.

HPDGI (Hydropower Planning and Design General Institute). 1989. China's water resources and uses. Beijing (China): China Water Resources and Hydropower Press.

NIHWR (Nanjing Institute of Hydrology and Water Resources). 1998. Water demand and supply in China in the 21st century. Beijing (China): China Water Resources and Hydropower Press.

People's Daily. Tuesday, 20 March 2001. China needs to raise water prices.

Pezzey J. 1992. The symmetry between controlling pollution by price and controlling it by quantity. Can. J. Econ. 25(4):983-991.

Qian Z, editor. 1991. China's water resources. Beijing (China): China Water Resources and Hydropower Press.

Raskin P, editor. 1997. Comprehensive assessment of the freshwater resources of the world. Stockholm (Sweden): Stockholm Environment Institute.

Rosegrant MW, Cline S. 2002. The politics and economics of water pricing in developing countries. Water Resources IMPACT 4(1):6-8.

Rosegrant WM, Cai X, Cline S. 2002. World water and food to 2025: dealing with scarcity. Washington, D.C. (USA): International Food Policy Research Institute.

Rosegrant MW, Paisner MS, Meijer S, Witcover J. 2001. Global food projections to 2020: emerging trends and alternative futures. Washington, D.C. (USA): International Food Policy Research Institute.

Shah F, Zilberman D, Chakravorty U. 1995. Technology adoption in the presence of an exhaustible resource: the case of groundwater extraction. Am. J. Agric. Econ. 77:291-299.

Varela-Ortega C, Sumpsi JM, Garrido A, Blanco M, Iglesias E. 1998. Water pricing, public decision making and farmers' response: implications for water policy. Agric. Econ. 19: 193-202.

Zilberman D, Chakravorty U, Shah F. 1997. Efficient management of water in agriculture. In: Parker D, Tsur Y, editors. Decentralization and coordination of water resources. Boston, Mass. (USA): Kluwer Academic Publishers.

Notes

Authors' addresses: M.W. Rosegrant, International Food Policy Research Institute; X. Cai, International Water Management Institute.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The conditions of effective irrigation system management by users' associations in the Philippines[1]

M. Kikuchi, M. Fujiie, and Y. Hayami

We examine the factors affecting the success and failure of irrigation system management by users by using cross-sectional survey data on the activities of irrigators' associations in the Philippines. The regression analysis finds that operation and maintenance activities by water users are difficult to organize where (1) the water supply is uniformly abundant, (2) the water supply is greatly different between upper and lower streams in the lateral, (3) the size of the association is large, (4) population density is low, (5) the ratio of nonfarm households to households is high, and (6) the history of irrigated farming is short. Our findings suggest that these difficulties can be overcome with adequate support by state agencies to promote community-level cooperation.

The critical importance of irrigation in the development of rice-based agriculture in monsoon Asia has long been established (Ishikawa 1967, Hayami and Ruttan 1985). The need to mobilize effective participation by farmer beneficiaries in the management of irrigation systems as well as other local commons has increasingly been voiced in recent years (Coward 1980, Korten 1982, Uphoff 1986, Ostrom 1992, Isham et al 1995, World Bank 1996). Yet, the cases of successful management of irrigation systems by irrigators are rather rare. What factors block the effective organization of water users for operation and maintenance activities? This paper aims to shed light on this question on the basis of a regression analysis of data collected from a cross-sectional survey of irrigation systems in the Philippines.

Irrigation systems under study

This study is based on our survey of 46 irrigators' associations (IAs) in 25 national irrigation systems under the command of the National Irrigation Administration (NIA)

---

[1] This paper is an abridged version of the report on the output of the IRRI-Japan Shuffle Project. For the results of more complete analysis, see Fujiie et al (2002).

over six provinces in the Philippines—Batangas, Cavite, Laguna, Occidental Mindoro, Oriental Mindoro, and Quezon. The survey consisted mainly of interviews with the leaders of IAs and the staff members of local NIA offices in charge of the national systems' operation and maintenance. We tried as much as possible to check the reliability of their answers with farmer beneficiaries as well as knowledgeable people in each system's service area. The pilot survey was conducted in February-March 1998 and the main survey in August-September 1998.

The area of our survey belongs to Region 4, one of 12 administrative regions of the NIA. Our survey tried to cover all the 30 national irrigation systems within Region 4, but five systems were excluded, which were not functioning because of natural hazards or they were located too far away to reach.

All the systems that we surveyed are of the simple gravity type, based on surface flows of water diverted from a river with no reservoir and no pump-up system being installed. Typically, a major canal runs from the diversion dam and branches out into several laterals (and further into sublaterals), which are connected to farm ditches for the distribution of water to individual fields. Usually, one IA is formed over an area served by one lateral; hence, several associations are organized within a large system. The national average of irrigation service areas under the command of NIA systems is just about 3,000 hectares, whereas the average of the systems that we surveyed was 1,553 ha, reflecting the hilly topography in Region 4 that is characterized by relatively small rivers that provide water for irrigation. This contrasts with the large flat plains such as those of Central Luzon. As is common to all the gravity systems under NIA's auspices, the systems under our survey are intended to serve solely for the imgation of rice fields.

As is common in tropical monsoon Asia, most canals and laterals in the systems under study are embanked by mud, except for the concrete structure to support water gates and water-gauging facilities at the junctures of laterals and the main canal and of sublaterals to laterals. There is no device for metering the intake of water into individual fields. In the absence of water-gauging devices, irrigation fees are not based on the quantity of water consumed but are charged proportionally to the area served at the rate of 100 kg of paddy per ha for the wet season and 150 kg for the dry season.

As such, water supplied from those systems is endowed with the attributes of "local commons," which are allowed for use by the people in a local community but are exhaustible if used in excess of their reproductive capacity. Since the water resource for a system is limited by the capacity of diversion from the river flow, it is exhaustible through overexploitation. Thus, an abuse by farmers in upper streams has negative externalities for downstream farmers. Yet, no incentive mechanism exists to prevent individual users from abusing water because water intake to their fields cannot be metered and hence is not chargeable in proportion to their consumption. It is costly to organize actions to save water (by such means as rotating water supply among users) or to augment the water supply (by such means as removing silt and cutting weeds in canals) because everyone is tempted to be a free rider on others' conservation activities. This problem is exacerbated in the case of gravity irrigation systems by an asymmetry in the distribution of means and benefits of the conservation activities. Typically, farmers in the head end of the system can reduce abuse in their water use, but receive no benefit from it, whereas those in the tail end receive benefits from the head-enders' water savings, but are not in a position to reciprocate to them (Ostrom and Walker 1994).[2] Thus, deterioration in the quality of gravity irrigation systems is universal in developing economies (Chambers 1988).

The NIA, which is mandated to administer national irrigation systems in the Philippines, is a "government-owned and controlled corporation." Until the end of the 1970s, with generous subsidies from the national treasury based on foreign aid, the operation and maintenance (O&M) of the NIA systems had almost totally been carried out by the teams of water masters and ditch tenders formally employed at NIA's local offices (called "irrigation systems offices"). However, with the collapse of the international rice market in the 1980s, the NIA lost its financial base to maintain sufficient field staff. Foreign aid decreased. It has been stipulated since 1981 that the NIA should be autonomous in financing its current expenditures for the O&M of existing systems from its revenue, which consisted mainly of irrigation fees collected from farmers.[3] However, as rice prices continued to fall, the monetary value of irrigation fees collected in paddy declined proportionally.

Pressed by the financial crisis, the NIA set up IAs for handing over a part of the responsibility for O&M. The NIA urged local community leaders to organize farmers into IAs through persuasion as well as some honorarium payments to the leaders. To enhance local participation and initiatives, the NIA designed various incentive schemes for IAs. First, if an IA agreed to take the responsibility for cleaning canals within its territory, the NIA paid 400 pesos per month (which is about equivalent to 3 person-days of farm work) per km of canal length. For repair work that cost more than 500 pesos, the NIA usually granted a contract to the IA. For a smaller repair costing less than 500 pesos, the IA was supposed to mobilize members' labor without pay but materials and machines were supplied by the NIA. The IA that takes charge of collecting irrigation fees is entitled to receive 2% of the collected fees if it could collect more than 50% of the total invoice and 15% if the collection rate exceeded 90%.

How successful have these efforts of the NIA been? What could have been the factors underlying success or failure in farmers' participation in O&M activities? These are the questions upon which we try to shed light in this study on the basis of cross-sectional variations in the degree of farmers' participation in collective actions organized by IAs.

---

[2] The tendency for the head-enders to abuse water is enhanced by the nature of rice plants, which are relatively tolerant of excess water application but not tolerant of drought.

[3] NIAs capital expenditures for the construction of new systems and major rehabilitation of existing systems are still financed by the national treasury that channels foreign aid money. For more details about the NIA, see Svendsen (1993) and Kikuchi et al (2001).

Measures of success in organizing farmers

Our analysis begins by developing a measurement of the degree of success of IAs in organizing farmers for O&M activities. The measures are first developed in terms of success in the organization of IA members for specific O&M activities separately. These separate measures are then aggregated into a composite index.

Individual activities for our measurement are (1) collective work for cleaning canals and laterals, (2) coordination in rice-cropping schedules, (3) the practice of water rotation, and (4) organized monitoring of cropping schedule and/or water rotation. For each collective action, successful implementation is measured as 1 and failure as 0.

Needless to say, the cleaning of canals and laterals by cutting grass and removing silt is a critical component of regular O&M activities for ensuring efficient delivery of irrigation water to farmers' fields. One method for achieving efficient and equitable distribution of a limited water supply is to coordinate rice planting (for which water demand is the highest) among farmers according to an agreed-upon schedule (commonly called the "cropping calendar"). For example, farmers in the head-end portion of a major lateral may be scheduled to plant rice in the first two weeks of a season, followed by those in the middle-stream portion for the next two weeks, and further followed by tail-end farmers. In this way, the water supply tends to be de facto rotated across sections along the lateral. Alternatively or simultaneously, the rule of water rotation can be explicitly agreed upon and practiced. Further, both the rules of cropping coordination and water rotation can be enforced more strongly if the system of monitoring against possible violators is established in the association, either by IA leaders' rotational patrolling or by employing a professional guard. In our sample of 46 IAs, those that successfully organized collective canal cleaning, cropping coordination, water rotation, and organized monitoring were 74%, 57%, 54%, and 52%, respectively (Table 1). In our sample, 13 IAs (28%) were successful in organizing all four collective activities, whereas 9 IAs (20%) failed in all four.

These collective actions can be both complementary and substitutionary to some extent. For example, the coordination of cropping schedules may be used as a

Table 1. Average characteristics of sample irrigators' associations about collective actions.

Item	Active (PC score >0)	Inactive (PC score <0)	Total
No. of associations	28	18	46
Percent of associations practicing:			
Collective canal cleaning	89	50	74
Cropping coordination	86	11	57
Water rotation	89	0	54
Organized monitoring	82	6	52
Total score of cooperation			
Principal component (PC) score	1.1	-1.8	0
Simple-sum score	0.7	-1.1	0

Table 2. Correlation matrix of collective actions across irrigators' associations.

Action	Collective canal cleaning	Cropping coordination	Water rotation	Organized monitoring
Collective canal cleaning	1.00	0.38	0.35	0.32
Cropping coordination		1.00	0.60	0.48
Water rotation			1.00	0.61
Organized monitoring				1.00

Table 3. Principal components of collective actions by irrigators' associations.

Item	1st	2nd	3rd	4th
Eigenvalue	2.39	0.75	0.52	0.35
Proportion (%)	60	18	13	9
PC vector				
Collective canal cleaning	0.40	0.90	0.15	-0.05
Cropping coordination	0.52	-0.09	-0.73	0.44
Water rotation	0.55	-0.28	-0.04	-0.79
Organized monitoring	0.51	-0.32	0.67	0.44

substitute for the explicit water rotation rule, but these actions are highly complementary because the former makes the implementation of the latter much easier. Likewise, augmented water supply by means of collective canal cleaning may reduce the need for equitable water distribution by means of water rotation, but it can be complementary with the implementation of water rotation as it mitigates conflicts between upstream and downstream farmers. Such intricate interrelationships seem to be reflected in the correlation matrix across four variables, in which all the correlation coefficients are positive and significantly different from zero at conventional levels but none is dominantly large (Table 2).

Since the variables representing the four types of collective action are not orthogonal, the simple summation is not very appropriate for aggregating them into a composite index of farmers' cooperation. A better approach is the principal component (PC) analysis. Application of the PC analysis to our four variables shows that the first component dominates in terms of its eigenvalue as well as proportion (Table 3). The PC vector of the first component is also economically meaningful because none of its coefficients is negative, unlike those of the other components' vectors. Thus, we use the PC score of the first component as the composite measure of cooperation or success of the IAs in organizing farmers in collective action (Table 1). This score is calculated as the sum of four variables weighted by coefficients in the PC vector, after normalizing each variable by subtracting its average from individual observations and dividing these differences by standard deviation, with the result that the average is zero. For the sake of comparison, the "simple-sum score," which is the unweighted sum of four variables normalized in the same manner as the PC score, is also calculated.

Table 4. Average characteristics of sample irrigators' associations about the determinants of collective action.

Item	Active (PC score >0)	Inactive (PC score <0)	Total
Number of associations	28	18	46
Water supply conditions[a]:			
(number of associations)			
0-0	1	4	5
0-M	11	5	16
0-S	2	5	7
M-M	3	0	3
M-S	9	3	12
S-S	2	1	3
Size of association			
Service area (ha)	421	608	494
Number of farm households[a]	371	379	374
Number of villages	4.9	5.1	5.1
Community characteristics			
Number of farm households per ha [b]	1.1	0.9	1.0
Ratio of nonfarm households (%) [b]	16	34	22
Prior existence of communal systems (%)	25	11	20
Policy factors			
Provision of special incentive from NIA (%)	18	6	13
Excellent local staff of NIA (%)	25	0	15

[a] 0 = no or rare water shortage, M = moderate water shortage, S = severe water shortage. [b] Average of 42 associations for which data are available, of which 28 are active and 14 are inactive.

If we classify IAs with their PC scores above 0 as "active" associations and those below 0 as "inactive" associations, the former numbered 28 and the latter 18. Among active IAs, the incidence of success in organizing any of the four collective actions was higher than 80%, whereas it was incomparably lower among inactive IAs (Table 1).

Determinants of collective management

A major question is what factors may underlie differences in the performance of IAs in mobilizing farmers' participation. From data collected from our survey, several variables are chosen as possible determinants of the degree of farmer participation, as summarized in Table 4.

Water supply conditions

The conditions of the water supply are obviously a crucial determinant for inducing farmers to organize collective action. If the water supply is abundant relative to demand so that no water shortage could possibly occur, there should be no incentive for farmers to undertake collective action to augment the supply of water or to save its consumption, as elucidated by Wade (1988) for the case of southern India. In contrast, if the water shortage is very severe, conflicts among water users might become SO large as to make cooperation difficult. As already discussed, in the case of gravity irrigation systems such as those under our study, differences in water supply between upstream and downstream farmers are critically important in determining lateral-wide cooperation within IAs.

In terms of water supply conditions in the upper and lower stream portions along the lateral before the formation of IAs, our observations fall into the following six combinations:

Upper	Lower
O	O
O	M
O	S
M	M
M	S
S	S

where O represents the case of no water shortage in that a significant water shortage seldom occurred, M represents the moderate water shortage case in that a water shortage often occurred but could be solved through coordination among farmers within a small district served by a common turnout gate for taking in water from a major lateral or sublateral, and S represents the severe water shortage case in that significant crop damage was bound to occur without lateral-wide coordination.

These classifications were based on the results of interviews with IA leaders and NIA officials as well as selected farmer beneficiaries. Surprisingly little disagreement among them was found in each IA. The water supply conditions that we have asked about are the situations that prevailed before the formation of IAs instead of the current situations at the time of the interviews. Therefore, our variables of water supply conditions are free from the problem of endogeneity when used in the regression analysis in the next section.

The distribution of IAs according to the six combinations of water supply conditions between upper and lower streams shows that the number of inactive IAs is higher than that of active IAs only in the cases of O-O and O-S (Table 4).

It is reasonable to expect that no inducement to organize collective action operates as long as all the farmers in both the upper and lower stream sections need not fear a water shortage (O-O). In contrast, it is possible that a major difference in water supply conditions between upstream and downstream farmers (O-S) makes it difficult to reach an agreement to their mutual satisfaction.

Size of association

The classic study by Olson (1965) suggests that collective action is more difficult to organize in larger groups. An obvious indicator of the group size in the case of IAs is the number of irrigators, which is roughly equal to the number of farm households within the association’s territory.

In the context of rural economies in Asia, including the Philippines, the village is a basic unit of people's lives, endowed with both formal and informal self-governing mechanisms. Therefore, it is relatively easy to reach an agreement and enforce it within a village, whereas coordination across different villages is more difficult. Therefore, the number of villages (*barangays* in the case of the Philippines) within the territory of an IA can be an important determinant of the cost for IA leaders to organize lateral-wide cooperation.

Further, the size of the association as measured by irrigation service area within its territory is likely to be a significant determinant because it is more difficult and costly to monitor over a wider area if the rules of collective action such as the schedules of planting and water rotation are duly observed.

In our data, the size of the IA as measured by its service area is on average about 50% larger in inactive IAs than in active IAs. However, there is no significant difference in the number of farm households or in the number of villages.

Community characteristics

Rural people in developing economies base their organization and enforcement of collective action on intense social interactions among people within a community, involving informal sanctions against free-riders by means of malicious gossip, social opprobrium, and eventual ostracism (Hayami and Kikuchi 1981). Therefore, the social structures and traditional norms of rural communities, along which IAs are organized, are critically important in determining the success of their collective action.

The characteristics of a community in this regard are difficult to quantify. One possible measure of the intensity of social interactions may be population density. It is expected that social interactions among people tend to be more intense if they are concentrated within a smaller area. For this consideration, we use the number of farm households per hectare in the service area as a proxy to represent the degree of social interactions among irrigators. Admittedly, this is a highly crude measure. However, its effectiveness can at least partially be judged in terms of its statistical significance in the regression analysis in the next section.

Another characteristic of the rural community, which may have a significant influence on the organization of collective action for irrigation management, should be the degree of exposure and access to market activities outside agriculture. If a rural community is largely self-sufficient with little exposure to urban market activities, the expectation should be strong for its members to indefinitely continue their collective action in the future; this is akin to the situation of infinitely repeating games to sustain a positive-sum cooperative outcome along the Folk theorem (Fudenberg and Maskin 1986, Bardhan 1993, Seabright 1993, Ostrom and Walker 1994). On the other hand, ready access of farmers to nonfarm market activities means availability of the "exit option" for them from collective action within the farming community in the sense of Hirschman (1970). If this option is available, it should be more difficult to force them to join collective action at the community level. In this study, the ratio of nonfarm households within the territory of one IA is calculated as a measure of farmers' access to market activities. Indeed, this ratio is more than twice as high in inactive IAs than in active IAs.

Theoretically, this variable can be marred by the endogeneity problem when used in regression analysis because successful cooperation may increase profitability in farming and, hence, retain a larger number of farming households in the community. In our context, however, such a causal effect is considered very minor relative to the dominant influence of the availability of nonfarm employment opportunities, which is mainly determined by the community's proximity to an urban market center as well as the size of the economic activities in the center.

A significant factor for facilitating the activities of IAs appears to be the past experience of collective action for the maintenance of communal irrigation systems. In about one-fifth of our sample IAs, communal irrigation systems tapping water from small streams in hilly areas by the collective work of farmers in a small group had been operating until large-scale national irrigation systems were built by the NIA. It is naturally expected that, where communal systems existed previously, communities are better endowed with social skills and norms to mobilize collective efforts to maintain and operate irrigation systems. This expectation is consistent with the observation that the percentage of IAs in which communal systems had previously existed is twice as high among active IAs than among inactive ones.

Policy factors

According to our field observations, the intensity and quality of activities by local NIA offices for the promotion of IAs made significant differences. One way for local NIA offices to promote IAs is to give special incentives. Although such incentives as payments to associations for regular cleaning and repair of canals and dikes (as explained earlier) are uniformly applied to all the IAs, each local office has some discretion in deciding on priority among IAs in the allocation of public works for major renovations such as the lining of laterals and the widening of access roads as well as on who should be chosen as contractors. It is also possible to give administrative guidance to contractors so as to employ farmers in a certain IA for the assigned public works project. Through the exercise of this discretion, a local office can induce activation of IAs. In fact, the percentage of IAs that received such special incentives was three times higher among active IAs than among inactive IAs. However, we must caution that causal relationships are ambiguous because these incentives tend to be given as a reward to the IAs that achieved (or were expected to achieve) a high rate of irrigation fee collection.

It is noteworthy that some managers of NIA's local offices exerted exceptionally fine leadership for the promotion of IAs. Beyond the routines as instructed by the headquarters, these local officers devoted much of their time and energy to persuading local community leaders to develop cooperation and coordination within the IA as well as among IAs, while assisting them not only in irrigation matters but often in solving their retained problems with other local government offices. The IAs that were favored by the service of the excellent local staff of the NIA, as identified unanimously by IA leaders as well as farmers, were only 15% of our sample, but all of them were able to achieve the status of active associations in our classification.

However, there is a little ambiguity about the causal relationship of this factor with the success in activating IAs, though probably less ambiguous than in the case of special incentives. The possibility cannot be ruled out that even the most capable and devoted NIA official might have failed to organize an effective IA under extremely unfavorable conditions with respect to water supply, association size, and community characteristics and, hence, have not been recognized as an excellent official. Therefore, these policy variables, when used in regression analysis, might create a serious endogeneity problem.

It must be noted that the list of possible determinants in Table 4 is not exhaustive. Such variables as farming systems, especially with respect to the share of nonrice crops, and distributions in farm size as well as land tenure relationships may have significant influences.[4] Our choice of explanatory variables is limited by the narrow coverage of our survey questionnaire used for a rather quick survey over a wide area.

Regression analysis

To measure the net contributions of possible determinants selected in the previous section, multiple regression analysis is conducted. The principal dependent variable is the PC score as measured in section 2 (“Measures of success in organizing farmers”), but the analysis using the simple-sum score is also tried for the sake of comparison. The regression analysis is conducted using the observations of 42 associations for which data are available for all the explanatory variables.[5]

Six combinations of water supply conditions between the upstream and downstream sections are represented by five dummy variables using the S-S case as the base, namely, assigning 0 to S-S and 1 for each of the other combinations. The irrigation service area, the number of farm households, and the number of villages to represent the size of the IA are tried interchangeably to avoid multicollinearity.

The number of farm households per hectare and the ratio of nonfarm households are parametric variables, but the prior existence of communal irrigation systems (abbreviated as “communal irrigation”), the provision of special incentives from the

---

[4] Local communities in the area under our study are predominantly inhabited by Tagalogs, involving few ethnic conflicts. Unlike Central Luzon, where large estate farms (haciendas) had prevailed until land reform, this area had traditionally been farmed by smallholders, mostly under sharecropping arrangements with relatively small-scale landlords living in local towns. With the implementation of land reform programs in the 1970s under President Marcos’s Martial Law regime, most farmers established their status either as leasehold tenants paying low fixed rents controlled by the government or “amortizing owners” who expected to become owner-farmers upon finishing amortization payments to the Land Bank, which purchased lands from landlords in lieu of the tenants. Since both the controlled rents and the amortization payments are fixed at about the same level, work incentives and farm incomes per hectare are largely the same between the leaseholders and the amortizing owners. For more details, see Hayami and Kikuchi (1981. 2000).

[5] The observations of four IAs are dropped from the regression analysis because both the IA leaders and the local NIA offices were not able to keep reliable records on the number of households as well as their farm-nonfarm classifications at the time of our survey because of rapid progress in urbanization in their territories.

NIA ("NIA's special incentive"), and the excellent local staff of the NIA ("NIA's staff quality") are the 1-0 dummies.

Table 5 summarizes the results of the regression analysis using all those variables. Estimation is based on the method of ordinary least squares (OLS). Among the five dummy variables representing water supply conditions, the coefficients of O-O and O-S alone are negative and statistically significant, whereas the others are nonsignificant. These results are consistent with the hypotheses: (1) collective action for irrigation O&M activities is difficult to organize where water supply is abundant over all the system of irrigation and, hence, returns to such collective actions are low, and (2) collective action is difficult to organize where water supply conditions are very different across sections of a lateral, so that the conflicts of interest between upstream and downstream farmers are difficult to resolve. Implicit in those results is that collective action is relatively easy to organize under conditions in which water shortage occurs uniformly across sections of an IA's territory.

The coefficients of service area and the number of farm households in regressions 1 and 2 are both negative and significant, reflecting the high cost to organize collective action for the IA that encompasses a wide territory and has a large number of farmer beneficiaries. It is somewhat anomalous, however, that the number of villages turns out to be not statistically significant at a conventional level in regression 3. It appears that more in-depth investigation is necessary to identify the role of villages in the organization of IAs.

The coefficients of three variables representing community characteristics have expected signs and are statistically significant at conventional levels. The positive coefficient of the number of households per hectare is consistent with the hypothesis that the high density of farm population strengthens social interactions as the basis of organizing community-wide collective action. The negative coefficient of the nonfarm household ratio implies that availability of the exit option for farm workers to nonfarm employment weakens their cooperation for improving agricultural production infrastructure such as irrigation. The highly significant positive coefficient of communal irrigation shows clearly that the prior experience of small-group cooperation in managing small-scale indigenous systems becomes an important basis of organizing collective action for the operation and maintenance of a large-scale modem system, representing a case of historical path dependency in the evolution of social systems.

Finally, the coefficients of two policy variables are all positive and significant. The results suggest that much room exists for the NIA to achieve greater participation of farmers in the management of national systems by designing greater incentives to IAs as well as upgrading NIA's staff quality.

On the whole, the results of regression analysis as reported in Table 5 are reasonable in terms of both signs and statistical significance of the coefficients as well as the values of R-square adjusted for the degree of freedom. These regressions using the PC score as the dependent variable may be compared with those using the simple-sum score as reported in Table 6. Reflecting relatively homogeneous PC weights for calculating PC scores (Table 3), the results based on simple-sum scores

Table 5. Results of organized least square regressions to explain the degree of cooperation by irrigators' associations as measured by principal component score, based on the observations of 42 associations.

Regression no.	(1)	(2)	(3)
Intercept	0.62	0.034	-0.24
	(1.02)	(0.064)	(0.44)
Water supply conditions			
0-0	-2.58***	-2.15***	-2.77***
	(3.19)	(2.63)	(2.59)
0-M	0.05	0.28	0.36
	(0.083)	(0.47)	(0.56)
0-S	-1.50**	-1.28**	-1.48**
	(2.35)	(1.90)	(1.96)
M-M	0.064	0.24	0.50
	(0.084)	(0.32)	(0.64)
M-S	-0.26	0.52	0.60
	(0.43)	(0.85)	(0.91)
Size of association			
Service area	-0.00086**		
	(2.36)		
No. of farm households		-0.0012**	
		(1.79)	
No. of villages			0.011
			(0.24)
No. of farm households per ha	0.34*	0.59**	0.45**
	(1.53)	(2.27)	(1.72)
Nonfarm household ratio	-0.018**	-0.017**	-0.019**
	(2.14)	(1.93)	(1.80)
Communal irrigation	1.37***	1.34***	1.24***
	(3.55)	(3.36)	(2.93)
NIA's special incentive	0.78**	0.88**	0.87**
	(1.95)	(2.11)	(1.92)
NIA's staff quality	1.08**	1.31**	0.83*
	(2.23)	(2.38)	(1.58)
Adjusted R^2	0.64	0.61	0.56

[a] Shown inside parentheses are t-values, significant at *** = 1%, ** = 5%, and * = 10%.

are not greatly different from those based on PC scores. Yet, adjusted R-squares in the regressions based on PC scores are about 15% higher than the counterpart regressions based on simple-sum scores. Also, several regression coefficients become nonsignificant at conventional levels with the use of simple-sum scores, such as those of the number of households per hectare and the NIA's staff quality. These comparisons seem to support the hypothesis that the PC score is a superior index in measuring the degree of farmers' cooperation in collective actions organized by IAs.

Policy implications

Results of our cross-section analysis over national irrigation systems in the Philippines are consistent with the hypothesis that organization of water users for the operation

Table 6. Results of organized least square regressions to explain the degree of cooperation in collective action by irrigators' associations as measured by simple-sum score, based on the observations of 42 associations.

Regression no.	$(4)^a$	(5)	(6)
Intercept	0.49	0.026	-0.14
	(1.12)	(0.068)	(0.36)
Water supply conditions			
O-O	–1.67***	–1.33**	–1.42**
	(2.91)	(2.29)	(2.31)
O-M	0.87	0.15	0.20
	(0.20)	(0.35)	(0.45)
OS	–1.00**	–0.83**	–0.94**
	(2.21)	(1.73)	(1.83)
M-M	0.14	0.11	0.27
	(0.27)	(0.20)	(0.50)
M-S	0.025	0.25	0.32
	(0.057)	(0.56)	(0.67)
Size of association			
Service area	–0.00063**		
	(2.35)		
No. of farm households		–0.00073*	
		(1.49)	
No. of villages			0.067
			(0.22)
No. of farm households per ha	0.21*	0.39**	0.31*
	(1.31)	(2.08)	(1.66)
Nonfarm household ratio	–0.010*	–0.0096*	–0.011*
	(1.65)	(1.48)	(1.46)
Communal irrigation	0.76***	0.75***	0.74**
	(2.69)	(2.52)	(2.38)
NIA's special incentive	0.78**	0.78**	0.45
	(2.17)	(1.93)	(1.17)
NIAs staff quality	0.39*	0.48*	0.47*
	(1.39)	(1.62)	(1.53)
Adjusted R^2	0.57	0.53	0.48

Shown inside parentheses are t-values, significant at *** = 1%, ** = 5%, ana * = 10%.

and maintenance of irrigation systems is difficult (1) where the water shortage rarely occurs, (2) where the difference in water supply is large between upstream and downstream farmers, (3) where the irrigators' association is large in terms of service area and in the number of farmer beneficiaries within its territory, (4) where the local community is sparsely populated, involving low social interactions, (5) where farm workers have the option of ready exit from farm to nonfarm economic activities, and (6) where farmers had traditionally practiced rainfed farming with no previous experience in managing communal irrigation systems. The results also suggest that collective action can be promoted by adequate incentives granted by the national irrigation agency and that the promotion of associations' activities is especially effective when handled by capable and devoted personnel in the agency's field staff.

Our findings obviously imply that the promotion of irrigators' associations is not sufficient to just hand over the responsibility of operation and maintenance by granting them a standard package of incentives. Where water supply conditions, sizes of associations, and community characteristics are unfavorable for the organization of irrigators, the national agency must increase support by such means as providing special incentives for associations' activities. Of course, granting discretion to the agency's local staff on the provision of special incentives can be a source of inefficiency as well as corruption, unless properly handled by competent and devoted personnel. Therefore, they vitally need adequate salaries and other forms of work incentives, appropriate education and training, and sufficient logistical support for their field work.

References

Bardhan P. 1993. Symposium on management of local commons. J. Econ. Perspectives 7:8-92.

Chambers R. 1988. Managing canal irrigation. New Delhi (India): Oxford & IBH Publishing.

Coward EW. 1980. Irrigation development: institutional and organizational issues. In: Coward EW, editor, Irrigation and agricultural development in Asia: perspectives from social sciences. Ithaca, N.Y. (USA): Cornell University Press. p 15-27.

Fudenberg D, Maskin E. 1986. The Folk theorem in repeated games with discounting or with incomplete information. Econometrica 54:533-534.

Fujiie M, Hayami Y, Kikuchi M. 2002. The conditions of collective action for local commons management: the case of irrigation in the Philippines. FASID (Foundation for Advanced Studies on International Development) Discussion Paper on International Development Strategies No. 2002-001. Tokyo (Japan): FASID.

Hayami Y, Kikuchi M. 1981. Asian village economy at the crossroads. Tokyo (Japan): University of Tokyo Press.

Hayami Y, Kikuchi M. 2000. A rice village saga: the three decades of the green revolution in the Philippines. Houndmills (UK): Macmillan.

Hayami Y, Ruttan VW. 1985. Agricultural development: an international perspective. Baltimore, Md. (USA): Johns Hopkins University Press.

Hirschman AO. 1970. Exit, voice, and loyalty: responses to decline in firms, organizations, and states. Cambridge, Mass. (USA): Harvard University Press.

Isham J, Narayan D, Pritchett L. 1995. Does participation improve performance? Establishing causality with subjective data. World Bank Econ. Rev. 9(2):175-200.

Ishikawa S. 1967. Economic development in Asian perspective. Tokyo (Japan): Kinokuniya Bookstore.

Kikuchi M, Fujita M, Hayami Y. 2001. State, community and market in the deterioration of an irrigation system in the Philippines. In: Aoki M, Hayami Y, editors. Communities and markets in economic development. Oxford (UK): Oxford University Press. p 265-294.

Korten FF. 1982. Building national capacity to develop water users associations: experience from the Philippines. Staff Working Paper 528. Washington, D.C. (USA): World Bank.

Olson M. 1965. The logic of collective action. Cambridge. Mass. (USA): Harvard University Press.

Ostrom E. 1990. Governing the commons. New York, N.Y. (USA): Cambridge University Press.

Ostrom E. 1992. Crafting institutions for self-governing irrigation systems. San Francisco, Calif. (USA): Institute for Contemporary Studies Press.

Ostrom E, Walker J. 1994. Rules, games, and common-pool resources. Ann Arbor, Mich. (USA): University of Michigan Press.

Seabright P. 1993. Managing local commons: theoretical issues in incentive design. J. Econ. Perspectives 7:113-134.

Svendsen M. 1993. The impact of financial autonomy on irrigation system performance in the Philippines. World Dev. 21:989-1005.

Uphoff N. 1986. Improving international irrigation management with farmer participation: getting the process right. Boulder, Colo. (USA): Westview Press.

Wade R. 1988. Village republics: economic conditions for collective action in South India. Cambridge (UK): Cambridge University Press.

World Bank. 1996. World Bank participation book. Washington, D.C. (USA): World Bank.

Notes

Authors' addresses: M. Kikuchi, Chiba University; M. Fujiie, Takushoku University, Faculty of International Development, Takushoku University, Faculty of International Development, Takushoku University, 815-1 Tatemachi Hachioji-shi, Tokyo 193-0985, Japan, E-mail: mfujiie@ner.takushoku-u.ac.jp; Y. Hayami, Foundation for Advanced Studies on International Development.

Acknowledgment: The invaluable assistance to this research from Esther Marciano, Mena Serrano, and many NIA officials in Region 4 is gratefully acknowledged.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Increasing water productivity in irrigated rice systems in Australia: institutions and policies

E. Humphreys and D. Robinson

Australian irrigation farmers, and rice growers in particular, are under tremendous pressure to increase water-use efficiency and water productivity. A host of institutions, programs, and policies, often interrelated, affect water availability and price, which drive the need to increase the water productivity of rice-based systems, and irrigated agriculture in general. These are driven by environmental and National Competition Policy agendas at the national, state, and local irrigation area levels. This paper outlines the various institutional and policy drivers that affect water productivity for rice-based cropping systems in Australia, with examples from the Murrumbidgee and Murray valleys. In addition to generic policies, for many years rice cultivation has been subjected to a range of environmental restrictions designed to reduce deep percolation and water-table rise, and increased water productivity has been an implicit outcome of these regulations. However, yield increases from improved varieties and management have been the main causes of increased field-level water productivity of rice.

Australian irrigation farmers, and rice growers in particular, are under tremendous pressure to increase water-use efficiency and water productivity. Irrigated agriculture accounts for about 75% of all water use in Australia, with about 18 million ML of irrigation water used on about 2 million hectares each year (NLWRA 2000). The extraction of water for irrigation has large effects on rivers and associated ecosystems and their ecological sustainability (MDBMC 2001 d).

The Australian rice industry uses about 1.5 million ML to produce about 1.2 million t of paddy annually, and virtually all of this is grown in the Murrumbidgee and Murray valleys of the state of New South Wales. Rice culture depends entirely on irrigation, with average rainfall of about 150 mm and evapotranspiration of about 1,150 mm during the growing season. The rice industry is a significant element in the economic and social prosperity of major regional communities (Dwyer Leslie 1992), with a farm-gate value of AUD296[1] million in 1997 (NSW Irrigators 2002).

The majority of the rice crop is grown in gazetted irrigation areas or irrigation districts, each of which is run by a large nonprofit-making private irrigation company (or cooperative), owned by all the landholders who are shareholders in the company. There are three such entities — Murrumbidgee Irrigation Ltd (MI), Coleambally Irrigation Cooperative Ltd (CICL), and Murray Irrigation Ltd (MIL). Large state government-owned and -operated dams in the upper catchments store water for irrigation. The areas and districts purchase river water from the NSW Department of Land and Water Conservation (DLWC). The areas and districts have well-managed channel systems supplying water directly to each farm; private groundwater pumping is also significant in some areas. Recycling of drainage water is significant at the system scale, and increasing on-farm.

Rice is the dominant broadacre crop in the irrigation areas and districts, occupying from 10% to 25% of the landscape for about 7 months, and accounting for 50-70% of the total irrigation water use. The majority of the rice crop is direct-seeded into fields that remain ponded for about 5 months. Large areas of winter cereals and a wide range of other summer and winter crops and pastures are also grown on "rice farms." Rice typically provides about two-thirds of farm income, and irrigation water is one of the major rice-growing costs, constituting approximately 22% of total variable costs and around 13% of gross revenue, compared with 0-2.5% of gross revenue at six sites across Asia (Valencia et al 2001).

The productivity of irrigated agriculture in the rice-growing regions is threatened by rising water tables and salinization. Up to half of the rise in water tables has been attributed to rice culture (GHD 1985, Dwyer Leslie 1992). Therefore, rice cultivation has been subjected to a range of environmental water-related regulations like no other crop (Humphreys et al 1994), and increased water productivity is an implicit outcome of these regulations.

A host of institutions, programs, and policies, often interrelated, affect water availability and price, which drive the need to increase the water productivity of irrigated agriculture in general, including rice-based systems. These are driven by environmental and National Competition Policy agendas at a range of levels, principally (1) national, (2) multi state/national, (3) state, and (4) local irrigation scheme. This paper outlines the various institutional and policy drivers that affect water productivity for rice-based cropping systems in Australia, with examples from the Murrumbidgee Irrigation Area (MIA).

Irrigation water productivity of rice

Farm-level irrigation water productivity of rice (g grain kg^{-1} water) has roughly doubled in the past 20 years, fluctuating from 0.6 to 0.8 g kg^{-1} in recent years in the MIA (Fig. 1). In comparison, Bouman and Tuong (2000) reported water productivities

---

[1] Australian dollars (AUD); AUD1 equaled approximately US$0.55 at the time of writing (October 2002).

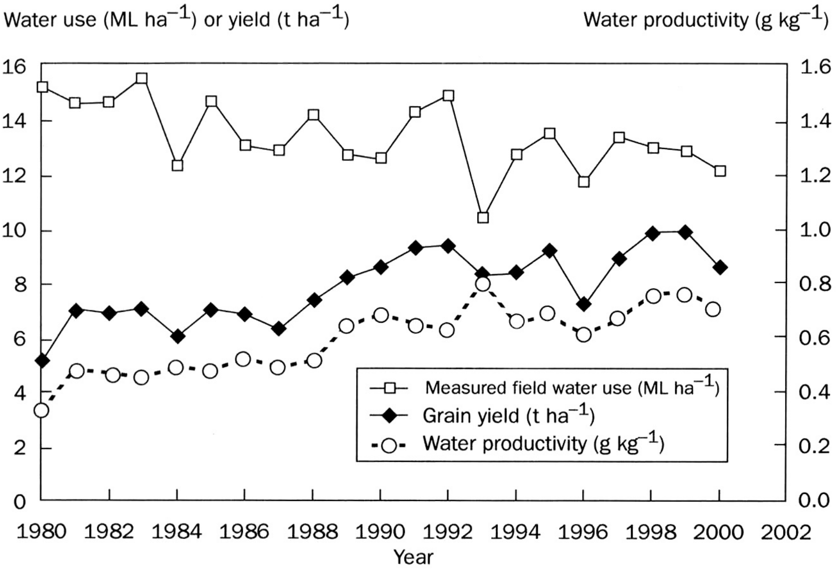


Fig 1. Trends in rice water productivity, grain yield, and field water use in the MIA.

of 0.2-0.4 g kg^{-1} in India and 0.3-1.1 g kg^{-1} in the Philippines for continuously flooded rice. The increase in water productivity in the MIA is largely due to a yield increase, a result of improved varieties and management (Lewin et al 1994, McDonald 1994), and to a smaller degree to declining water use (Fig. 1). The dips in the yield trend in Figure 1 are due to unfavorable seasonal conditions (especially low temperatures during the reproductive period, e.g., 1996 and 2000). The theoretical crop water-use requirement also fluctuates considerably in response to the highly variable seasonal conditions experienced in the rice-growing regions (Fig. 2). The trends in rice-field water use closely match the trends in theoretical crop water use; however, irrigation water-use efficiency (crop water-use requirement/irrigation amount) appears to have increased from about 0.8 in the early to mid-1980s to an average of about 0.9. This change coincided with the introduction of the rice water-use target policy in 1985-86 (Humphreys et al 1994).

Government natural resource management institutions and policies

Integrated catchment management

Australian water policies, programs, and institutions affecting irrigated agriculture and rice systems need to be understood in the context of the overall natural resource management (NRM) agenda at the national, state, catchment, and irrigation area levels. The peak body is the Natural Resource Management Ministerial Council (NRMMC), a coalition of commonwealth, state, and territory ministers formed in

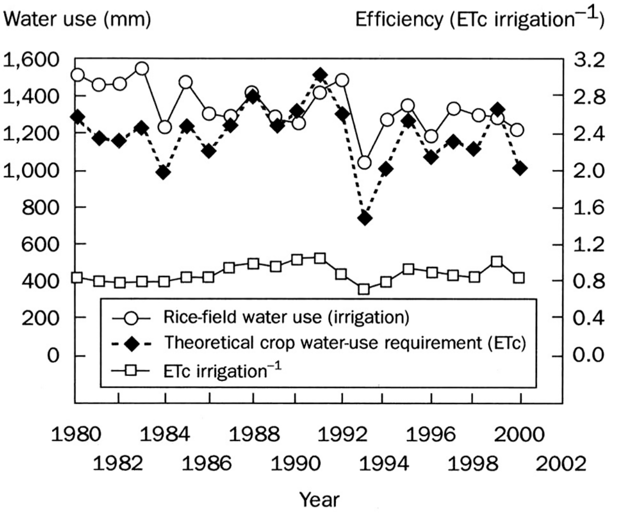


Fig 2. Trends in rice-field water use, crop water-use requirement, and irrigation efficiency in the MIA (1 ML ha^{-1} = 100 mm).

2001 to ensure a national approach to NRM. The Council oversees major NRM funding initiatives, including the National Action Plan (NAP) for Salinity and Water Quality. These initiatives are implemented by the states at the catchment and subcatchment levels, but with joint commonwealth/state funding. The NAP is a recent initiative that involves the setting of targets and standards for NRM, including salinity, water quality, and flows, and biodiversity for priority catchments.

Draft catchment "blueprints" have been prepared and made available for public comment for the Murrumbidgee and Murray catchments (MCMB 2001a,b). These draft "blueprints" specify the objectives for each catchment, and detail and prioritize the targets, management actions, and activities required to achieve the objectives. For example, the water management targets with direct implications for irrigation for the Murrumbidgee catchment are to (1) "manage the hydraulic fall and rise rates in the regulated river system to reduce bank slumping" and (2) "ensure the implementation of water-sharing plans."

An important aspect of the NRM process at all levels has been the involvement of the community in the planning and implementation of NRM plans by establishing catchment and river management committees comprising representatives of all stakeholders. A key component of this process is the community commitment and ownership of the decisions that have considered the socioeconomic and environmental effects of policy change.

The Murray-Darling Basin

Seventy-five percent of Australia's irrigation, and all rice cultivation, occurs within the Murray-Darling Basin (MDB). This Basin contains Australia's largest and most developed river system, covering more than 1 million km^2 across four states and the Australian Capital Territory. Coordination within the MDB, particularly sharing the water, began with the intergovernmental MDB Agreement under the 1914 Murray-Darling Basin Act. However, since the 1980s, deteriorating water quality, salinization (especially dryland), and acidification of agricultural lands, and loss of biodiversity, have led to the development of the Basin NRM Strategy, the Basin Integrated Catchment Strategy (MDBMC 2001a), the Basin Salinity Management Strategy (MDBMC 2001b), and the cap on water use. Salinity levels in the Basin rivers have been increasing as a result of land-use changes over the past 200 years, which cause rising water tables and mobilization of salt in the subsurface materials. The main cause of increasing salinity in the rivers of NSW is dryland salinity, and the irrigation regions of the NSW Murray and Murrumbidgee catchments are in fact net importers of salt. The MDB Ministerial Council (MDBMC), formed in 1985, has the power to make decisions for the Basin as a whole, while the states in partnership with regions have responsibility for within-valley or catchment outcomes. Water supply and management throughout the Basin have historically been focused on ensuring reliable supplies for irrigation. However, increased priority is now being given to environmental flows to protect water quality for both urban use and river ecosystem health. Furthermore, large-scale revegetation in parts of the catchment to reduce groundwater recharge (the cause of dryland salinization) will significantly affect catchment water yields in the future.

Government institutions, programs, and policies for water management

The Murray-Darling Basin "cap" on diversions

Extraction of water from the river system has increased greatly over the past 100 years, contributing to declining river health. The 1995 audit of water use in the MDB showed that, with 1994 levels of irrigation development, median minimal flows to the sea are only 21% of those that would occur under natural conditions (MDBMC 1995). The audit also showed that the lower Murray River experiences severe drought-like flows in 60% of years compared with 5% of years in natural conditions. Furthermore, in the five years preceding the audit, only 63% of all water entitlements were used, leaving considerable scope for further increases in consumption if inactive entitlements were activated. On average, diversions could have increased by 15% if all existing water entitlements were activated, which would greatly reduce the security of supply for existing irrigators.

In 1995, implementation of a cap on diversions began. Each year, the volume of allowable diversions is set at the volume of water that would have been used with 1993-94 levels of development, assuming climatic conditions similar to those of the year in question. Implementation of the cap is the responsibility of the states and is done on a catchment basis, and performance is reviewed annually. If the cumulative cap is exceeded in any catchment, the state government has to report to the MDBMC on proposed measures to bring diversions within cap limits.

The operation of the cap was reviewed after five years of implementation (MDBMC 2000a). The review found that, without the cap, there would have been a significantly increased risk of environmental degradation, but that the current cap does not necessarily provide for a sustainable ecosystem and should be refined as more knowledge becomes available, and that all forms of water use should be incorporated in cap management arrangements. The review also found that the cap has benefited the security of supply and provided a more certain environment for long-term investment and development, and accelerated water trade. In 2002, the MDBMC agreed to recovery of a further 350,750, or 1,500 GL for the Murray River to boost environmental flows and management, with the final decision to be announced in October 2003 (MDBMC 2002). An AUDl billion package will be provided, which includes investment in improved structures and other water-efficiency initiatives, some water purchase for the environment through the market, and a native fish strategy. The Council also reaffirmed the importance of water property rights issues in dealing with the nation's salinity and water quality problems, and noted the need to consider the implications of changes in water property rights for investment and the effects of the changes on water users, particularly farmers.

The Council of Australian Governments (COAG) water reforms

The COAG is a high-level council of heads of state representing the commonwealth, states, and territories, with the power to influence commonwealth funding to the states and territories. The COAG water reforms aim to maximize the economic contribution of water to the Australian community and achieve a better balance between environmental and consumptive uses (Crase et al 2000, Crean and Young 2001). The main components of the COAG water reform framework are

- pricing reform based on principles of full cost recovery and transparency
- a comprehensive system of water allocations, backed by separation and clarification of water property rights
- formal determination of water allocations, including allocations for the environment
- water trading, including cross-border (state) sales of water allocations or entitlements
- institutional and organizational reforms involving the separation of resource management and regulatory roles of government from roles of providing water services
- improved public participation and community consultation in water management decisions

The COAG policy was strengthened by its inclusion in the Commonwealth Government's 1995 National Competition Policy, which provides payments to individual states and territories for a total of AUD 16 billion for staged implementation of the recommendations. Implementation of the COAG water reforms is the responsibility of the states (see below). Significant achievements to date include pricing reform and determination of volumetric water allocations. Downsides have been the failure to adequately define and implement water property rights (particularly in advance of trading) (Cullen 2002) and insufficient separation of regulatory and water service roles in some states (NCC 2001).

The Snowy River Agreement

The Snowy River Agreement is another example of coordination and cooperation between the states and commonwealth. In October 2000, the Victorian, NSW, and Commonwealth governments announced an AUD375 million agreement to restore the environmental health of the Snowy River by increasing flow to 28% of its natural flow, from the current level of about 10% because of diversion for hydropower and irrigation in the Murrumbidgee and Murray systems. To achieve this, the government will invest in capital water-saving projects such as pipelining, better water accounting, improved maintenance of irrigation distribution systems, and major engineering works. The water agreement will release up to 294 GL into the Snowy River and 70 GL into the Murray River annually.

The NSW Water Management Act 2000

The Water Management Act 2000 prescribes that the first priority of water sharing is to protect the water resource and its dependent ecosystems. An interim State Water Management Outcomes Plan (SWMOP) has been prepared to provide strategic direction and guidance for water management in NSW. The five-year plan outlines the policy context, targets, and strategic outcomes desired from the management and use of water across the state. The SWMOP was supposed to have input from peak irrigator groups, but in fact the interim plan was developed in isolation by government agencies, and, in the case of Murrumbidgee, delivered with little time (3 days) to provide input by irrigator groups to the committee 3 days before submission of the draft plan (M. Linnegar, personal communication). The Plan is currently with the state cabinet, and all ground- and surface-water sharing plans (see below) must be in accord with the SWMOP.

Water supply and allocation

In response to the COAG requirement to separate regulation and resource management from service, NSW State Water (a commercial business entity within DLWC) was created in 1997 to deliver water to users. However, it is questionable whether there is a sufficient degree of separation between State Water and DLWC (NCC 2001). Water administration and licensing are conducted by DLWC, which is responsible for sharing the available regulated and unregulated water resources between competing water uses to achieve optimum economic, environmental, and social benefits.

Licenses are divided into normal and high security entitlements, reflecting the type of water use. High-security entitlements are usually issued for town water supplies, stock and domestic use, industrial use, and permanent plantings (e.g., orchards, vineyards), and are usually a small component of the total valley entitlement. For most license entitlement categories, no new licenses have been issued since 1977.

DLWC's main tool in the sharing process is the announcement of allocation levels as a percentage of each license's annual entitlement. Allocation announcements are made on a seasonal basis for each river system depending on the amount of water in storage and the minimum expected inflows (in 99% of years) during the season. The 99% reliability ensures that the allocation will not need to be subsequently reduced during the irrigation season (unless conditions more severe than the worst recorded drought occur). The choice of such a conservative reliability was made on the basis that the risk of supply shortfall should be a matter for the individual licensees, and not the result of government decision. Allocations may be updated during the season because of increases in available water.

Water sharing plans (WSP). Under the Water Management Act 2000, WSP are being developed for all river and groundwater sources in the state. Once finalized, the plans will be binding for 10 years. The WSP for the regulated Murrumbidgee River has 11 objectives to protect water access among various uses, including irrigated agriculture, town water supply, and the environment (DLWC 2001). Environmental flow rules were originally developed by river management committees comprising representatives of all stakeholders and first implemented in 1998. The rules were designed to ensure minimum outflow from the dams, minimum end-of-system flows, and some degree of natural flow and variability downstream of the dams, and to maintain an environmental contingency allowance. Hydrological modeling indicates a 3% long-term average reduction in diversions for irrigation as a consequence of the WSP, but in extreme years the reduction would be as high as 17% (DLWC 2001).

Announced allocations in the Munumbidgee (1980-81–1994-95) averaged 116% (range 100-120%) before the introduction of the cap and environmental flows compared with an average of 81% (range 72-90%) from 1998-99 to 2001-02. Similarly, announced allocations in the NSW Murray have changed from an average of 126% (range 85-140%) to an average of 68% (range 29-87%) over the same periods. Economic modeling suggests a reduction in long-term average farm gross margin of 2% as a result of the WSP (DLWC 2001). However, irrigation industry groups consider that the government has grossly underestimated the social and economic effects of the reductions in water availability because of the WSP. For example, the effect for the major irrigation valleys in NSW was estimated to be a total loss of gross production of AUD0.3 billion per year, or 24% of the total farm-gate value of irrigated production in NSW, and with additional effects on employment on- and off-farm (NSW Irrigators 2002). The annual losses for the Murrumbidgee and Murray valleys were estimated to be AUD73 million and AUD18 million, respectively, with a total loss of AUD14 million (4.7% of farm-gate value) for the rice industry. Almost 400 submissions have been received on the Murrumbidgee WSP, and there is considerable tension between irrigators and the state government, and the threat of a legal challenge from the Australian Conservation Foundation. In her “Reflections on developing a water sharing plan,” Bowmer (2002) outlines the successes and failures of the process, and suggests that the challenge for the future is to demonstrate that local solutions can work inside an overarching set of state and national policies and principles.

Water pricing

The Independent Pricing and Regulatory Tribunal (IPART) regulates pricing in NSW. In the past, price played a small role in the allocation of scarce bulk water resources as the state water authorities allocated water to agricultural use in large volumes and at prices that generally did not cover the operating and maintenance costs, let alone the high capital costs of the infrastructure (IPART 1996). Since 1995, IPART has independently determined the path of water prices back to full recovery of both operational and asset refurbishment costs, using a process that is both transparent and independent.

The infrastructure required to manage the water resource for irrigation also provides benefits to the wider community such as flood mitigation and environmental protection; therefore, IPART also has a role in determining the cost-sharing arrangements between irrigators and the other beneficiaries, which are continually under review. IPART originally aimed for full recovery of allocated costs to be achieved by 2003-04. Current water prices recover varying proportions of the costs allocated to users; however, almost complete cost recovery occurs in the Munumbidgee (91% in 2000-01) and Murray (82% in 2000-01) valleys.

Water charges are two-tiered, consisting of a fixed charge to the license holder that must be paid regardless of water use to cover asset refurbishment, administration, and other overhead costs, and a volumetric charge to cover delivery costs. Bulk water prices determined by IPART are incorporated in the charges set by irrigation companies, which include their own operating and fixed charges. Wholesale irrigation customers receive discounts on their bulk water charges. These are not justified on cost grounds but because wholesalers provide information that assists DLWC in performing its functions (IPART 2001). The current discounts for MIL, MI, and CICL are 40%, 29%, and 32%, respectively.

Water trading

The introduction of water trading has been instrumental in breaking the nexus between property rights for land and property rights for water, and has provided a mechanism for allowing water to be traded from low-value uses to high-value uses. Marsden Jacob Associates (1999) conservatively estimated that the increase in the gross value of irrigated agriculture in NSW from permanent and temporary trade in 1997-98 was AUD60-100 million. A water market may also increase the financial incentive for irrigators to become more water-use efficient by changing management practices and/or investing in technologies, providing there is potential to sell the achieved water savings.

The level of water trading in the MDB has increased significantly since the introduction of the cap in 1995, from 502 GL in 1996-97 to 820 GL in 1999-2000 (10% of total diversions). Approximately 90% of trades are temporary, and almost all trades are within-valley. Similar statistics apply to trade in NSW, with total trading of 421 to 548 ML over 1996-97 to 1999-2000 (Table 1).

The effectiveness of water trading in increasing the economic value of water will depend on an efficiently functioning water market. There are several impediments to

Table 1. Water trading in New South Wales.

Year	irrigation diversions (GL)	Permanent transfers (GL)				Temporary transfers (GL)				Total trade (GL)	Intra valley trade (%)	Inter-valley trade (%)	Inter-state trade (%)	Total trade to diver-sions (%)
		Intra valley[a]	Inter-valley	Inter-state	Total	Intra valley	Inter-valley	Inter-state	Total					
1996-97	7,034				37.5				384	421				6.0
1997-98	6,476				47.3				501	548				8.5
1998-99	6,216	56.6	0.0	-3.2	59.8	463.0	0.0	-17.6	481	540	96.2	0.0	3.8	8.7
1999-00	4,940	48.1	-2.6	-2.6	53.3	380.5	3.5	3.5	388	441	97.2	1.4	1.4	8.9

[a] The intravalley transfer is a *gross* value, whereas the intervalley and interstate transfers are a *net* value.

Source: MDBMC (1998, 1999, 2000b, 2001c).

tShe formation of an efficient water market, in particular for permanent trading (Crase et al 2000, Goesch 2001). These include

1. *Unclear or poorly defined rights to access and use the resource.* The lack of a uniform national system with a clear definition of rights, central registration, and uniform market rules is currently a major impediment. There are now about 20 different water products on the market with a different security of supply (Cullen 2002).
2. *Irrigation authority restrictions.* Currently, irrigation authorities impose a raft of restrictions on permanent and intervalley and interstate transfers of water entitlements. For example, permanent trade out of MI is not permitted, and is subject to restrictions in CICL and MIL (Bell and Blias 2002). The major reasons for trade restrictions are the need to protect against the prospect of stranded assets, to maintain the economic viability of the region, and to prevent environmental problems. Such restrictions may contribute to the fact that most temporary water traded in the Murrumbidgee is surplus to needs and goes from high-security entitlements (high-value, high water-use efficiency—horticulture) to general-security entitlements (lower value, lower water-use efficiency—rice) (MI 2001).
3. *Imperfect market information.* Market information for permanent transfers is not very transparent because they are usually done by private treaty and price is not disclosed. The temporary market is more transparent with transactions through various water exchanges, with the information easily accessible from the Internet. For example, the Southern Riverina Irrigation Districts Council operates a water exchange through MIL (www.murrayirrigation.com.au/watexch/), which posts the historical monthly minimum, maximum, and average prices as well as the quantity traded.
4. *Hoarding behavior and speculation.* Natural supply variability and increased uncertainty surrounding possible changes in environmental allocations have led to the retention of surplus entitlements for greater security and associated speculation that entitlements are increasing in value.
5. *Excessive transaction and transfer costs.* In general, the transaction costs of permanent trade are significantly higher than for temporary trade because of higher search costs to determine the market price for permanent trades, more onerous conveyancing requirements, higher administrative costs, taxation implications, and administrative delays.

The price of temporary traded water is greatly influenced by the availability of water. For example, in 1999-2000, a year of very low allocation (approximately 30%), the mean monthly prices in the Murray Valley reached AUD80 ML^{-1}, whereas, in a year of higher allocation (approximately 80%), the price remained below AUD25 ML^{-1}.

Table 2. Irrigation area, entitlement and estimated annual farm-gate value of irrigated production in rice-growing areas.

Irrigation company	Total area (ha)	Area developed for irrigation (ha)	Entitlement (GL)			Value of production (AUD million)
			General security	High security	Total	
MI	490,000 [a]	198,000	930	283	1,213	350
CICL	79,000 [b]	77,000	477	8	485	55
MIL	716,000	429,600 [c]	1,445	–	1,445	250
Total	1,285,000	704,600	2,852	291	3,143	655

[a] Includes Wah Wah District, which is 272,000 ha, with only 25,000 ha (10.3%) being irrigated. [b] Not included is the Coleambally Outfall District, which is approximately 320,000 ha, of which 9,000 ha are irrigated. [c] An estimate of irrigation area is approximately 60% of total area, with less than half of this irrigated in any one year (personal communication, Adrian Smith, MIL, 2002).

Irrigation area institutions, programs, and policies for water management

Privatization of irrigation

The move toward privatization commenced under the NSW Irrigation Corporations Act 1994 and local ownership commenced in the mid- to late 1990s. All three irrigation companies are now privatized and are responsible for managing their businesses as nonprofit companies, and for implementation of Land and Water Management Plans (LWMPs), which are the vehicle for achieving and demonstrating sound environmental management. The area, water entitlement, and approximate farm-gate value of irrigated production for the three irrigation companies are summarized in Table 2.

The irrigation companies purchase water from the state and are responsible for all sales, operations, and assets within the irrigation areas. The price of water charged to irrigators is set to meet all costs and in 2000-01 was approximately AUD15–19 ML^{-1} for irrigators in the MIA, AUD17 ML^{-1} in the CIA, and AUD18 ML^{-1} in the Murray Districts (includes fixed and variable costs at 80% allocation).

The primary goals of the irrigation companies are profitable and environmentally sustainable irrigation regions. Both goals are drivers to maximizing water-use efficiency or minimizing wastage (surface and deep drainage losses) and its effects on water tables and salinization. Therefore, there is considerable investment in automation of flow monitoring and control of flow structures, such as SCADA (supervisory control and data acquisition) technology, to increase water-use efficiency. Targeted investment in sealing leaky sections of channels causing local environmental problems is also important; however, the economics of this is not conducive to large-scale works.

Bulk license conditions for irrigation areas and districts

The right to supply water each year to the three irrigation companies is contingent on meeting the requirements of two licenses issued by the NSW government under the Pollution Control Act 1970 (administered by the NSW Environmental Protection Agency) and the Irrigation Corporations Act 1994 (administered by NSW DLWC). Compliance with the license requirements involves reporting on and meeting up to 50 conditions each year, some of which are rice environmental monitoring, groundwater pressure levels and salinity, and drainage volumes and quality (salinity, chemicals, etc.) (MI 2001, CICL 2001, MIL 2001).

Land and Water Management Plans (LWMPs)

The land and water management planning process began in the early 1990s and was largely driven by concerns about rising water tables and salinization. The development of LWMPs was a community-driven process to identify options for improved management, and with the opportunity to acquire government-funded incentives over a period of 15 years to encourage adoption of the best management practices. The LWMPs have been officially under way for one to six years in the different regions, and include education programs in addition to on-farm and regional actions. The incentives include subsidies for undertaking intensive soil surveys (using electromagnetic inductance—EM31) to detect areas unsuitable for ponded rice, channels, and on-farm storages, for on-farm recycling systems, and for groundwater pumping. These technologies all promote increased water productivity.

Rice environmental policy

Rice environmental policy has had a major influence on increasing the water productivity of rice since the 1940s (Humphreys et al 1994). The policy aims to minimize the rate of development of high water tables and subsequent secondary salinization. Rice growing is restricted to medium and heavy clay soils and to fields where water use does not exceed a seasonal adjusted target based on the theoretical crop water-use requirement. The volume of water supplied to each farm is measured and farmers are required to specify the area of rice (and other crops) they are growing and which crop(s) the water is going to. The area of rice is measured each season from aerial photos or satellite imagery and rice water use for each farm or field is calculated directly by the irrigation companies.

Rice environmental policy was implemented and administered by the state (NSW DLWC) until the late 1990s, when the irrigation companies took over management of the irrigation areas and districts; however, they largely retained the existing policy (DLWC 1995). Since 1984, the development of rice environmental policy has been guided by the Rice Environmental Policy Advisory Group (and its predecessors) comprising representatives of the rice industry, irrigation companies, and government agencies.

Conclusions

A host of institutions, programs, and policies, often interrelated, affect water availability and price, driving the need to increase the water productivity of irrigated agriculture. Rice water productivity (g grain kg^{-1} water) at the farm level has almost doubled in the past 20 years in the MIA; however, this has largely been due to increased yields. Water-use efficiency (crop water-use requirement per irrigation amount) appears to have increased by about 10%, starting in the mid-1980s, coincident with the introduction of the target rice water-use policy, to assist water table control. There is little scope for further increasing rice water-use efficiency at the farm level while rice is grown under continuous ponding, and research is under way to develop alternative systems and varieties with sufficient cold tolerance to remove the need for ponding during the early reproductive phase.

The main driver for increasing water-use efficiency and water productivity now and in the future is the reduced availability of water because of increased allowances for the environment. Pricing policy will have little influence, as in the rice-growing areas prices are almost at full cost recovery already. To date in the MIA, water trading has shifted surplus water from horticulture to rice, contrary to the theory of water shifting to higher-value, higher-productivity uses, probably because of market restrictions. As the availability of water decreases further, this will further affect prices and the direction of trade. Therefore, irrigation companies and irrigators are strongly focused on improving water-use efficiency at the irrigation area level, in particular through automation of flow structures and monitoring, and through the implementation of Land and Water Management Plans that promote on-farm efficiency measures such as whole-farm planning, recycling, and the identification of suitable soils for rice, channels, and water storage.

References

Bell R, Blias A. 2002. Capturing benefits from the removal of impediments to water trade: a modelling framework. 46th Annual Conference of the Australian Agricultural and Resource Economics Society, 13-15 February, Canberra, Australia.

Bouman BAM, Tuong TP. 2000. Field water management to save water and increase its productivity in irrigated lowland rice. Agric. Water Manage 49:11-30.

Bowmer KH. 2002. Reflection on developing a water sharing plan. Fenner Conference on the Environment, 31 July-1 August 2002, Canberra, Australia.

CICL. 2001. Environment report 2001. Coleambally Irrigation Cooperative Ltd, Coleambally, Australia. http://env.colyirr.com.au/aer2001/.

Crase L, O'Reilly L, Dollery B. 2000. Water markets as a vehicle for water reform: the case of New South Wales. Aust. J. Agric. Res. Econ. 44(2):299-321.

Crean J, Young R. 2001. Modelling the farm level implications of water reforms in NSW, Australia. Invited paper at the ACIAR water policy workshop, Bangkok, Thailand, June.

Cullen P. 2002. Sort out water property rights. Australian Landcare, June 2002, p 14-15.

DLWC. 1995. Rice environmental policy guidelines. Discussion Paper. NSW Department of Land and Water Conservation, Leeton, Australia.

DLWC 2001. Draft water sharing plan for the Murrumbidgee regulated river water source. NSW Department of Land and Water Conservation, Wagga Wagga, Australia.

Dwyer L. 1992. Rice 2000: environmental policy paper. Dwyer Leslie Pty Ltd, Canberra, Australia.

GHD. 1985. Waterlogging and land salinisation in irrigated areas of NSW. Vol. 1. The problems. Gutteridge, Haskins, and Davey for the Water Resources Commission, Sydney, Australia.

Goesch T. 2001. Delivery charges for water: their impact on interregional trade in water rights. Aust. Commodities 8(4):626-634.

Humphreys E, van der Lely A, Muirhead WA. 1994. The development of on-farm restrictions to minimise recharge from rice in New South Wales. Aust. J. Soil Water Cons. 7(2):11 - 20.

IPART. 1996. Interim report on bulk water prices, independent pricing and regulatory tribunal. Sydney, Australia.

IPART. 2001. Department land and water conservation bulk water prices from October 1st, 2001. Independent Pricing and Regulatory Tribunal of New South Wales.

Lewin LG, Reinke RF, Williams RL. 1994. Yield performance of rice cultivars in NSW. In: Temperate rice: achievements and potential. Proceedings of the Temperate Rice Conference, 21-24 February 1994, Yanco, Australia. p 125-130.

Marsden Jacob Associates. 1999. Water trading development and monitoring. Final Report to NSW Department of Land and Water Conservation, Paramatta, Australia.

McDonald DJ. 1994. Temperate rice technology for the 21st century: the New South Wales example. In: Temperate rice: achievements and potential. Proceedings of the Temperate Rice Conference, 21-24 February 1994. Yanco, Australia. p 1-12.

MCMB. 2001a. Draft Murmmbidgee catchment blueprint 2001. Murmmbidgee Catchment Management Board, Wagga Wagga, Australia.

MCMB. 2001b. Draft Murray catchment blueprint 2001. Murray Catchment Management Board, Albury, Australia.

MDBMC. 1995. An audit of water use in the Murray-Darling Basin. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 1998. Water auditing monitoring report 1996197. Report of the Murray-Darling Basin Commission on the Final Year of the Interim Cap in the Murray-Darling Basin. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 1999. Water auditing monitoring report 1997198. Report of the Murray-Darling Basin Commission on the Cap on Diversions. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2000a. Review of the operation of the cap. Overview Report of the Murray-Darling Basin Commission. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2000b. Water auditing monitoring report 1998/99. Report of the Murray-Darling Basin Commission on the Cap on Diversions. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2001a. Integrated catchment management in the Murray-Darling Basin 2001-2010. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2001b. Basin salinity management strategy 2001-2015. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2001c. Water auditing monitoring report 1999/2000. Report of the Murray-Darling Basin Commission on the Cap on Diversions. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2001d. Snapshot of the Murray-Darling Basin River condition. Murray-Darling Basin Ministerial Council, Canberra, Australia.

MDBMC. 2002. The living Murray. A discussion paper on restoring the health of the river Murray. www.thelivingmurray.mdbc.gov.au.

MI. 2001. Environmental performance and compliance report 2000/1. Murrumbidgee Irrigation Limited, Griffith, Australia.

MIL. 2001. Environment report 2000/1. Murray Irrigation Limited, Deniliquin, Australia.

NCC. 2001. National Competition Council 2001: assessment of government progress in implementing the National Competition Policy and related reforms: June 2001. Canberra (Australia): AusInfo.

NLWRA. 2000. Australian water resources audit, national land and water resources audit. Land and Water Australia, Canberra, Australia. http://audit.ea.gov.au/ANRNwater/docs/national/water_contents.html.

NSW Irrigators. 2002. Fact sheet: socio-economic impacts of NSW water sharing plans—major irrigation valleys July 2002. Prepared by NSW Irrigators Council, Cotton Australia, and Ricegrowers' Association of Australia.

Valencia MS, Dawe D, Moya P, Pabale D. 2001. Water fees for irrigated rice. Int. Rice Res. Notes 26(2):78-79.

Notes

Authors' address: CSIRO Land and Water, Griffith Laboratory; Liz.Humphreys@csiro.au, phone 61 2 6960 1500, fax 61 2 6960 1600, CSIRO Land and Water PMB 3 Griffith, NSW 2680, Australia.

Acknowledgments: Our work is supported by the Cooperative Research Centre for Sustainable Rice Production and the Australian Centre for International Agricultural Research (ACIAR). We thank Mr. Matt Linnegar, executive director of the Ricegrowers' Association of Australia, for his feedback on this paper; Mr. Jason Crean, NSW Agriculture, for providing information; the Ricegrowers' Cooperative Ltd for yield data; and Mumumbidgee Irrigation Ltd for water-use data.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Farm pesticide use, rice production, and human health

J. Huang, F. Qiao, S. Rozelle, and F. Lu

China, like many developing countries, has seen a dramatic increase in the use of pesticides over the last 20 years. Various kinds of pesticides have been used on a large scale to protect crops from damage inflicted by insects and diseases. The overall goal of this paper is to have a better understanding of the effects of farm pesticide use on rice production and farmers' health. To meet this goal, a unique primary data set from 100 rice farmers randomly selected from four villages with different rice-cropping patterns in Zhejiang Province was used in the analyses. The rice farmer survey gathered detailed information on rice production, farmers' perceptions of pest-related crop losses, their knowledge and attitudes on pests, safety of pesticide use, and their practices for pesticide use. The study also used laboratory tests that examined the blood, liver, kidneys, and neurological and other systems of these 100 farmers. The results showed that, although pesticides contributed significantly to rice production by limiting yield losses, the marginal contributions of pesticide use declined considerably with the increased use of pesticides and approached zero at the current average pesticide use level of rice farmers. Given the current rice and pesticide prices, pesticides were being grossly overused. On average, rice farmers were overusing pesticides by more than 40%. The study found that the farmers' perceptions of yield loss had the largest effect on how they applied pesticides. Farmers were found to grossly overestimate the crop loss caused by pests. The average farmer perceived yield losses to be nearly twice the loss that actually occurred when no pest control was used. Econometric analysis also showed that education and quality of the extension system are the major determinants of how farmers perceive yield loss. Once it was clear that pesticides were being misused, the paper then looked at the health effects this was having. The farmers interviewed reported eye problems, headaches, skin problems, liver problems, and neurological effects, among others. Of 100 farmers examined, 22 had impaired liver function and 23 had abnormal levels of key chemicals in their kidneys, which indicated that overuse of pesticide was having a marked negative effect on farmers' health and their economic well-being. The study concluded that a reduction in farm pesticide use is not likely to occur without policy interventions. Reforms in the public agricultural extension system, providing farmers with better information, changes in agricultural training, and alternative methods of pest management, are crucial for reducing pesticide use.

Pesticides of various kinds have been used on a large scale in China since the 1960s to protect crops from damage inflicted by insects and diseases. Annual pesticide production reached more than 500,000 metric tons after the mid-1990s (Ministry of Chemical Industry, n.d.). China was the second-largest pesticide-using country in the world in the 1980s and was the largest pesticide-using country in the world in the 1990s (Huang et al 2000).

The Chinese government has made numerous efforts to prevent grain production losses from pest attacks and to control the rapid growth of farm pesticide use. Before the 1980s, policies focused on the safe handling of agricultural chemicals. Since the 1980s, regulations have been developed for the safe use of pesticides, with bans imposed on highly hazardous organochlorine (BHC and DDT), organomercurial, and organoarsenical pesticides. Standards for an acceptable daily intake level and maximum allowable residue on crops have also been developed. More recent efforts have focused on promoting integrated pest management (IPM) in certain areas. Developing pest-resistant crop varieties has become a top priority in conventional plant breeding programs since the 1970s and in biotechnology programs since the early 1990s.

However, experience has shown that the effect of many previous efforts (except for research and technology development on crop resistance) has been minimal. The promulgation of rules and regulations did not guarantee improvements in the proper and safe use of pesticides. Farm pesticide use has increased rapidly in recent years.

Worldwide, numerous studies have questioned whether current patterns of pesticide use are economically and socially efficient (e.g., Pimentel and Lehman 1992, Pingali and Roger 1995). Some studies showed that the costs (both economic and social) related to pesticide use in crop production were higher than the gains from the reduction in crop yield losses (e.g., Rola and Pingali 1993). However, few researchers have assessed farmers' pesticide use and its impacts on production, environment, and human health in China.

In seeking to have a clear understanding of the consequences of increasing farm pesticide use in China, and to identify the policies that will help farmers reduce their pesticide use yet maintain the profitability of crop production, several critical questions arise. How much pesticide is applied to crop production? Do farmers overuse pesticides? If they do, what major factors underlined their overuse of pesticides? What are the effects of pesticide use on crop production, the environment, and farmers' health? Answers to the above questions are by no means clear in China. The overall goal of this paper is to have a better understanding of farm pesticide use and its effects on crop production and farmers' health.

To narrow the scope of analysis, however, rice in Zhejiang Province was selected as the research focus. Rice accounts for about 40% of grain production in China and more than 80% in Zhejiang Province (NSBC, n.d.). A unique primary data set from the farm level in Zhejiang Province is used in the analysis. A total of 100 rice farmers were randomly selected from four villages with different rice-cropping patterns in two counties, Jiaxing and Anji, of Zhejiang Province. The paper is organized into the following sections: a profile of pesticide use in rice production, determinants of farm pesticide use, the effects of pesticide use in rice production, the effects of pesticide use on rice farmers' health, and a summary of the findings of the study and their policy implications.

Pesticide use in rice production

An overview of pesticide use in rice and other production in China

Pesticide expenditures in all crop production increased considerably in the past two decades. After deflating the current value of pesticide use by the retail price index of pesticide, the results indicate that the real cost of pesticide per hectare rose 2.5 times for rice, 3 times for wheat, and 4.8 times for maize in 1980-97. The real cost of pesticide per hectare of cropped area increased by 1.5-2.6 times for fruits, vegetables, and cotton in the same period (Table 1).

The rates of pesticide application varied significantly among crops, reflecting that the extent of pest-related problems differed across crops. On a per-hectare basis, fruit and vegetable production used much more pesticide than other crops. Cotton farmers applied 3 times more pesticide than rice farmers. In grain production, rice was the most intensive pesticide user. Per-hectare rice production cost 231 yuan (US$1 = 8.3 yuan) of pesticide in 1997, nearly 3 times that of wheat and 4 times that of maize (Table 1).

It is worthwhile to note that the increase in pesticide use over time had been higher than that of other inputs in all crop production. The cost share of pesticide in total material inputs rose from 5.8% in 1980 to 7.3% in 1997 in rice production, from 1.9% to 2.9% in wheat, and from 1.0% to 2.4% in maize. The most significant increase in pesticide cost share occurred in cotton production, rising from 13.1 % in 1980 to 21.7% in 1995.

On an aggregate basis, rice is the largest pesticide user. National data showed that rice farmers spent more than 7.3 billion yuan for chemical pesticides to control pest problems in 1997 (Table 1). This was followed by apples (5.4 billion yuan), cotton (3.3 billion yuan), wheat (2.5 billion yuan), oranges (2.3 billion yuan), and maize (1.4 billion yuan). For these six crops altogether, farmers spent about 22.2 billion yuan (or US$2.67 billion) for pesticide in 1997. These six crops accounted for about 61.5% of the total crop area in the past two decades. Using a similar rate of pesticide use for the rest of the crops that are not included in Table 1, the study estimated that Chinese farmers might have spent as much as 36.1 billion yuan (US$4.34 billion) annually for chemical pesticides in the late 1990s. In 1992, Japan was the world's largest pesticide consumer with a total of US$3.5 billion (Wood

Table 1. Pesticide use of selected major crops in China, 1980-97. [a]

Year	6 crops	Rice	Wheat	Maize	Cotton	Apple	Orange
Per-hectare pesticide cost (yuan at 1997 prices)							
1980		94	27	12	277	1,131	1,127
1985		127	25	13	315	1,473	2,203
1990		139	41	22	411	1,810	2,286
1995		223	69	64	900	2,221	1,845
1997		231	83	59	728	1,888	1,741
Pesticide cost share (%) in total material costs of crop production							
1980		5.8	1.9	1.0	13.1	36.1	17.8
1985		6.0	1.4	0.8	11.5	29.1	17.7
1990		7.5	2.7	1.6	18.1	29.3	25.6
1995		7.0	2.8	2.7	21.7	27.0	20.8
1997		7.3	2.9	2.4	18.2	23.2	22.1
Million yuan at 1997 prices							
1980	6,722	3,184	797	248	1,363	835	294
1985	9,050	4,086	731	221	1,621	1,276	1,117
1990	14,022	4,602	1,276	463	2,299	2,956	2,427
1995	23,988	6,864	1,986	1,453	4,883	6,562	2,240
1997	22,149	7.346	2,497	1,401	3,267	5,358	2,280
Million US$ converted at official exchange rate							
1980	1,382	655	164	51	280	172	60
1985	962	434	78	23	172	136	119
1990	2,173	713	198	72	356	458	376
1995	2,661	762	220	161	542	728	248
1997	2,672	886	301	169	394	647	275

[a] The rural retail price index of pesticides was used to deflate the current value. Six crop sown areas accounted for 61.5% of the total crop sown area in 1980-97.

Source: State Development and Planning Commission for cost of production data: crop area data used in computing the total pesticide cost and exchange rates were from NSBC.

Mackenzie Co., Ltd., 1993, as cited in Yudelman et al 1998). Although no comparable data are available for Japan in 1997, estimates showed that, based on China's current rate of pesticide use, China is likely to have been the largest pesticide consumer in the world since the mid-1990s.

Pesticide use in rice production in the sample households

The average farm size (0.50 ha) in the sample (100 households) was slightly smaller than the country average (0.57 ha). Farmers allocated more than 80% of their land to grain production. Rice was the most important grain and accounted for 58% of the total crop area. In the two villages of Jiaxing County, rice was planted under a double-season rice-cropping system, which accounted for 69% of the total rice area in Zhengbei village and 80% in Yuangzhuang village. In these two villages, the common cropping patterns were rice-rice and cash crop-wheat. In Yushanwu and Shuikou villages of Anji County, rice was planted under a single-season rice-cropping system.

Table 2. Pesticide use by rice season on the surveyed farms, 1998. [a]

Rice season	Sample size (no.)	Pesticide use per hectare Times (no.)	Dose (kg)	cost (yuan)	Yield (t ha^{-1})
All rice	200	8.0	27.7	287.1	6.4
Doubleseason early rice	47	5.7	20.6	174.5	6.0
Doubleseason late rice	47	8.7	28.4	288.9	6.4
Single-season middle rice	35	10.0	31.0	325.0	6.5
Single-season late rice	71	7.9	30.2	341.8	6.7

[a] Data were from 100 farm households in four villages of Jiaxing and Anji counties in Zhejiang Province. Because some farms plant doubleseason rice in some plots and also plant single-season rice in other plots, the total sample size (200) is larger than the number of farm households (100).

The common cropping patterns in Anji County were rice-wheat, rice-rape seed, and multiple cash crops.

Average rice yield in the sample households ranged from about 6 t ha^{-1} for double-season early rice to 6.7 t ha^{-1} for single-season late rice (Table 2), which was slightly higher than the national average. On average, farmers used 179 labor days and 282 kg of fertilizer for every hectare of rice crop.

Compared with those of other Asian countries, farmers in the surveyed areas applied exceptionally large amounts of pesticide. The average pesticide use per hectare reached 27.7 kg (or about 12-14 kg of active ingredient) for each rice-growing season, which cost the farmers 287 yuan (or US$34.70). This was similar to the usage level in Japan (14.3 kg of active ingredient) and the Republic of Korea (10.7 kg of active ingredient), but much higher than that of the rest of the Asian countries (Barker and Herdt 1985).

On average for each season, farmers applied pesticides 8 times: about 3 times during the seedling period and 5 times in the field (Huang et al 2000). During the field survey, the local farmers reported that the frequency of pesticide application in the 1970s was only about 4-5 times for each rice-growing season. The frequency of pesticide application increased significantly in the early 1980s when the collectively owned land was distributed to individual households. Although the reform increased the production incentives of farmers, there is also evidence that China's technology generation and extension systems may have been weakened after the reform, which could have resulted in an increase in the cost of technology use (Lin 1991).

Pesticide use also differed by rice-cropping system. While double-season rice used a much higher dosage of pesticides on an annual basis (i.e., add double-season early and late rice), on a per-crop-season basis, pesticide use in single-season rice was higher than that in double-season rice (Table 2). The lower level of pesticide application in double-season early rice was mainly due to fewer applications of pesticide during the rice seedling period and fewer pest-related problems in April to June. The longer the rice-growing period such as single-season middle and late rice, the higher the level of pesticide use (Table 2).

Based on the same survey data, Huang et al (2000) showed that the overuse of pesticides is very common among rice farmers. Among the various factors that determine the amount of farm pesticide use, farmers' own perceptions of the yield loss caused by pest problems (risk aversion), the quality of pesticides available in the market, local agricultural and extension services (particularly the plant protection service), and the opportunity cost of farm labor were the most important determinants. Therefore, in seeking a better solution to pest problems, they suggested that the regulations and policies that would ban some pesticide use in crop production were necessary, but not sufficient. Convincing farmers that their perceptions of crop yield loss caused by pest-related problems are overestimated and improving farmers' knowledge of pest management and pesticide safety issues are critical.[1] The results presented in Huang et al (2002b) also raised some questions on the services currently provided by the agricultural extension system, a public extension system that has been participating heavily in pesticide marketing activities as a result of the financial crisis.

Effects of pesticide use in rice production

Damage control production function with endogenous pesticide use

To estimate the effects of chemical use on rice productivity, a production function approach was used. However, the roles of pesticide and other inputs in rice production differ by nature. Inputs such as fertilizer and labor were treated as "normal" inputs that contribute to a yield increase, while pesticide was a damage abatement input. The production function was a combination of yield loss and output that was recoverable by limiting this loss with damage control or abatement inputs. Following the work by Lichtenberg and Zilberman (1986), a damage abatement function was incorporated into the traditional models of agricultural production.

The nature of damage control suggests that the observed crop yield, Y, can be specified as a function of both standard inputs and damage control measures, that is,

$$Y = f(X)\ G(Z) \qquad (1)$$

where X is a vector of standard inputs such as labor, fertilizer, and other inputs and $G(Z)$ is a damage abatement function that is a function of the level of control agent Z (e.g., pesticide-use level). The abatement function possesses the properties of a cumulative probability distribution. It is defined on the interval of [0, 1]. $G(.) = 1$ indicates a complete abatement of crop yield losses caused by pest attacks with a certain high level of control agent, while $G(.) = 0$ represents a complete destruction

---

[1] The effort to convince farmers to reduce their pesticide use relies mainly on the factors that could significantly reduce the farmers' risk aversion. These may include pest management-related information, education, training, and extension services (Huang et al 2000). Huang et al (2000) also suggested that increasing farmers' awareness of the hazard of the pesticides to the environment and human health should be included in the local extension activities so that farmers could partially internalize the externalities of pesticide use.

of crop production by the pest at a certain low level of control measures. *G(.)* is a nondecreasing function of Z and approaches 1 as the use of the damage control agent increases. Assuming a Cobb-Douglas (C-D) production function for *f(X)* and the damage abatement function *G(Z)* with an exponential specification, equation 1 can be written as

$$Y = a_0 \Pi_i^n X_i^{a_i} [1 - exp(- c Z)] \qquad (2)$$

where a_0, a_i, and c are parameters to be estimated, i indexes inputs including labor and various fertilizers (N, P, and K), and Z is farmers' pesticide use. Model 2 is estimated using nonlinear methods. To compare the results from the traditional production approach, a C-D production function is estimated using ordinary least squares (OLS), where pesticide use is specified as the same as other inputs such as labor and fertilizer.

The models specified above, however, do not account for endogenous problems in pesticide use. Since pesticides are applied in response to pest pressure and high levels of infestations are correlated to lower crop yields, a relationship between pesticides and negative residuals in the production function might bias parameter estimates for pesticide and other variables. To empirically account for this endogenous problem, the farmers' pesticide adoption model is estimated first. The predicted values of the pesticide use are then used in the estimation of model 2. Following Huang et al (2000), the farmers' pesticide adoption behavior is hypothesized to depend on the incentive gained from pesticide application (i.e., pesticide prices and farmers' expected yield losses caused by pest problems), farmers' characteristics, and environments where the crop production activities are based.

Estimation results and discussion

To compare the results of the damage control model with the C-D production model, both linear (C-D production function) and nonlinear estimates of damage control rice production functions with endogenous pesticide use are summarized in Table 3.

After control for the other input uses and location-specific effects, a higher yield for both single-season middle and late rice (compared with double-season early and late rice) is expected. Similar to the findings of early studies on very low elasticity values of both labor and fertilizer in rice production (Huang et al 1994, 1995, Widawsky et al 1998), the estimated labor elasticity is about 0.07 and the marginal contribution of fertilizer on the sample farms is about zero. The low labor elasticity in rice production is consistent with the observation of a large labor surplus in rural China. The insignificant marginal contribution of fertilizer to rice production may be due to the overuse of fertilizer in our sample households (farmers applied 282 kg fertilizer ha $^{-1}$, one of the highest levels in the world). Table 3 also shows that, given the same amount of fertilizer but raising the proportion of potash fertilizer by 10%, rice yield would increase by 1.7%. This result confirms early findings by Huang et al (1994).

Table 3. Estimated parameters for rice yield, Ln (yield).[a]

Variables	Cobb-Douglas function	Damage control function
Intercept	1.00	1.35
	(0.37)***	(0.21)***
Ln (labor)	0.07	0.07
	(0.03)**	(0.03)**
Ln (fertilizer)	-0.002	-0.002
	(0.03)	(0.03)
Ratio of phosphate fertilizer	0.10	0.09
	(0.15)	(0.15)
Ratio of potash fertilizer	0.16	0.17
	(0.07)***	(0.07)**
Dummies		
Double-season late rice	0.01	0.02
	(0.04)	(0.04)
Single-season middle rice	0.14	0.13
	(0.05)***	(0.05)**
Single-season late rice	0.09	0.10
	(0.04)**	(0.04)**
Higher than middle school	-0.02	-0.02
	(0.04)	(0.04)
Village dummies		
Zhengbei	0.14	0.12
	(0.06)**	(0.05)**
Yangzhuang	0.08	0.07
	(0.05)*	(0.05)
Yushanwu	-0.05	-0.04
	(0.04)	(0.04)
Ln (predicted pesticide)	0.06	
	(0.06)	
c (in exponential model)		0.03
		(0.01)**
Adjusted R^2	0.14	0.13

[a]The numbers in parentheses are standard errors of estimates. ***, **, and * denote significance at 1%. 5%, and 10%, respectively.

Between the two alternative models, only the production function with exponential damage control specification shows a statistically significant effect of pesticide use on rice production (Table 3). There are two explanations for the statistically insignificant parameter of the pesticide use in the C-D model. One explanation is that this result may suggest that the marginal contribution of pesticide use at the current level to rice production is zero, which could be one possible indicator of overuse of pesticide by farmers in rice production. The alternative explanation may be the inability of the C-D production function approach to capture the effect of pesticide use in rice production because pesticide use is not a normal input but a damage abatement input.

Using the parameter *c* and mean values of rice yield and all right-hand-side variables as bases, average and marginal products of pesticide use in rice production at the mean level of other inputs were computed. On average, farmers applied 287

Table 4. Pesticide productivity in rice production.

Item	Average
Pesticide use (yuan ha^{-1})	287
Yield (t ha^{-1})	6.4
Average product (kg rice for every yuan of pesticide use)	22
Elasticity	0.0033
Marginal product (kg rice for additional yuan of pesticide use)	0.07
Optimal pesticide use (kg ha^{-1})	201
Ratio of actual/optimal use of pesticides	1.43

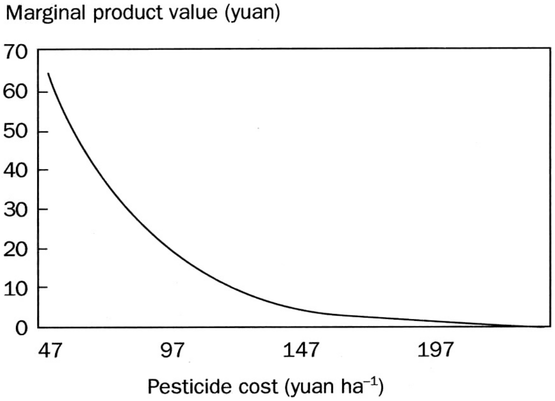


Fig. 1. Marginal product value of pesticide use in rice production.

kg ha^{-1} of pesticides. The average rice production was 22 kg per kg of pesticide use (Table 4). Pesticides do significantly contribute to rice production through yield loss abatement. However, at current high levels of pesticide use, the rice output elasticity of pesticide use is close to zero and the marginal product of pesticide is only 0.07 kg.

Figure 1 shows the trend of rice marginal product values with respect to pesticide cost evaluated at the means of all nonpesticide variables. The marginal rice production value declines significantly with increases in pesticide use. The increase in rice output approaches zero as pesticide use increases to a level above 200 yuan ha^{-1} . Based on the trend, the optimal pesticide use is 201 yuan ha^{-1} evaluated at the mean value of rice price (Table 4). This is substantially lower than the actual expenditure on pesticide use. Pesticide use by farmers in the sample areas was 42% higher than the optimal level (287/201 = 1.43).

Effects of pesticide use on farmers' health

Pesticide poisoning affected about 40,000-50,000 persons, among which 300–500 died, because of the improper use and overuse of pesticide in crop production each year in China in the past decade (Huang et al 2000).[2]

Evidence from rice farmers

To determine the effects of pesticide use on farmers' health, the farmers were examined by a medical team of two physicians and two nurses. The examinations included obtaining general information on the farmers' physical and medical situation, observing for acute poisoning symptoms, as well as conducting biochemistry, blood, and pathology tests. The pesticide-related health indicators include visible and invisible ones. The visible indicators are those that can be obtained directly by interviewing farmers. The invisible indicators are those that accumulate in the human body and are reflected by the functions of the liver, kidneys, and neurological and other systems.

Visible effects. The results of the study show that, although many farmers reported to have felt some discomfort when they applied pesticides, only a few of them considered the discomfort as severe. For example, among 100 farmers interviewed, only three farmers considered that the effects of pesticide use were serious on their eyes, seven farmers reported having experienced serious headaches, 10 farmers reported having skin pain, and three farmers experienced nausea or decreasing chest expansion when they applied pesticides during the last rice-growing season.

More sophisticated tests of the effects of pesticide use on farmers' health were made through farmers' laboratory tests.[3] The health indicators have been developed to measure possible effects (particularly chronic effects) of pesticide on human health and are provided in Huang et al (2000). They include indicators for the blood system and functions of the liver, kidneys, neurological system, and others. Table 5 summarizes the major indicators.

Cardiovascular effects. Acute pesticide poisoning is mainly caused by the pesticide entering the blood. As soon as the pesticide enters the body, it enters the blood system, which makes it difficult to observe its effects by a simple diagnostic check. The blood test results in Table 5 showed abnormalities in the blood platelets and white blood cells of many farmers. However, further analysis by stratifying results based on pesticide use did not lead to a significant difference in these statistics among different pesticide-use groups.

Liver function. Pesticides can enter the gastrointestinal tract accidentally through the mouth. When ingested, carbamate insecticides formulated in methyl alcohol may cause severe gastroenteritic irritation (Morgan 1977). Organophosphates and copper

---

[2] These figures do not include the purposive use of pesticides (e.g.. suicide) or careless handling/use of pesticides.

[3] This study benefited greatly from several meetings in Beijing and Nanjing, where medical doctors from hospitals provided very useful comments on pesticide-related health problems and health Indicators for both general and laboratory tests.

Table 5. Summary of results of laboratory tests for 100 farmers in Zhejiang Province.

Effects[a]	Normal range	Abnormal cases Less than lower boundary	 Greater than upper boundary	 Total
Blood effects				
Hgb	110-160	8	0	8
PLT	100-300	69	0	69
Liver effects				
ALT	0-40	0	22	22
AST	0-40	0	14	14
Kidney effects				
BUN	3-7.2	1	22	23
UA	150-430	1	3	4
Neurological effects				
CHE	30-80 (4.500-13,000)	5	0	5

[a] Hgb = hemoglobin, PLT = platelet, ALT = alanine transaminase, AST = aspartic transaminase, UA = uric acid, BUN = urea nitrogen, CHE = choline esterase.

salts irritate the gastrointestinal tract, resulting in intense nausea, vomiting, and diarrhea. Alanine transaminase (ALT) and aspartic transaminase (AST) are two important indicators of the liver's function. Many factors affect ALT and AST, and pesticide is one of them. When people are exposed to pesticide, their ALT and AST values will rise with the level of pesticide exposure. In 100 farmers examined, 22 had ALT values higher than the normal range and 14 had AST values exceeding the normal range (Table 5). Stratifying the ALT and AST by pesticide use indicated that there was a close linkage between the abnormality of ALT and AST and level of pesticide application of farmers.

Kidney effects. The kidneys help to ensure the efficient functioning of body cells through several mechanisms: regulation of extracellular fluid volume, control of electrolytes and acid-base balance, excretion of toxic and waste products, and conservation of essential substances. High exposure to circulation toxins and long-term exposure to organophosphate compounds could lead to renal tubular abnormalities. Nephrotoxic agents such as endrin and endosulfan can also cause kidney abnormalities. Cases of pesticides affecting kidney function have been reported by many researchers (Lei et al 1998). Among the 100 rice farmers in the sample, 23 had abnormal levels of blood urea nitrogen (BUN) and 22 had BUN values exceeding the upper boundary for the normal population (Table 5).

Neurological effects. Most pesticides are neurotoxicants. Choline esterase (CHE) is a major indicator in monitoring the neurological effects of pesticide use. When pesticides enter the human body, they mix with the protein enzyme and affect its function. When this happens, the value of CHE will decrease. In the survey sample, 5% of the farmers had CHE values less than the lower limit of the range for a normal population (Table 5).

Table 6. Pesticide use and statistics on farmers who underwent a health examination.

Item	Mean[a]	Standard error
Age (years)	45.4	9.1
No. of males (%)	90	30
Smoking history (years)	11.1	12.1
No. of smokers (%)	51	50
Amount of pure alcohol consumption (kg d^{-1})	0.03	0.03
No. of drinkers (%)	69	46
Pesticide use (kg y^{-1})		
Category I and II	2.47	3.41
Category III and IV	11.59	10.87
Total (I + II + III + IV)	14.07	13.46
Pesticide use (yuan y^{-1})		
Category I and II	28.18	33.10
Category III and IV	116.09	113.05
Total (I + II + III + IV)	144.27	137.94
No. of pesticide applications (times y^{-1})	15.93	6.06
Health cost (yuan)	21.69	55.75

[a] The numbers in the table were from 100 farmers in four villages in Zhejiang.

Health costs of pesticide use in rice production

Health costs related to pesticide use are computed based on the treatment required to restore farmers' health. They include the expenses for medication and a physical examination and the opportunity costs of farmers' time lost to recuperation. Because of the difficulty in estimating the costs related to the treatment required to restore farmers' health to its normal state, the health costs are limited to visible health impairments. A correlation analysis shows a strong linkage between farmers' health costs for visible health impairments and pesticide use. On average, each rice farm applies 14.07 kg of pesticide (Table 6). The health cost related to this level of pesticide application is 21.68 yuan. However, for farmers who use more than 15 kg of pesticide, their health costs are nearly 3 times as much as those of farmers who use less than 9 kg of pesticide (33.09 vs 8.59 yuan).

Health costs may also be linked with farmers' health or physical condition such as age, sex, and smoking/drinking habit, and various pesticides used. To arrive at a firm conclusion on the causal relation between farmers' health cost and pesticide use, a control treatment on the effects of the above factors would be required.

Table 6 shows the basic statistics of the 100 farmers examined and pesticide use by category. Males are the major pesticide users. More than half of the farmers smoked and 69% drank alcoholic beverages. Most pesticides belong to categories III and IV and these pesticides are expected to cause more chronic diseases. Of the 14.07 kg of pesticide used by rice farmers per year, 11.59 kg belong to categories III and IV. This accounted for 82% of the total pesticides used by farmers in rice production in 1998 (Table 6).

Models of health impairments and costs

The hypothesized effects of farmers' pesticide use on their health and costs related to health impairments were examined using health risk models and health cost models, respectively. A health risk model can be specified in a general functional form as follows:

$$Hrisk_i = f(F_i, P_i, Z_i, e_i) \tag{3}$$

where *Hrisk* denotes a health indicator and is equal to 1 if the health effect occurred or the health indicator is not in the range of normal cases; it is equal to 0 otherwise. Indicators for the health impairments are headaches, nausea, and skin pain for visible health impairments and abnormal laboratory test results for the liver, kidney, and neurological functions for invisible health impairments. *F* is a vector of farmers' characteristics, including sex, height, weight, and smoking/drinking habit. *P* is pesticide used by farmers. *Z* is regional fixed factors such as local quality of drinking water and environment. The *i's* denote farmers. The small number of cases of health impairments for each individual illness disables the study from running the model separately for each impairment. Instead, the study constructed *Hrisk* as equal to 1 if any health impairment was present and 0 otherwise. In the empirical estimation, the health impairment model is specified as follows:

$$\begin{aligned} Hrisk_i = {} & a_0 + a_1 * Dmale_i + a_2 * Ln(Age_i) + a_3 * Ln(Smoke_i) \\ & + a_4 * Ln(Drink_i) + a_5 * Weight_i/height_i \\ & + a_6 * Pesticide_i + a_7 * Dregion_i + e_i \end{aligned} \tag{4}$$

Variables with continuous values such as *Age, Smoke* (amount d^{-1}), and *Drink* (kg d^{-1}) are specified in natural log form. For those with a zero value for *Smoke* and *Drink,* a small value (0.0001) is assigned. Pesticide is specified in volume or cost and by category. *Weight* is specified as two alternatives: weight and weight/height. *Dmale* is a dummy variable and is equal to 1 for male and 0 for female. Since the dependent variable in this equation is a discrete variable, ordinary least squares may produce biased and inconsistent parameter estimates (Maddala 1983). Therefore, a probit model is used to estimate the parameters.

A health cost was specified similarly as in the health impairment model except for the dependent variable. The estimated health cost model is as follows:

$$\begin{aligned} Ln(Hcost)_i = {} & b_0 + b_1 * Dmale_i + b_2 * Ln(Age_i) + b_3 \\ & * Ln(Smoke_i) + b_4 * Ln(Drink_i) \\ & + b_5 * Weight_i/height_i + b_6 * Pesticide_i + b_7 \\ & * Dregion_i + e_i \end{aligned} \tag{5}$$

where *Ln(Hcost)* denotes health cost in natural log form. For those with zero cost of health, a small value (0.0001 yuan) was assigned. Model 5 was estimated by the OLS method.

Table 7. Estimates of health impairments (headaches, nausea, and skin illness) and multiple abnormalities (BUN, ALT, and CHE) of rice farmers in the sample villages.

Variables	Health impairments[a]		Multiple abnormality in rice farmers	
	Model I	Model II	Model I	Model II
Intercept	4.97	1.77	6.35	5.39
	(6.32)	(6.09)	(4.87)	(4.82)
Respondents' characteristics				
Male dummy	1.27	1.37	–0.69	4.68
	(1.07)	(1.05)	(0.26)***	(0.26)***
Ln (age)	–2.83	–2.95	–0.20	–0.19
	(1.45)**	(1.44)**	(0.27)	(0.27)
Ln (smoke)	0.02	0.02	0.003	0.003
	(0.05)	(0.05)	(0.009)	(0.010)
Ln (drink)	0.04	0.05	4.02	–0.02
	(0.07)	(0.07)	(0.01)*	(0.01)*
Ln (weight)			–1.89	–1.76
			(1.49)	(1.48)
Weight/height	7.60	7.80	7.94	7.48
	(5.86)	(5.77)	(4.64)*	(4.61)*
Chemical use (kg y^{-1})				
Ln (categories I and II)	–0.02		–0.003	
	(0.09)		(0.02)	
Ln (categories III and IV)	1.21		0.15	
	(0.53)**		(0.09)*	
Chemical cost (yuan y^{-1})				
Ln (categories I and II)		0.02		–0.002
		(0.07)		(0.016)
Ln (categories III and IV)		0.95		0.17
		(0.50)**		(0.10)*
Ln (number of applications)	–0.86	–0.15	–0.16	–0.12
	(1.16)	(1.06)	(0.23)	(0.22)
County dummy: Jiaxing	–0.63	–0.74	0.08	0.06
	(0.79)	(0.80)	(0.15)	(0.15)
c^2 (9 degrees of freedom)	16.68	14.69	16.72	16.98

[a] The numbers in parentheses are standard errors of estimates. ***, **, and * denote significance at 1%, 5%, and 10%, respectively.

Estimated results of health impairment and health cost models

The estimates of the health impairment models for equation 4 are presented in Table 7. As Table 7 shows, pesticide use significantly affected farmers' health impairments. The statistically significant and positive coefficient for category III and IV pesticides indicates that the incidence of farmers' health impairments (headaches, nausea, and skin illness) rises with the increase in pesticide use. The same result is obtained when pesticide specifications are given in either volume or value.

The insignificant coefficient for category I and II pesticides might be due to the small amount of this category of pesticide used by the farmers. It is interesting to note the significant negative coefficient for age, which is consistent with the

Table 8. Estimates of health cost of rice farmers in the sample villages.

Variables	Ln (health cost)[a]			
	Model I	Model II	Model III	Model IV
Intercept	4.02	2.92	4.48	3.19
	(4.13)	(4.11)	(4.03)	(4.10)
Respondents' characteristics				
Male dummy	0.94	1.01	0.87	0.98
	(0.68)	(0.68)	(0.68)	(0.69)
Ln (age)	-1.13	-0.85	-1.28	-1.12
	(0.90)	(0.91)	(0.89)	(0.91)
Ln (smoke)	0.02	0.02	0.02	0.02
	(0.03)	(0.03)	(0.03)	(0.03)
Ln (drink)	0.03	0.03	0.03	0.04
	(0.04)	(0.04)	(0.04)	(0.04)
Weight/height	5.59	5.23	5.14	5.28
	(3.64)	(3.57)	(3.71)	(3.71)
Ln (chemical use: kg y^{-1}):				
Ln (categories I and II)	0.06		0.04	
	(0.06)		(0.06)	
Ln (categories III and IV)	0.54		0.87	
	(0.30)*		(0.29)***	
Ln (I + II + III + IV)		0.03		0.03
		(0.01)*		(0.01)**
Ln (number of applications)	4.72	-0.34	-0.28	-0.46
	(0.74)	(0.66)	(0.65)	(0.51)
Village dummies	Estimated, but not reported			
R^2/adjusted R^2	0.24/0.15	0.23/0.15	0.18/0.10	0.13/0.06

[a] The numbers in parentheses are standard errors of estimates. ***, **, and * denote significance at 1%, 5%. and 10%, respectively.

researchers' observations during the field survey, that is, the older the farmer, the more experience in pesticide use. Using BUN, ALT, and CHE as indicators for the functions of the liver, kidney, and neurological system, respectively, the estimates of multiple abnormality models of farmer health (Table 7) confirm previous findings on the effects of category III and IV pesticides on chronic diseases of the liver and kidney.

The regression results also show that the incidence of health abnormality is higher among male farmers than females. The significant positive sign for the ratio of weight to height is contrary to expectations. More observations on BUN abnormality enabled the researchers to run a separate model on the effects of pesticide use on kidney function. The results (Huang et al 2000) confirm the expectations that category III and IV pesticides have significant effects on farmers' kidney function.

Table 8 presents the estimated parameters for farmers' health cost models based on the volume of pesticide use. The insignificant coefficients of the farmers' specific

Table 9. Health cost of pesticide use in rice production. [a]

Item	Based on pesticide use in yuan	Based on model I in Table 8	
		Original number in model is kg	Converted kg to yuan
Pesticide I + II			
Pesticide-use level	28.2	2.5	26.9
Average health cost per pesticide use (yuan yuan^{-1} or kg^{-1})	0.77	8.76	0.80
Marginal health cost (yuan per additional unit of pesticide use)	0.05	0.53	0.05
Elasticity	0.07	0.06	
Pesticide I + II			
Pesticide-use level	116.1	11.6	126.3
Average health cost per pesticide use (yuan yuan^{-1} or kg^{-1})	0.19	1.87	0.17
Marginal health cost (yuan per additional unit of pesticide use)	0.12	1.01	0.09
Elasticity	0.65	0.54	

[a] The sample mean value for health cost per farmer was 21.7 yuan and the pesticide price was 10.89 yuan kg^{-1}. The numbers for pesticide I + II were based on a statistically insignificant coefficient of pesticide (I + II) use in the health model. They are presented here for reference only.

characteristics in the model might be due to the different coverage of health costs. In the study, only the costs of health impairments that are severe and require time for the patient to recover or rest were included.[4]

Based on the parameters presented in Table 8, the farmers' health costs from pesticide use are computed at the average and marginal levels (Table 9). At the average level of pesticide use, the health cost per yuan of category III and IV pesticides is 0.19 yuan (1st column, Table 9) or 0.17 yuan (3rd column). The marginal health cost value indicates that each additional yuan of category III and IV pesticide use will cause the health cost to increase by 0.12 yuan (1st column) or 0.09 yuan (3rd column).

Conclusions

Pesticide use in grain production has more than tripled in 20 years. Among grains, rice uses pesticides the most intensively. The productivity analyses of pesticide use in rice farming based on this study indicate that, although pesticides contribute significantly to rice production by limiting yield losses, the marginal contributions of pesticide use decline considerably with the increased use of pesticides and approach

---

[4] Although slight health impairments such as headaches and those related to the eyes and skin were recorded, the medical team strongly rejected inclusion of these in the estimation of "explicit" health costs for the following two reasons: (1) inconsistent measurement among the respondents even if the interviews were conducted by the medical team and (2) difficulty in estimating the health costs of small, short-duration health impairments.

zero at the current average pesticide-use level by rice farmers. Given current rice and pesticide prices, the average overuse of pesticides by farmers is more than 40%. Our study also shows that the effect of pesticide use on farmers' health is significant. If costs related to farm health and external costs (e.g., consumer health and environmental costs that are not examined in this study) were included with the cost of purchasing pesticides, the social optimal use of pesticide in rice production could be far below half of the current level of pesticide used by farmers.

Given the above results, identifying measures for and alternatives to current agricultural chemical pesticide practices should be of critical importance in China. Our study shows that the level of farmers' pesticide applications could be reduced significantly by providing farmers with better information on the real effects of pest diseases, improving the quality of pesticides, and strengthening the local agricultural extension system. Although extending IPM technology is facing a greater challenge in small-farm-dominated agriculture and with the rise in the opportunity cost of farm labor, efforts should be continued. Last, but not least, recent developments in biotechnology are likely to be one of major avenues that could lead to substantial savings in pesticides without reducing crop yield. Our recent studies (Huang et al 2002a,b, Pray et al 2000) show that *Bt* cotton can reduce pesticide use in cotton production by more than 70% and increase cotton yields by more than 10% for a relatively modest increase in seed costs.

References

Barker R, Herdt RM, with Rose B. 1985. The rice economy of Asia. Washington, D.C. (USA): Resources for the Future with IRRI.

Huang J, Qiao F, Zhang L, Rozelle S. 2000. Farm pesticide, rice production, and human health. CCAP's Project Report 11. Chinese Academy of Sciences. A Project Report Submitted to EEPSEA, Singapore.

Huang J, Chen Q, Wang Q. 1994. Rice productivity and fertilizer balance use in China's major rice regions. J. Agrotech. Econ. 5:36-41.

Huang J, Rozelle S, Pray C, Wang Q. 2002a. Plant biotechnology in China. Science 295:674-677.

Huang J, Hu R, Rozelle S, Qiao F, Pray C. 2002b. Transgenic varieties and productivity of smallholder cotton farmers in China. Aust. J. Agric. Res. Econ. 46(3):1-21.

Lei H, Dai L, Liu L, Gu L, Xu W, Ding Y. 1998. The relationship between poison and flesh blood protein. Chinese J. Preventive Med. Volume 32, No. 3, May 1998.

Lichtenberg E, Zilberman D. 1986. The econometrics of damage control: why specification matters. Am. J. Agric. Econ. 68:261-273.

Lin JY. 1991. The household responsibility system and the adoption of hybrid rice in China. J. Dev. Econ. 36:353-373.

Ministry of Chemical Industry. n.d. China chemical yearbook. Various issues (unpublished).

Mongan DP. 1977. Recognition and management of pesticide poisonings. 2nd ed. U.S. Environmental Protection Agency, Office of Pesticide Programs, Washington, D.C.

NSBC (National Statistical Bureau of China). n.d. Statistical yearbook of China. Beijing (China): China's Statistical Publisher. Various issues.

Pimentel D, Lehman H. 1992. The pesticide question: environment, economics, and ethics. New York N.Y. (USA): Chapman and Hall.

Pingali PL, Roger PA. 1995. Impact of pesticides on farmer health and the rice environment. Boston, Mass. (USA): Kluwer Academic Publishers.

Pray C, Danmeng Ma, Huang J, Qiao F. 2001. Impact of *Bt* cotton in China. World Dev. 29:813-825.

Rola AC, Pingali PL. 1993. Pesticides, rice productivity, and farmers' health: an economic assessment. Los Baños (Philippines) and Washington. D.C. (USA): International Rice Research Institute and World Resources Institute.

Widawsky DS, Rozelle S, Jin S, Huang J. 1998. Pesticide productivity, host-plant resistance and productivity in China. Agric. Econ. 19:203-217.

Yudelman M, Ratta A, Nygaard D. 1998. Pest management and food production: looking to the future. Food, Agriculture and the Environment Discussion Paper 25. Washington, D.C. (USA): International Food Policy Research Institute.

Notes

Authors' addresses: J. Huang is professor and director of the Center for Chinese Agricultural Policy, Chinese Academy of Sciences; F. Qiao and S. Rozelle are graduate student and professor of the University of California at Davis; F. Lu is associate professor of Southeast University of China.

Acknowledgments: The authors would like to acknowledge the help, comments, and insights received from Linxiu Zhang, David Glover, Agnes Rola, Prabhu Pingali, Ruifa Hu, Herminia Francisco, Carl Pray, and Shengxiang Tang, and to thank Jun Song, Yanmei Lu, Lei Minguo, Mingming Fan, Caiping Zhang, Yuxian Lin, and Li Wang for their assistance in data collection and field surveys. Financial grants from the Economy and Environment Program for Southeast Asia (EEPSEA) and China National Natural Sciences Foundation (79800026 and 79725001) are greatly appreciated.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

IPM in cotton: lessons from rice IPM

P.A.C. Ooi

Successes in implementing integrated pest management (IPM) in rice suggested that a similar success could be achieved in cotton. There are many similarities, such as a similar starting point of insecticide-induced resurgence and an indigenous plant with native pests and natural enemies, small farm sizes, poor farmers with limited resources, and a tropical environment rich in biodiversity. In rice, the breakthrough in IPM implementation was the development of a farmer field school (FFS) approach. The focus moved from a transfer of technology to farmer education. This avoided the pitfall observed in a topdown approach- a lack of understanding what to do. The FFS approach allowed farmers to learn science, facilitated a scientific method of acquiring knowledge, and improved the ability to make decisions.

That pesticides are not a production factor should be an entry point and encourage the study of the rich biodiversity of the tropical cotton ecosystem. A second point concerns providing an opportunity for farmers to learn and achieve greater control over the conditions they face at the field level.

Based on lessons learned from rice IPM, the management team of the FAO-EU IPM Programme for Cotton in Asia embarked on a participatory farmer field school approach to implement cotton IPM. In 2001, studies of Bt cotton by farmers in the province of Hubei, China, suggested that IPM helped them to better realize the potential that science and technology can offer.

Impetus for developing integrated pest management (IPM) came from successes achieved in cotton in the Cañete Valley of Peru in the 1950s. However, cotton production in Asia did not benefit from this achievement. In many Asian countries where cotton is produced, producers continued to rely on chemical insecticides, with devastating results. In India, up to 50% of all insecticides used in the country ended up on cotton. In some countries, up to 65% of the cost of production of cotton was chemical control. This inefficient production system led to many outbreaks with health and economic consequences. Indeed, such inefficient cotton production had led to a sharp decline in production in the Philippines and Thailand.

With the threat of a decline in cotton production in major cotton producers such as China, India, and Pakistan, policymakers looked toward the achievements of IPM in rice for inspiration. Many similarities exist between rice and cotton. For instance, rice production was once threatened by irrational dependence on chemical pesticides. Ecological studies (Kenmore et al 1984, Ooi 1988, Gallagher et al 2002) showed that chemical insecticides killed natural enemies that kept insect pests in check. This resurgence was halted by teaching farmers to recognize biological control and conserve natural enemies. This same entry point exists in cotton. Other similarities included the indigenous nature of the plant in Asia with corresponding indigenous herbivores, small farm size, poor farmers with limited resources, and a tropical environment rich in biodiversity. The farmer field school (FFS) approach pioneered in rice appeared equally suitable for cotton farmers who work on small farms.

This paper examines the achievements made in educating rice farmers and how this applies to a cotton ecosystem. Indeed, it provides an opportunity to examine progress in the farmer education process when it is transferred to cotton.

Achievements of rice IPM

When the FAO Intercountry Integrated Pest Control Programme began in 1980, it started with a traditional mixture of different components. It was only in the 1990s that a participatory learning method with groups of farmers evolved, initially in Indonesia and then elsewhere. However, Matteson et al (1994) pointed out that learning in a group using conventional teaching methods with field demonstrations and class experiments was reported earlier by Goodell et al (1981). A focus on understanding rather than following instructions or adopting a package was basically still little understood then. The approach to farmer education that has been named the rice IPM farmer field school (FFS) was built on lessons from the Philippines' experience in farmer IPM training (Pontius et al 2002). Further information on the implementation of the FFS may be obtained from Roling and van der Fliert (1994), Schmidt et al (1997), and ter Weel and van der Wulp (1999). The FFS is a season-long learning session attended by 25 to 30 farmers (Dilts and Pontius 2000). These FFSs are organized by PM facilitators, who are often graduates from the season-long training of facilitators (ToF) program.

The FFS approach is based on four IPM principles. These principles guide farmers on what to do when they participate in an FFS. They are (1) grow a healthy crop, (2) conserve natural enemies, (3) conduct regular field observations, and (4) become IPM experts.

Over the last 10 years, this participatory approach has challenged the stereotyping of farmers, and in particular rice farmers. The success of this empowerment process is reflected in Table 1. The five former heresies associated with educating farmers were broken down over the years, but resistance toward this approach continued despite evidence by Ooi (1998, 2000) and Ooi et al (2001). A top-down process

Table 1. Emerging above the heresies surrounding the capabilities of rice farmers (adapted from Pontius et al 2002).

Former heresies	Accomplishments
Farmers as experts	Few believed that farmers could identify pests and natural enemies and, based on an understanding of field ecology, could decide whether biological control was working. A quality indicator for the farmer field school (FFS) is that farmers can explain why they avoid calendar spraying.
Farmers as IPM trainers	In many countries, graduates of the FFS have demonstrated that they are good IPM facilitators. This approach has encouraged many donors to urge national programs to focus on this as a sustainable development.
Farmers as scientists	Farmer field research is now a common goal of the FFS in many countries. The curiosity initiated in the FFS has encouraged farmers to produce new knowledge and enhance their skills in conducting field research.
Farmers as organizers, planners, advocates, and activists	That farmers can organize meetings to share their knowledge from farmer field research, plan area-wide campaigns, and press for district-level support for their activities confirms that indeed farmers can be good organizers. (See Warsiyah et al 1999.)
Farmers as policymakers	With confidence that they are experts, capable of being IPM facilitators, can undertake scientific studies, and can organize themselves, the next step involves farmers becoming policymakers. In Indonesia, many IPM farmer-leaders have taken up leadership in district politics to bring about changes.

developed in the 1950s treated farmers as passive recipients of technology developed by research institutions. This “telling farmers what to do” assumed that farmers were able to comprehend the recommendations without being educated.

Hence, it was not surprising that rice farmers did not recognize the rich diversity of natural enemies in their fields. They were not taught that spiders were natural enemies of rice pests and it was common for farmers to assume that all arthropods in the rice fields were pests. Perhaps it was this lack of knowledge of natural enemies that led to the widespread use of chemical insecticides, resulting in the outbreaks of the rice brown planthopper in tropical Asia in the 1970s. Farmer field schools teach farmers the skills of studying arthropods to determine whether these are natural enemies or pests. With this skill, rice farmers in Thailand were able to increase their knowledge of beneficial organisms (Table 2). A consequence of this combination of skills and knowledge resulted in the decline in the use of chemical insecticides in rice fields (Table 3). These simultaneous developments led to a more efficient production system as a result of farmer education.

After ten years of implementing IPM using the FFS approach, experiences accumulated were analyzed. Dilts and Pontius (2000) summarized these experiences

Table 2. Knowledge about beneficial organisms in rice before and after the farmer field school (FFS) event (after Praneetvatakul and Walbel 2002).

Items	Means of no. of types of beneficial insects[a]		t-test
	Before	After	
Assessment of FFS farmers	1.73	2.28	–3.46***
Assessment of non-FFS farmers	1.12	0.91	1.49 ns
Assessment of control group of farmers	1.24	1.12	0.82 ns
F-test	6.61***	34.88***	

[a] ns = no significant difference, *** = significant at 99%.

Table 3. Summary of use of insecticides in rice before and after the farmer field school (FFS) event (adapted from Praneetvatakul and Waibel 2002).

Items	Means of cost of insecticide use (bath rai^{-1})		t-test
	Before	After	
Report by FFS farmers	41.2	17.3	3.45***
Report by non-FFS farmers	50.3	49.8	0.06 ns
Report by control group of farmers	31.7	28.4	0.59 ns
F-test	0.78 ns	7.11***	

[a] ns = no significant difference, *** = significant at 99%.

from Indonesia as lessons learned (Table 4). These are the lessons that are brought into cotton IPM.

IPM in cotton

The FAO-EU IPM Programme for Cotton in Asia was established in late 1999. The program worked in six countries: Bangladesh, China, India, Pakistan, the Philippines, and Vietnam. Like rice, cotton is a plant indigenous to Asia. The small farms operated by resource-poor farmers are also similar to those found in rice. A common entry point for IPM is the inefficient production caused by reliance on chemical insecticides. Indeed, the overuse of chemical insecticides helped reduce the area under cotton in the Philippines from 35,000 ha in the early 1990s to 1,000 ha in 2000. As in rice, cotton farmers complained that the more they sprayed, the more worms they found in their crop. Based on the lessons learned from implementing rice IPM, the program embarked on a training of IPM facilitators and focused on farmer education that built up skills to seek knowledge so that these farmers could become better decision makers.

Table 4. Lessons learned in implementing a participatory rice IPM using farmer field schools (FFS) in Indonesia (after DIlts and Pontius 2000).

1. **Have values and be clear about these values.** This provides farmers with an opportunity to learn and achieve greater control over the conditions they face at the field level-empowerment is the value that influenced the design and implementation of IPM activities. Why empowerment? Farmers live and work in a world where they face a variety of contending forces, including those related to technology, politics, markets, and society.
2. **Farmers can train other farmers.** This approach is easily replicable. The FFS approach allows farmers to master learning methods that are reinforced during an FFS. These require commitment and good process skills and leadership training during farmer IPM trainers' meetings, more technical workshops are needed to upgrade skills, and management and technical support are important.
3. **Farmers are effective organizers.** Farmer IPM trainers and IPM alumni are an effective "core cadre" for farmer-led community IPM programs. Farmers organize IPM activities with the support of local government. Farmers learn critical thinking skills in the FFS, thus helping them in problem analysis.
4. **Farmers can do science.** Indeed, as alumni, farmers conduct their own field research, thus helping to increase their understanding of the ecology of the agroecosystems. There is a need to strengthen their ability to better design and analyze results.
5. **Farmers can bring about policy change.** Well-organized FFS alumni who understand ecology, think critically, and possess the relevant facts can change local policies. Having the facts at hand and with a clear presentation of these facts, farmers have been able to successfully change local policy.
6. **There is a spread effect.** IPM-trained farmers talk to other farmers and farmer IPM trainers organize activities to help other farmers learn about IPM.
7. **Intensity of activities is important.** This includes the number of FFSs conducted in a village as well as follow-up activities, such as a support group for IPM-trained farmers. The more FFSs in a location, the greater the likelihood that there will be more farmer IPM trainers in that location.
8. **Pesticides are not a production factor.** In tropical rice production in particular, not using pesticides coupled with using good agronomic practices increases the likelihood of higher yields. Insecticides cause pest outbreaks. The risk of pest outbreaks increases with every application of insecticide.
9. **Field schools are cost-effective.** The cost per farmer trained in a rice FFS is US$10, and farmer-funded FFSs are much less expensive than those funded by the national program.
10. **Follow-up activities for farmers are an obligation.** These activities will help farmers increase their understanding of field ecology as well as organize their own local IPM programs.

The crop may be different but many of the natural enemy groups are similar to those found in rice. Farmers were able to go to the field, observe the condition of the cotton plants, collect information on the population of arthropods, and return to their classroom to prepare a cotton ecosystem analysis (CESA). As in rice, the cotton field is the laboratory for learning. Twenty-five to 30 farmers gather weekly to learn and practice how to use field information to make decisions. Results from selected FFSs in the 2001-02 season in all six countries are summarized in Figure 1. The net returns from IPM tend to be higher and this has encouraged farmers to have confidence in their ability to make decisions.

As in rice, the program management team encouraged follow-up activities. One such activity was the evaluation of *Bt* cotton in China. As in rape, soybean, and maize, toxin genes from the bacterium *Bacillus thuringiensis* (*Bt*) were engineered

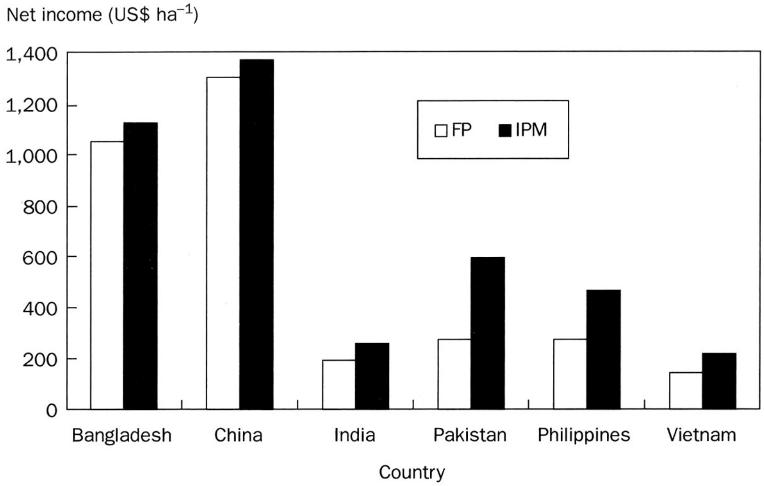


Fig. 1. Comparison of net income from fields managed using an IPM approach (IPM) and those managed without IPM (FP) from selected villages in the six countries making up the FAO-EU IPM Programme for Cotton in Asia. The villages are as follows: Arpara (Bangladesh), Xlao Sun (China), Mummadi (India), Tarah (Pakistan), Candon City (Philippines), and Thua Dua (Vietnam).

into cotton plants. This was quickly adopted by cotton farmers as this promised a way out of the pesticide treadmill that burdened their production. The program decided that since *Bt* cotton was so widespread in China, the program would initiate farmer field research. In past studies, *Bt* cotton was compared only with the farmers' practice. IPM as an option was not studied. The net returns from three treatments were studied (i.e., fields managed by farmers with IPM education [IPM], fields managed by farmers without IPM education [FP], and fields cultivated without any pesticide inputs [BD, or biodiversity plots]). An analysis of these net returns from Xiantao City, Hubei Province, showed that IPM education, by increasing farmers' capacity to critically evaluate inputs and their effects, and by reducing nonbollworm pesticide use, has the potential to help farmers maximize the value of *Bt* cotton (Fig. 2). This experience may apply equally well for rice when transgenic rice is introduced. It may help avoid a reoccurrence of the debacle associated with the development of chemical pesticides as a technological breakthrough for pest control in the 1950s.

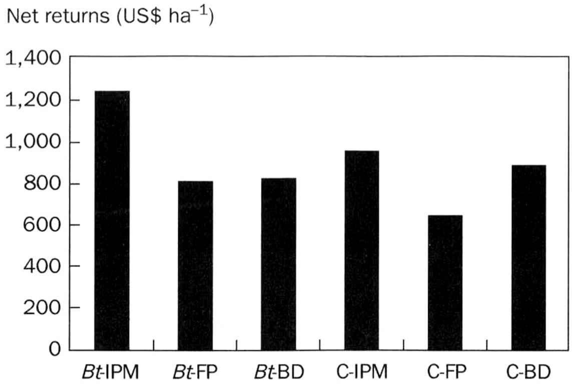


Fig. 2. Net returns from a farmer field research in Xiantao, Hubei, in 2001 under three conditions with both *Bt* cotton (*Bt*) and non-*Bt* cotton (C). The three conditions are as follows: (1) fields managed by farmers with IPM education (IPM), (2) fields managed by farmers without IPM education (FP), and (3) fields cultivated without any pesticide inputs (biodiversity plot, or BD).

References

Dilts R, Pontius J. 2000. IPM and farmer-led development: lessons from Indonesia. In: Ooi ACP, editor. Farmer-led integrated pest management. Tokyo (Japan): Asian Productivity Organization. p 34-42.

Gallagher KD, Ooi PAC, Mew TW, Borromeo E, Kenmore PE. 2002. Integrated pest management in rice. Int. Rice Comm. Newsl. 51:9-23.

Goodell GE, Litsinger JA, Kenmore PE, 1981. Evaluating integrated pest management technology through interdisciplinary research at the farmer level. In: Proceedings of the Conference on Future Trends of Integrated Pest Management, Bellagio, 30 May-4 June 1980. IOBC Special Issue/Centre for Overseas Pest Research, London, UK. p 72-75.

Kenmore PE, Carino FO, Perez CA, Dyke VA. 1984. Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stal) within rice fields in the Philippines. J. Plant Prot. Trop. 1:19-37.

Maneson PC, Gallagher KD, Kenmore PE. 1994. Extension of integrated pest management for planthoppers in Asian irrigated rice: empowering the user. In: Denno RF, Perfect TJ, editors. Ecology and management of planthoppers. London (UK): Chapman and Hall. p 656-685.

Ooi PAC. 1988. Ecology and surveillance of *Nilaparvata lugens* (Stal): implications for its management in Malaysia. Ph.D. thesis. University of Malaya, Kuala Lumpur, Malaysia. 275 p.

Ooi PAC. 1998. Beyond the farmer field school: IPM and empowerment in Indonesia. Gatekeeper Series No. 78. London (UK): International Institute for Environment and Development. 13 p.

Ooi PAC. 2000. From passive observer to pest management experts: science education and farmers. In: Guijt I, Berdegue JA, Loevinsohn M, Hall F, editors. Deepening the basis of rural resource management. Proceedings of a Workshop, RIMISP and ISNAR. p 167-178.

Ooi PAC, Warsiyah, Nanang Budiyanto, Nguyen Van Son. 2001. Farmer scientists in IPM: a case of technology diffusion. In: Mew TW, Borromeo E, Hardy B, editors. Exploiting biodiversity for sustainable pest management. Los Baños (Philippines): International Rice Research Institute. p 207-215.

Pontius J, Dilts R, Bartlett A, editors. 2002. Ten years of IPM training in Asia from farmer field school to community IPM. Food and Agriculture Organization of the United Nations, Regional Office for Asia and the Pacific, Bangkok, Thailand. 106 p.

Praneetvatakul S, Waibel H. 2002 A socio-economic analysis of farmer field school (FFS) implemented by the National Program on Integrated Pest Management of Thailand. Paper presented at the CIMMYT impact assessment conference, 4-7 February 2002, San José, Costa Rica.

Roling N, van der Fliert E. 1994. Transforming extension for sustainable agriculture: the case of integrated pest management in rice in Indonesia. Agric. Human Values 11:96-108.

Schmidt P, Stiefel J, Hurlimann M. 1997. Extension of complex issues: success factors in integrated pest management. Lindau (Switzerland): Swiss Center for Agricultural Extension. 100 p.

ter Weel P, van der Wulp H. 1999. Participatory integrated pest management: policy and best practice. Document No. 3. The Hague (Netherlands): Netherlands Ministry of Foreign Affairs, Development Cooperation. 67 p.

Warsiyah, Sobarih, Wahyudin, Yusuf H, Arif Lukman Hakim, Sukara, Madamin, Busyairi MA, Warum, Sumarjo. 1999. Membangun Pengetahuan Emansipatoris. Kasus Riset Aksi Petani di Indramayu. Studi Kehidupan dan Gerakan Pengendalian Hama Penggerek Batang Padi Putih. Jakarta (Indonesia): Lakpesdam NU. 191 p. (In Indonesian.)

Notes

Author's address: FAO-EU IPM Programme for Cotton in Asia, c/o FAO Regional Office, Phra Atit Road, Bangkok 10200, Thailand. Email: Peter.Ooi@fao.org.

Acknowledgments: The author is grateful to the organizers of the conference, especially to Professor Piao Yongfan and Dr. Peter E. Kenmore, for the kind invitation to share the progress with a participatory approach developed in rice that has been transferred to cotton. The encouragement of Dr. Tom Mew has been an inspiration to the author to believe that good researchers are finding out that the participatory approach of the FFS provides an improved way to diffuse research findings to farmers.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Economic impact of integrated pest management

B.H. Lee

Integrated pest management (IPM) training was assessed through comparison trials of IPM and the farmers' practice on rice from 1996 to 1998. The results of IPM validation studies show that the number of pesticides sprayed can be reduced by 34% to 54% without significant changes in yield. The number of applications and the amount of active ingredients of pesticide were also reduced. The comparison of returns, receipts, and operation costs showed that there were no significant differences because of the savings in pesticide, a result from not mixing unnecessary pesticides at some crop stage. According to the production efficiency analyzed by the nonparametric efficiency analysis model, the efficiency scores of IPM plots were higher, respectively, than those of the farmers' practice plots: 0.5824 vs 0.4192 in 1996, 0.5558 vs 0.5195 in 1997, and 0.6961 vs 0.6281 in 1998. Although IPM implementation by the field-oriented approach was very effective in improving plant protection practices and production efficiency, several constraints must also be examined.

Since the concept and practice of integrated pest management (IPM) first appeared in the 1950s and '60s, IPM has been acknowledged worldwide as the best practice for managing crop pests and diseases to reduce input costs and increase yields. IPM has expanded to all plant protection principles and is now established as the main focus of pest management (Barfield and Swisher 1994, Kogan 1998). Current IPM programs are designed to improve economic, social, and environmental conditions and replace pesticides, fertilizers, and other off-farm inputs with improved management skills.

Economic evaluations of IPM programs have been in progress for more than 30 years and the methods of analysis and subjects have expanded from emphasis on simple budget analyses of IPM and non-IPM to the assessment of pesticide risk reduction, and to aggregate evaluations of social impacts of IPM programs on producers and consumers, including environmental benefits (Norton and Mullen 1994). Various methods to analyze the costs and benefits of pest management and pesticide use were attempted to support pesticide risk reduction. However, relatively little empirical work regarding on-farm training that attempts to estimate the economic benefits of an IPM program has been completed.

The purpose of this paper is to illustrate the effects of IPM on pesticide use on rice and to quantify the economic impact of IPM practices. Constraints and possible solutions are also discussed.

The IPM program: extension and farmer education

From 1993 to February 2000, the IPM Program in Korea was developed in collaboration with the United Nations Development Programme (UNDP), Ministry of Science and Technology (MOST), and Rural Development Administration (RDA). The project aimed to transform the existing pest control system by using field extension staff members responsible for plant protection at the City/County Agricultural Development and Technology Centers (ADTCs) to disseminate relevant IPM methods during farmers' training. This attempt was agreed upon to build an IPM program based on Korean and regional research using the new field training methods emerging from the FAO Intercountry Program for Integrated Pest Control in Rice in South and Southeast Asia (Gallagher 1995).

To achieve an effective orientation program, field staff members were required to participate in extensive field training, called training of trainers (TOT). The training involved agronomic practices; main disease symptoms and development; detritivore, herbivore, and natural enemy recognition and population dynamics; pest control methods (cultural, biological, and chemical); pesticide effects on the ecosystem and health; weed management; decision-making using agroecosystem analysis methods; training methods for farmers; and group dynamic exercises.

Usually, all topics were explored during each crop stage through field experiments, field observation and analysis, discussion, and presentation by resource persons.

Graduates of TOT set up season-long farmer field meetings (FFMs) based on a highly modified version of farmer field schools (FFS) implemented in other FAO Intercountry Program countries. The FFMs consisted of approximately 25 farmers, a trainer, and training fields. The chosen training fields were the same throughout the season and allowed a subset of the TOT activities and included defoliation and detillering experiments, agroecosystem analysis, and experiential learning activities on predation, pesticide effects, and pest population dynamics. The decision-making during each critical crop stage (roughly monthly) was followed by the discussion of FFMs based on intensive field practice. IPM fields were observed regularly to determine plant production and protection needs. No economic thresholds were used; rather, the potential for insect pest development was determined by assessing current field levels in relation to weather and natural enemies present in the field. Disease assessment in IPM fields considered weather and crop development stage. Herbicides were used in IPM on the basis of conventional practices. In conventional treatments, the local recommendations used were based on crop stage and weather forecasting.

Effects of IPM implementation

To validate IPM methods, an assessment was carried out in 79 cities/counties in 1996, 66 cities/counties in 1997, and 25 cities/counties in 1998. Each site consisted of one IPM plot and one farmers' conventional plot. Each plot was 0.1 ha. The trials were carried out in farmers' fields and were supervised by the extension staff.

Effects of pesticide use

Typical results indicated that pesticide use (including the number of pesticides sprayed and the number of applications) was reduced with no significant difference in rice yield. The number of pesticides sprayed decreased by 54.4% in 1996 (58.0% of fungicide and 62.1 % of insecticide), 44.8% in 1997 (57.1 % of fungicide and 43.3% of insecticide), and 33.7% in 1998 (46.2% of fungicide and 45.9% of insecticide). The reduction in applications increased from 35% to 49% (Fig. 1).

The active ingredient (ai) of pesticides also decreased by 40.4% in 1996 (45.5% of fungicide and 52.1% of insecticide), 36.5% in 1997 (46.8% of fungicide and 45.1% of insecticide), and 27.5% in 1998 (21.0% of fungicide and 39.6% of insecticide). Herbicide use decreased slightly by 5.7% to 19.3% (Fig. 2). The total amount of pesticides and the total number of sprays decreased because IPM methods do not allow for mixing of pesticides during application, unlike the conventional recommendation, which suggests mixing during each spray for "preventive" control.

Economic evaluation

Receipts, production costs, and net returns between IPM plots and farmers' conventional plots are compared in Table 1. The net returns have no significant differences between IPM plots and farmers' conventional plots. However, the cost of pesticides decreased in IPM plots, while the costs of fertilizer and other inputs increased. It seems that anxiety about income loss allowed for IPM-trained farmers to use more fertilizer (Lee 1999). However, Kim et al (1985) showed that increasing nitrogen input increases the levels of disease in the rice field because weather conditions are conducive to epidemics. Nitrogen is also known to slightly promote the growth rates of some planthoppers (Uhm et al 1985). Furthermore, studies on fungicides have shown that some common fungicides and insecticides are active against natural enemies (Yoo et al 1984). Thus, nitrogen causing higher pathogen development can lead to natural enemy mortality because of increased fungicide applications.

Production efficiency

To compare the production efficiency of IPM plots with that of farmers' conventional plots, a nonparametric efficiency analysis model belonging to the data envelopment analysis (DEA) model, developed by Banker et al (1984) and Fare et al (1985), was

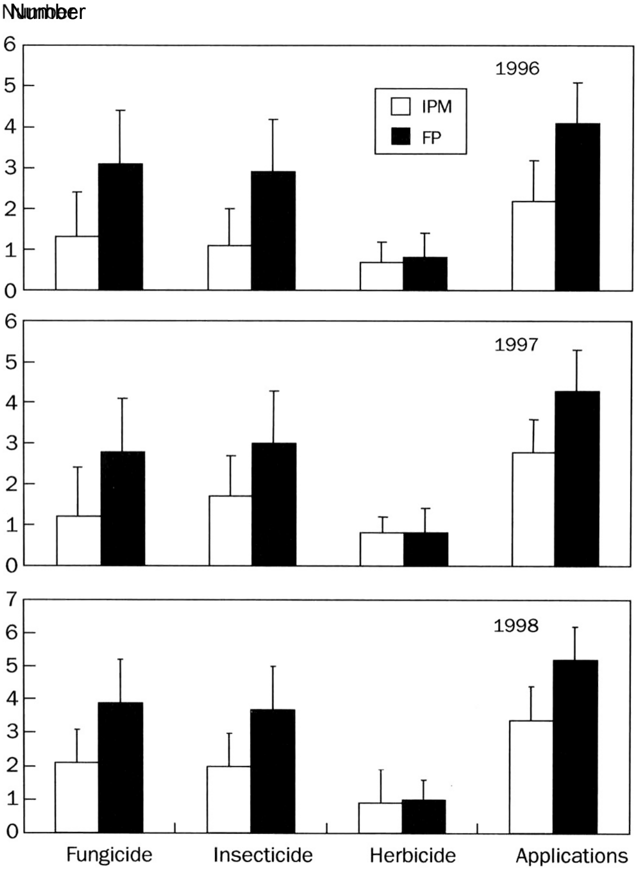


Fig. 1. Number of pesticides sprayed and applications in 1996-98 (= $P < 0.01$, * = $P < 0.05$).**

employed. The nonparametric model used for this study has the advantage of analyzing the production technology without imposing any functional specifications on the production frontier (Kwon 1998, An 1998).

For the nonparametric efficiency analysis model, define $x \in R_+^N$ as the input vector used by a farmer to produce rice yield $y \in R_+$. The production technology can be represented by the following input requirement set $V(y)$:

$$V(y) = \{x \in R_+^N : y \text{ can be produced with } x\} \qquad (1)$$

V(y), which is a subset of R_+^N, is a set of inputs that are required to produce a certain level of rice output y. V(y) does not include 0 for any positive y and is a closed

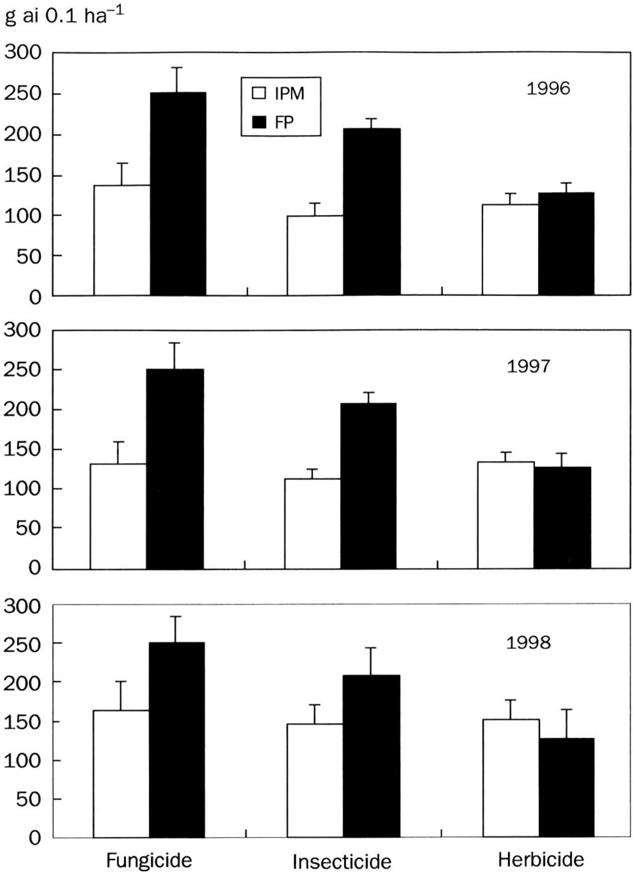


Fig. 2. Pesticide use (g ai 0.1 ha^{-1}) in 1996-98 (= P<0.01, * = p<0.05). IPM = integrated pest management, FP = farmers' practice.**

set. A nonparametric production model constructs the set $V(y)$ with an observed data set of input and output and analyzes the characteristics of the farmer's production technology on the basis of the constructed set. In an actual analysis, some assumptions on technology need to be employed, and the constructed set of $V(y)$ depends on those assumptions. First, free disposability of inputs and outputs is assumed, that is, if a certain level of output can be produced with a given input, then it is possible to produce any level of output lower than that with the same input. In addition, if a certain level of output can be produced with a given input, then this level of output can always be produced when more input is used.

If we suppose there are I farmers in the economy, under the assumption of the variable returns to scale (VRS), no restrictions on returns to scale are imposed. The

Table 1. Descriptive statistics. Values are in Korean won (US$1 = 1,200 won).

Year/variable	Method [a]	Mean ± SD	Min.	Max.
1996				
Receipts	IPM	824,718 ± 142,195	562,470	1,355,750
	FC	830,056 ± 107,000	586,470	1,150,000
Pesticide costs	IPM	12,026 ± 8,080	0	40,000
	FC	23,783 ± 15,969	4,100	75,000
Fertilizer costs	IPM	37,740 ± 29,063	8,500	180,000
	FC	33,025 ± 21,281	1,150	128,200
Other costs	IPM	103,174 ± 63,451	19,500	292,000
	FC	114,607 ± 95,128	20,045	767,500
1997				
Receipts	IPM	875,949 ± 127,127	660,956	1,247,100
	FC	888,395 ± 113,850	683,922	1,260,800
Pesticide costs	IPM	15,059 ± 7,023	2,800	39,000
	FC	24,166 ± 10,178	4,500	54,000
Fertilizer costs	IPM	38,869 ± 42,113	9,800	260,000
	FC	33,001 ± 34,599	9,290	222,000
Other costs	IPM	125,161 ± 61,071	23,820	341,466
	FC	131,639 ± 62,450	30,120	371,376
1998				
Receipts	IPM	921,148 ± 100,279	652,500	1,194,500
	FC	942,148 ± 96,532	702,500	1,194,500
Pesticide costs	IPM	19,584 ± 8,751	6,500	36,000
	FC	30,121 ± 15,636	14,000	93,000
Fertilizer costs	IPM	47,864 ± 44,795	11,825	169,430
	FC	37,735 ± 35,542	12,300	169,430
Other costs	IPM	158,559 ± 78,689	8,154	411,070
	FC	158,981 ± 83,901	8,154	413,290

[a] IPM = integrated pest management, FC = farmers' conventional practices.

input requirement set $V(y)$ can be approximated by the following set, $\hat{V}(y)^{v}$ which is constructed with each farmer's input and output data:

$$\hat{V}(y)^{v} = \{x : x \geq \sum_{i=0}^{I} \lambda_i x_i \,,\, y \leq \sum_{i=1}^{I} \lambda_i y_i \,,\, \lambda_i \in \mathrm{R}+, \sum_{i=1}^{I} \lambda_i = 1\} \qquad (2)$$

where x_i is the production input of the i th farmer while y_i is his rice output, 1_i is a nonnegative scalar, and $\{1_i\}$ is an intensity vector that allows for $\hat{V}(y)^{v}$ to approximate $V(y)$ by increasing or decreasing the input and output of each farmer. Suppose that a convex combination of some farmer's output levels is greater than or equal to y. Then, the definition in 2 implies that the input requirement set $\hat{V}(y)^{v}$ is the set of inputs that are greater than or equal to the convex combination of those farmers' inputs. The set $\hat{V}(y)^{v}$ contains all the properties of $V(y)$.

The input requirement sets, which correspond to the aforementioned production technologies, are produced by solving the following linear or mixed-integer programming problem for each farmer:

$$S(y_i, x_i)^{v} = \min_{\tau \succ 0, \{\lambda_i\}} \{\tau : \tau x_i \in \hat{V}(y)^{v}\} \qquad (3)$$

By solving the problem, it can be figured out where each farmer is located in the input requirement set. $S(y_i,x_i)^v$ is the ratio of the ith farmer's minimum input required to produce yi to his actual input usage under the assumption of VRS. Hence, $S(y_i,x_i)^v$ lies between 0 and 1. The ith farmer is located on the frontier of $\hat{V}(y)^v$ if the value of $S(y_i,x_i)^v$ is equal to 1, whereas he is located inside of the set when the value of $S(y_i,x_i)^v$ is less than 1. The ith farmer is regarded as efficient (inefficient) when the value of $S(y_i,C_i)^v$ is equal to (less than) 1. Therefore, both technical efficiency and scale in efficiency of each farmer can be investigated by calculating his efficiency scores. The size of the efficiency score calculated by model 3 represents the degree of technical inefficiency of each farmer. However, no restrictions on returns to scale are imposed by $\hat{V}(y)^v$, which may exhibit constant, increasing, or decreasing returns to scale.

Define another set of $\hat{V}(y)^C$, which is constructed by removing the constraint $\sum_{i=1}^{I}\lambda_i = 1$ from $\hat{V}(y)^v$:

$$\hat{V}(y)^C = \{x : x \geq \sum_{i=0}^{I}\lambda_i x_i, y \leq \sum_{i=1}^{I}\lambda_i y_i, \lambda_i \in R+\} \tag{4}$$

The production technology represented by $\hat{V}(y)^c$ exhibits constant returns to scale (CRS). Then, the input requirement sets that correspond to the CRS production technologies are produced by solving the following linear or mixed-integer programming problem for each farmer:

$$S(y_i, x_i)^C = \min_{\tau > 0, \{\lambda_i\}} \{\tau : \tau x_i \in \hat{V}(y)^C\} \tag{5}$$

The solution to this problem, λ_i, lies between 0 and 1 as in the case of VRS. The same interpretations are given to the $S(y_i,x_i)^c$ calculated by 5 as well.

Since the input and output data of rice production from IPM validation plots and farmers' conventional plots were measured as 0.1 ha instead of total cultivated area, the production technology should be assumed as CRS. Thus, in this study, the efficiency score was measured by 5. The production technology was analyzed using only the data of three kinds of production costs (pesticide cost, fertilizer cost, and other cost) and output of 340 plots, which consisted of 170 IPM plots (79 in 1996, 66 in 1997, and 25 in 1998) and 170 farmers' conventional plots (79 in 1996, 66 in 1997, and 25 in 1998).

Comparison of efficiency scores

According to production efficiency analysis, IPM plots scored 0.5824 and farmers' conventional plots scored 0.4192 in 1996. The differences in scores showed a similar tendency in 1997 and 1998 (Table 2). This meant that the IPM method is more efficient than the farmers' conventional method.

Table 2. Production efficiency.

Year	Method[a]	Mean of efficiency score
1996	IPM	0.5824**[b]
	FC	0.4192
	Total	0.5008
1997	IPM	0.5558*[b]
	FC	0.5195
	Total	0.5377
1998	IPM	0.6961*[b]
	FC	0.6281
	Total	0.6621

[a] IPM = integrated pest management, FC = farmers' conventional practices. [b] * = $P<0.05$, ** = $P<0.01$.

Discussion

The results of validation trials showed that the IPM method can reduce pesticide use without significant differences in yield and net returns. However, all data collected for rice cultivation in Korea indicate that the current conventional level of pesticide use and government recommendations for pesticide use are about twice what is necessary to maintain yields. Pesticide use presently amounts to 9,103 metric t ai per year and the area treated with some type of pesticide reaches 9.9 times the total planted area. On a national scale, rice yield has reached a production maximum since the 1980s, but pesticide cost and use have continued to grow. In other words, production with respect to pesticides has become less efficient and more polluting in recent years. Pesticide use and costs continued to increase from the 1980s to now even though average yields remained relatively steady (Fig. 3). Therefore, the verification trials show that the IPM method plays an important role in reducing the reliance on chemical pesticides and in preventing pest problems through better crop management.

The figures derived from the economic evaluation of IPM benefits would not be useful to farmers for adopting IPM. This is because the cost of pesticides is relatively small in proportion to production costs. Immediate economic effects on farmers will not be sufficient to capture the true impact of IPM.

In most countries, the results of research are transferred to farmers by the extension or advisory service. In Korea, IPM research has been undertaken since the 1970s to understand the basic ecological relationships of weeds, insect pests, and diseases in most crops. At the same time, the national forecasting system and other extension activities were developed to lessen the likelihood of crop failure and large-scale pest outbreaks. Although these programs have been effective, in many cases, an overdependence on pesticides has been practiced continuously and has resulted in an overuse of pesticides on a calendar basis by farmers (Hyun 1978).

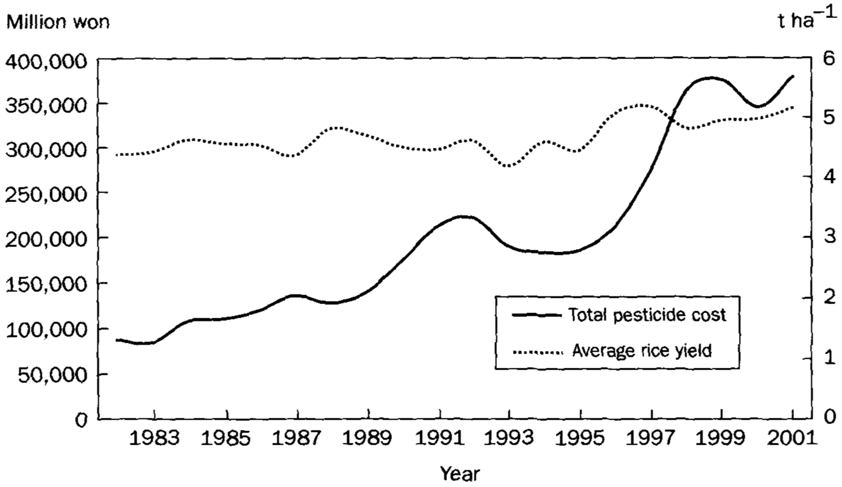


Fig. 3. Total pesticide cost and average rice yield in Korea from 1982 to 2001.

The results also indicated that the training for farmers and extension personnel was an important strategy for implementing IPM in the field. The FFM usually meet four times in a season, with each meeting conducted at a critical point in the crop cycle. By the end of the farmers' training, most farmers were able to make an appropriate management decision based on their field's situation by merely observing their field for a few minutes. This is a major move away from conventional calendar sprays that often mix several pesticide compounds in one application.

Since IPM requires higher quality training for both extension officers and farmers than most existing extension systems (Kenmore et al 1987), IPM training should continue to reach more farmers and be applied to more crops. There is strong interest in doing IPM and in developing farmer field-based training to improve plant production and protection skills of farmers. Therefore, it could be possible to reduce pesticide use by 30% by 2005, which was announced by the Ministry of Agriculture and Forestry (MAF) as the "Sustainable Agriculture Promotion Act" in 1997. However, farmers who received IPM training indicated a reluctance to adopt IPM because of their anxiety about income loss and difficulty in shifting their way of thinking and in selecting safe pesticides (Lee 1999). Thus, a reevaluation of the role of extension agencies and the broadcasting system and stressing the importance of pesticide management have been strongly recommended. When farmers implement IPM, negative environmental and health effects will be reduced while profits will be increased. The key to better IPM is better farming by farmers who are empowered with the knowledge to manage their own ecosystem in ways that benefit themselves and society as a whole (Matteson et al 1994). Public concern intensified over the effects on the environment and human health of pesticide use and the return on public investments in general, and attempts to quantify and qualify the economic consequences of IPM practices expanded to include environmental and social benefits (Norton and Mullen 1994, Hermann et al 1999). Such an evaluation will help to determine the effectiveness and long-term viability of IPM.

References

An DH. 1998. An analysis of productivity change in Korean rice farms: decomposition of productivity change into efficiency and technical changes. PhD dissertation. Seoul National University. 151 p. (In Korean with English abstract.)

Banker RD, Charners A, Cooper WW. 1984. Some models for estimating technical and scale inefficiencies in data envelopment analysis. Manage. Sci. 30(9):1078-1092.

Barfeld CS, Swisher ME. 1994. Integrated pest management: ready for export? Historical context and internationalization of IPM. Food Rev. Int. 10(2):215-267.

Färe RS, Grosskopf S, Lovell CAK. 1985. The measurement of efficiency of production. Boston, Mass. (USA): Kluwer-Nijhoff Publishing.

Gallagher KD. 1995. Lessons learned and new concepts for farmer IPM training from the FAO inter-country IPM program. Korean J. Appl. Entomol. 34:15-19.

Hermann W, Fleischer G, Kenmore PE, Feder G. 1999. Evaluation of IPM programs: concepts and methodologies. Paper presented at the First Workshop on Evaluation of IPM Programs, 16-18 March 1998. Hannover, Germany. 67 p.

Hyun JS. 1978. An urgent problem and prospect of plant protection. Korean J. Plant Prot. 17(4):201-215. (In Korean.)

Kenmore PE, Litsinger JA, Bandong JP, Santiago AC, Salac MM. 1987. Philippine rice farmers and insecticides: thirty years of growing dependency and new options for change. In: Tait J, Napompeth B, editors. Management of pests and pesticides: farmers' perceptions and practices. Boulder, Colo. (USA): Westview Press. p 98-108.

Kim CK, Ra DS, Min HS. 1985. Ecological studies on rice sheath blight caused by *Rhizoctonia solani:* cultural method and disease development. Korean J. Plant Prot. 24(1):7-10,

Kogan M. 1998. Integrated pest management: historical perspectives and contemporary developments. Annu. Rev. Entomol. 43:243-270.

Kwon OS. 1998. The rice production technology of Korean farmers: a nonparametric analysis of technical and scale efficiencies. Korean Soc. Sci. J. 25(1):179-196.

Lee BH. 1999. A study on the effects of integrated pest management implementation on rice in Korea. PhD dissertation. Seoul National University, Korea. 105 p.

Matteson PC, Gallagher KD, Kenmore PK. 1994. Extension of integrated pest management for planthoppers in Asian irrigated rice: empowering the user. In: Denno RF, Perfect TJ, editors. Planthoppers, their ecology and management. New York, N.Y. (USA): Chapman and Hall. p 656-685.

Norton GW, Mullen J. 1994. Economic evaluation of integrated pest management programs: a literature review. Virginia Cooperative Extension, Virginia State University. 112 p.

Uhm KB, Hyun JS, Choi KM. 1985. Effects of the different levels of nitrogen fertilizer and planting space on the population growth of the brown planthopper (*Nilaparvata lugens* Stal). Research Report RDA. 27(2):79-85.

Yoo JK, Kwon KW, Park HM, Lee HR. 1984. Studies on the selective toxicity of insecticides for rice insect pests between some dominant rice insect pests and a predacious spider, *Pirato subpiraticus.* Korean J. Appl. Entomol. 23(3):166-171.

Notes

Author's address: UNDP Developing and Promoting Support System and International Cooperation on Environment-Friendly Agriculture Programme, Rural Development Administration, 250 Seodundong, Suwon 441-707, Republic of Korea. E-mail: leebh@rda.go.kr.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Trade liberalization

Rice trade liberalization and poverty

A. Gulati and S. Narayanan

Rice is the lifeline of almost 70% of the world's poor residing in Asia, where more than 90% of world rice production and consumption takes place. Rice trade liberalization therefore has tremendous implications for poverty. The world rice market is highly distorted, partly because of the high degree of intervention in rice markets across the world. While poor countries such as Thailand, Vietnam, and India tend to "disprotect" rice sectors, the rich countries of East Asia (Japan and Korea), Europe, and the United States heavily support their rice producers. As a result, there is great diversity in domestic rice price levels, with very high prices in the latter countries and very low prices in the former. Trade liberalization would thus result in flows from these poorer Asian countries to East Asia and Europe. This is predicted to have beneficial effects for poverty, through producer price increases and second-round effects (wages, employment, and investment) in exporting countries, and to augment short-term food security in poor importing countries.

However, if rice trade liberalization is to contribute to poverty alleviation in developing countries, there is a need to streamline distortionary agricultural policies, particularly in developed countries. Also important are "behind the border" reforms in developing countries aimed at reducing transaction costs for farmers, rationalizing input pricing policies, ensuring access to risk management institutions and safety nets, improving access to food, and combating adverse environmental conditions. In the long run, rice trade liberalization might have to be coupled with initiatives to enhance agricultural productivity and rural economic growth to be able to make a dent in poverty.

Ever since the Uruguay Round Agreement on Agriculture (URAA) kickstarted trade liberalization in agriculture in 1995, there has been considerable concern in developing countries about its implications for poverty. This is particularly true of rice, which is the lifeline of almost 70% of the world's poor residing in Asia. Asia alone accounts for more than 90% of world rice production of 397 million t in 2001 (FAOSTAT 2002) and an overwhelming share of world consumption. Rice trade liberalization therefore has tremendous implications for poverty.

This paper explores this important link between rice trade liberalization and poverty, seeking specifically to respond to two broad questions: What would be the effect of freer trade in rice on trade flow patterns? How will rice trade liberalization and consequent rice price equalization across countries influence the prevalence of poverty in the poorer economies? In doing so, this paper focuses primarily on Asia. The paper is organized in six sections. The second section, which follows, characterizes the world rice market. The third section maps briefly the policies affecting the rice sector across different countries. The fourth section assesses the competitiveness of the major players in the world rice trade. Based on the relative competitiveness of different countries, it offers a prognosis of the change in trade patterns that liberalization would entail. The fifth section attempts to gauge the implications for poverty drawing on existing literature to do so. The sixth section identifies areas that need specific attention to see how poorer countries can best take advantage of opportunities in rice trade.

Characterizing the world rice market

The world rice market has been expanding over the years, particularly rapidly in the 1990s. Currently, around 24 million t of rice are traded annually, close to double the volume in 1990. However, the world rice market is still characterized by thinness, volatility, and segmentation. Despite growing absolute volumes, trade constituted only about 4.5% of world rice production from 1961 to 2000, compared with 18% for wheat and 13.6% for maize. This is partly attributable to the fact that much rice is consumed where it is produced and partly because of the nature of policies pertaining to rice sectors across the world.

The rice market also tends to be highly concentrated. During the 1990s, around 80% of the exports came from just six countries—Thailand, Vietnam, India, China, Pakistan, and the United States (Childs 2001). The import side has comparatively more players. However, here too there are a few large importers and many small ones. Among the major importers in Asia in the recent past have been Indonesia, the Philippines, Bangladesh, Malaysia, East Asia (Japan and Korea), and the Middle East. The thinness and concentration of world rice markets imply that changes in production or consumption in major rice-trading countries have an amplified effect on world prices. Volatility is also due to frequent shifts in the sources of supply and demand.

Finally, the world rice market is also highly segmented by type and quality. Trade flows are thus determined by what varieties are demanded and the ability of countries to supply them. For instance, while East Asia's demand for japonica is serviced by the U.S., Australia, and China, Africa's indica demand is met primarily by India and Thailand. Europe, on the other hand, obtains its high-quality grain from South Asia while importing indica rice from the U.S. While Middle East imports are primarily basmati from South Asia, most trade in South America is in paddy supplied by the U.S., mainly because of locational advantages. Indica rice accounts for the bulk of global rice trade (75-80%), followed by japonica (10-12%) and aromatic rice such as basmati and jasmine (10%), with glutinous rice accounting for the rest. There are limited substitution possibilities across varieties in both production and consumption, but they tend to be less for the latter given strong regional preferences in consumption.

While these three features of thinness, volatility, and segmentation set the context for any discussion on rice trade liberalization, perhaps the most important feature of the rice market is that it is among the most distorted of all cereals, with countries-developed and developing—using a plethora of controls both externally and domestically. These policies, in fact, collectively contribute to the thinness and volatility of the world market. What are these policies and how do they affect the relative competitiveness of different countries?

Overview of rice policies in different countries

Rice sectors across the world attract a high level of government intervention. This is true of both developed countries and developing countries, which are rather cautious in liberalizing rice trade for the sake of food security. Indeed, rice is regarded as a strategic commodity in many of these countries. But the policies in these two sets of countries differ in a fundamental way. While the former have high producer prices to maintain farmer incomes, the latter have tended to tax producers to ensure the availability of cheap staples for the mass of poor consumers.

Rice policies in rich countries

The wealthier countries use a combination of domestic market interventions and border protection or export subsidies depending on whether they are importers or exporters.

Border protection through bans, high tariffs, and state trading enterprises (STE) is widespread among wealthy rice importers such as Japan, Korea, and the EU. Both Japan and Korea, which, in the past, banned imports of rice, committed to minimum access quotas under Annex 5 of the URAA; this partially opened up imports of rice, albeit with markups on imports.[1] Although with tariff rate quotas (TRQ), over-quota imports are now possible, in practice, both countries use high over-quota tariffs-491% for grains other than wheat in Japan and 89% for rice in Korea in 1999 (Elbehri et al 1999)—which virtually prevents any imports above the quota. Moreover, both Japan and Korea control imports through monopoly STEs, Japan's Food Agency being among the world's largest importer STEs. The EU import regime for rice seeks essentially to protect its rice millers. Although the EU was required to tariffy its

---

[1] Japan's quota was to have risen from 4% of base-period (1986-88) consumption to 8% by 2000, expanding at 0.8% per annum. In 1999, Japan opted for tariffication, which meant that over-quota imports were now permitted but growth of the minimum-access quota was halved to 0.4% of base-period consumption. Korea too opted for a quota system, the quota being 1% to 2% of base-period consumption during the first five years, eventually rising to 4% over the next five years.

import duties and reduce them by 36% in 2000-01, the Blair House agreement enabled the EU to use a variable levy on husked and milled rice imports subject to the ceiling of the UR Bound rate (Nielsen 2002). The preferential quotas of the European Union are another factor that undermines market access.

Domestically also, rich countries heavily support rice producers through a combination of market price interventions and direct payments. Among OECD countries, the producer support estimate (PSE)[2] was 76% in 1997-99, the highest among agricultural commodities. While, in Japan and Korea, 70-90% of farm receipts were due to policy interventions, the figure was lower at 10-30% in the EU and U.S. Japan and Korea rely particularly heavily on market price support—which accounted for about 88% and 96% of the PSE, respectively, during 1997-99 (Nielsen 2002). The U.S., in contrast, uses direct payments, while the EU has shifted away from market price support in favor of direct payments only recently.

Finally, developed-country exporters also use export subsidies to promote their exports. Although export subsidies on rice constituted less than 1% of all notified export subsidies in agriculture during 1995-99, given the thinness of rice markets, even this could be significant. While the EU accounted for 95% of these subsidies, the U.S. accounted for the rest. In fact, as much as 65% of the EU's total rice exports enjoyed export subsidies, as high as US\$322 t^{-1} on average from 1995 to 1998.

The U.S., in contrast, uses export credit guarantees extensively to promote rice exports. Further, both the U.S. and EU channel significant quantities of rice through food aid on concessional terms. In the triennium ending in 2000, of the total US. rice exports, more than 22% either benefited from credit guarantees or constituted concessional food aid (USDA 2001). Interestingly, the volume of rice exported as food aid in general is inversely related to world prices, which is counterintuitive, as one would expect net-importing countries to need more food aid when world prices are high (Fig. 1).

To sum up, while developed-country importers such as Japan and Korea insulate their rice markets through heavy border protection, exporters such as the U.S. and EU resort to export support to make their rice more competitive—with both groups maintaining high domestic prices for producers.

Rice policies in the poor countries

In contrast to the wealthy countries, poorer developing countries in South and Southeast Asia have been taxing rice producers, with domestic prices often less than three-fourths of world prices. Domestic controls are aplenty and diverse. Most have some form of price support system. In the past, these support prices have been way below the international prices, as have been the domestic wholesale prices. Public procurement and government stocking are undertaken in almost all these countries, for public distribution of food grains (India), as buffer, or for market interventions (Vietnam, Thailand, China, and Indonesia).

---

[2] Briefly, PSEs refer to the share of transfers to producers in the total value of gross receipts, i.e., the share of farm receipts brought about by policy.

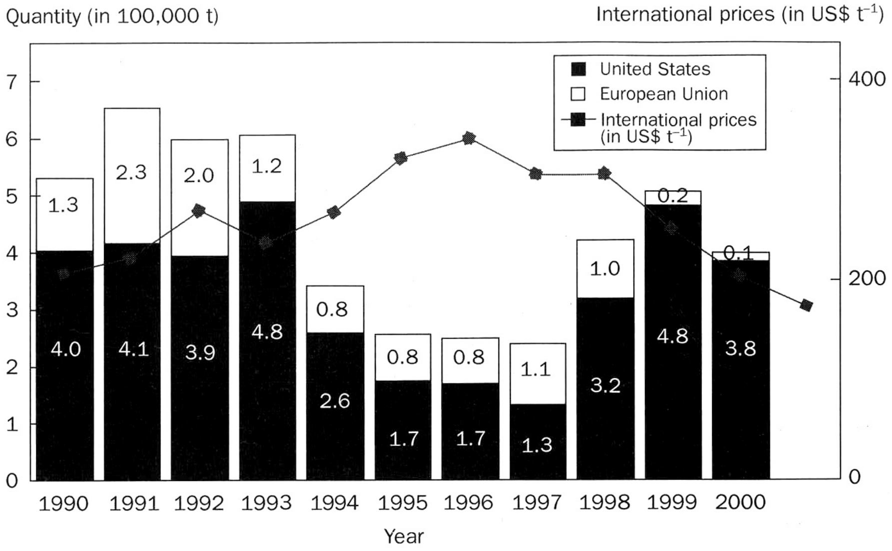


Fig. 1. Inverse relation between prices and food aid: rice food aid by the United States and European Union in the 1990s. Source: Data on Food Aid Shipments from FAO; prices from USDA.

Importantly, stocking limits on private traders, levies on millers, and movement restrictions are pervasive. In parts of India, for instance, levies on millers can be as high as 75%. India also had movement restrictions until recently. Vietnam had internal movement restrictions between the north and south before 1997, trade between regions being under monopoly control of the state. In China, domestic marketing continues to be the exclusive responsibility of state grain agencies. In Indonesia, too, it was only after 1998. that some effort was made to limit the role of BULOG (parastatal organization) in domestic trade.

Many developing-country exporters also tend to restrict and control exports for the sake of food security. Exports of common rice from India were banned until 1994. Exports were not permitted in Vietnam until 1987 and, even after that, Vietnam continued with export quotas until as recently as May 2001. Despite recent changes, the government continues to play a large role in rice exports so that, in 1999, only 4% of Vietnam's rice exports were by the private sector (Nielsen 2002). Thailand, traditionally a rice exporter, also had an export quota until 1986, along with an export tax called the "rice premium." Ironically, over the years, this has come to be replaced by subsidized export credit.

Despite the marked shift toward less trade controls, state trading enterprises continue to play a dominant role in many of these countries, particularly among importers. Indonesia's BULOG, among the largest agricultural importing STEs in the world, retained monopoly control over imports until 1999. However, even in exporting countries such as Vietnam, India, and China, imports have often been routed through the STEs, with a limited role for private traders, if at all. Other importers such as Malaysia use high tariffs to protect their relatively inefficient rice sectors. Recent years have seen regional trade agreements contributing to progress in liberalization in Asia. For example, under the ASEAN Free Trade Agreement (AFTA), all ASEAN member states have agreed to a lifting of all quantitative restrictions on rice trade by 2010. However, typically in these developing countries, progress toward greater trade liberalization is constrained by the dynamics of political economy considerations, given the importance of rice.

Thus, for rice, the high degree of intervention across countries has led to great diversity in rice price levels across countries and has created huge distortion in world markets and trade flows. In fact, it is acknowledged that rice markets are so distorted that countries compete less on productivity gains or efficiency and more on policy levers that make their exports competitive (Tabor et al 2002). Under the circumstances, the critical question is: How would world rice markets change with liberalization? Who would gain and who would lose?

Rice trade liberalization: Which way would the rice flow?

To find out who stands to gain from rice trade liberalization, it is essential to examine the competitiveness of the major rice-trading countries. One way of doing this is through the use of nominal protection coefficients (NPCs)—a competitiveness indicator that encapsulates the effects of diverse policies on the wedge between domestic and world prices. NPCs for selected countries for 1998 and 1999 indicate much diversity, with Japan at the high end of the spectrum with an NFC of 6.5 (Fig. 2; Nielsen 2002). Korea is also becoming uncompetitive, as are the United States and the European Union. In contrast, countries such as China, India, Vietnam, and Pakistan, with NPCs less than 1, are competitive.

The case of Thailand and Indonesia deserves elaboration. It must be remembered that the NPCs can vary widely for each country and are particularly sensitive to movements in world prices and exchange rates. With Indonesia's currency depreciating the way it did in 1997-98, although Indonesia is a major importer, it is becoming competitive. Similarly, Thailand is highly competitive, but the decline in world prices combined with a hike in domestic paddy pledging rates has caused Thailand to seem uncompetitive in 1998-99.

What the NPCs indicate in terms of domestic price levels is that, relative to world prices, domestic prices range from very high in Japan, Korea, the United States, and EU to very low in China, India, Vietnam, and Thailand (where domestic prices either approximate world prices or are even lower).

More significant perhaps is the link between poverty and price levels. It is evident that the countries with the highest domestic prices are the wealthiest countries, while those that are competitive in rice tend to have not only lower levels of per capita income but also a large number of poor people (Fig. 2). For instance, about 44% of the world's 1.2 billion poor live in South Asia and around 24% in East Asia, whereas, in terms of per capita income, countries such as the United States are 15 times better off than those in South Asia. This relationship reflects the historical tendency for

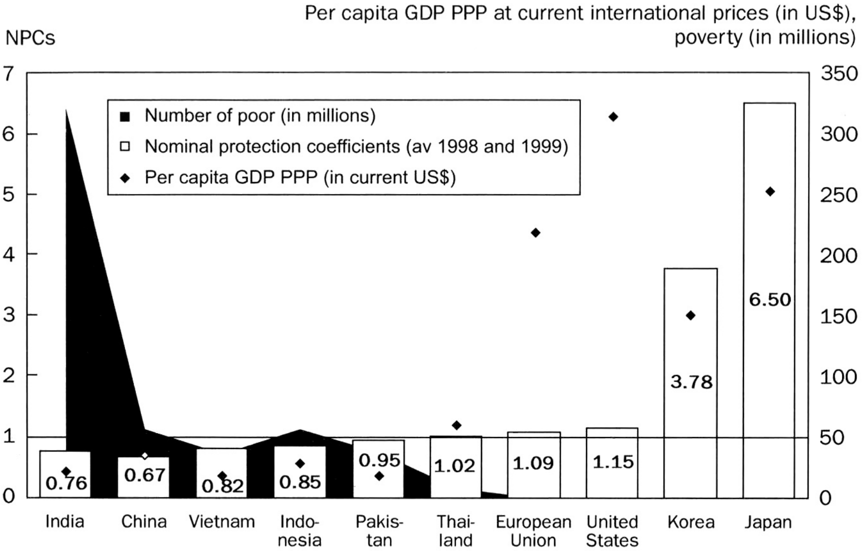


Fig. 2. Nominal protection coefficients (NPCs) (average 1998 and 1999). Source: NPCs from Nielsen (2002), poverty and per capita GDP from World Development Indicators (2002).

poor countries to tax their agricultural sectors (in the interests of availability of cheap food for consumers) and for rich countries to protect their farmers, as elaborated in the previous section.

Given the competitiveness of different countries, what would happen with rice trade liberalization? Prima facie, in a completely free trade scenario, rice should flow from countries where prices are lower, that is, rice is not protected relative to world prices, to where prices are higher, where rice is accorded some protection. Generally speaking, this would imply rice flows from poorer to richer countries. Thus, it can be expected that poorer countries such as Vietnam, Thailand, and India would be important net exporters while the richer countries such as Japan, Korea, and the EU would be net importers. However, some poorer countries in Asia would also be net importers, notably the Philippines, Indonesia, and Malaysia, just as richer countries such as the U.S. are predicted to remain net exporters.

The Arkansas Global Rice Model, for instance, predicts that, in 2010, major net exporters of medium- and long-grain rice would be Thailand, Vietnam, and India, followed by the United States and Pakistan (Fig. 3), reinforcing existing trade patterns. China would also emerge as a net exporter (Wailes et al 2000). At the other end of the spectrum, the major net importers would continue to be Indonesia, along with countries in the Middle East, East Asia, South America, and the European Union, plus Canada and South Africa.

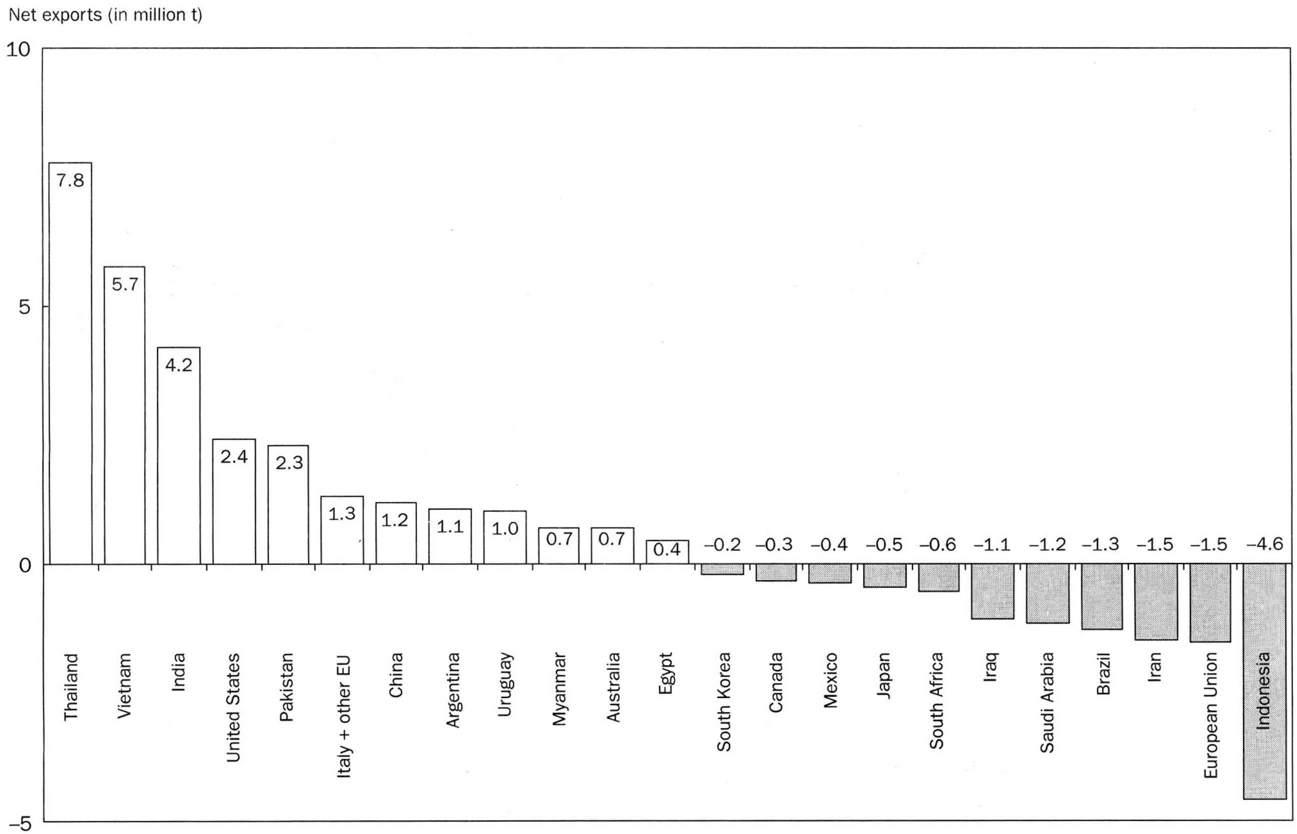


Fig. 3. Net exports of selected countries in 2010 (Arkansas Rice Model). Source: Wailes et al (1999).

Implications for poverty

How do rice trade liberalization and the consequent predicted changes in trade flows affect poverty in developing countries? To answer this question, it is important to recognize that the link between incomes and rice trade flows operates at different levels and in complex ways.

The immediate *impact effect* is through change in price levels. In a competitive country, trade liberalization would trigger exports and domestic prices would rise to equalize with world prices. This would benefit the net sellers of rice, while net buyers of rice face higher prices. In a country that is not competitive, imports would flow in to pull down the high domestic prices to world levels, to the advantage of consumers. It is important to remember that there may be both winners and losers in each country and the net gains are difficult to predict.

However, there seems to be clear empirical evidence that countries that are competitive stand to gain substantially from trade liberalization. Several studies have predicted beneficial effects on poverty from rice trade liberalization in these countries. Deaton (1989), for instance, observed that an increase in rice prices in Thailand would benefit all rural households. More recently, Minot and Goletti (1999) predicted, using a spatial equilibrium multimarket model, that the elimination of the rice export quota in Vietnam would raise prices by 14% to 22% on average, and can be expected to reduce both the incidence and depth of poverty.

While one might argue that only net sellers in these exporting countries benefit, this is not necessarily true when one considers that significant second-round effects operate. For instance, apart from the direct effect of rice trade liberalization on rice farmers, there could also be a lagged effect operating through agricultural wages and employment. Higher rice prices in exporting countries could stimulate production, which can be expected to increase demand for agricultural labor, driving up wages or offering more gainful employment. Thus, while an increase in rice prices may adversely affect net buyers of food in the short run, agricultural laborers and small farmers who supplement their income from agricultural wage earnings could gain through wage and employment increases in exporting countries. This price-wage linkage has been found to hold true for Thailand. In a study of a proposed rice export tax, it was found that the consumption benefit of lower rice prices as a result of an export tax was outweighed by a negative income effect of the driving down of wages for unskilled labor (Warr 2001). Given that the rural poor often derive about 40% of their income from unskilled employment, export liberalization would benefit net buyers as well. A similar linkage between rice prices and wages is apparent in Bangladesh (Rashid 2002, Ravallion 1990) and India (Fig. 4).

Another effect of changes in relative prices in the second round is on investment. As prices in competitive countries increase, terms of trade shift in favor of agriculture, thus spurring private investment, which in turn has a positive effect on growth. This is apparent in India, for instance, where changing terms of trade in favor of agriculture brought about growth in private investment to an extent to which it more than compensated for a decline in public investments (Fig. 5).

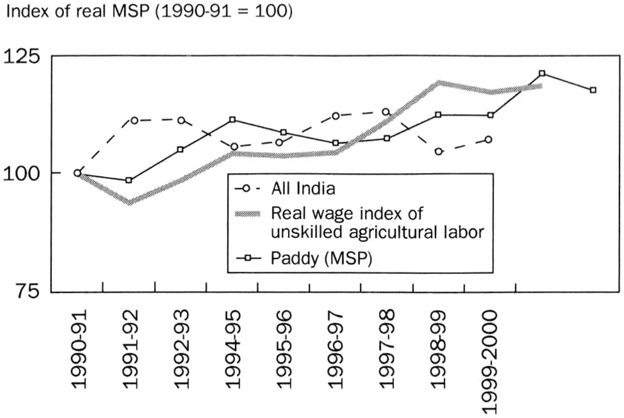


Fig. 4. Wage and rice prices in India. MSP = minimum support price.

Further, in the long run, there are also strong linkages between the farm and nonfarm sector in most countries. In Asia, a one-dollar increase in agricultural income resulted in an additional 80 cents for nonagricultural income for local enterprises, whereas, for selected countries in Africa, it was estimated to be more than two dollars (Delgado et al 1998). Much of the multiplier effect was driven primarily by household consumption demand and production linkages predominantly within the rural farm and nonfarm economies (Hazell and Hojjati 1995). Rice trade liberalization could then trigger increased rice production in some of the poorer-country exporters, helping to create more dynamic rural economies overall. Because most poverty in these countries is in rural areas, often with a share as high as 75%, a more dynamic rural economy would make substantial contributions to poverty alleviation.

While the positive link between rice trade liberalization and poverty discussed above pertains mainly to exporting countries, rice-importing countries can also benefit. However, because rice-importing countries tend to be far more diverse than exporting countries, it is critical to make a distinction between the richer importing countries and the poorer importers. As outlined in the fourth section, the richer importers such as Japan and the European Union, in protecting their producers, maintain domestic prices far higher than world prices, implicitly taxing consumers. Import liberalization in this case would benefit the net consumers in these countries. In the poorer countries, imports have always been viewed with some misgivings since they are feared to be a threat to domestic food security and livelihoods. However, contrary to popular opinion that trade liberalization would be inimical to food security and poverty alleviation, some research shows that trade liberalization in importing countries, by providing a "low-cost rapid response mechanism" to increase domestic supply and stabilize prices, can help enhance food security. For instance, following Bangladesh's poor harvest of rice in 1997, and floods the following year, trade liberalization measures in rice both in Bangladesh itself and in neighboring India made possible imports from India

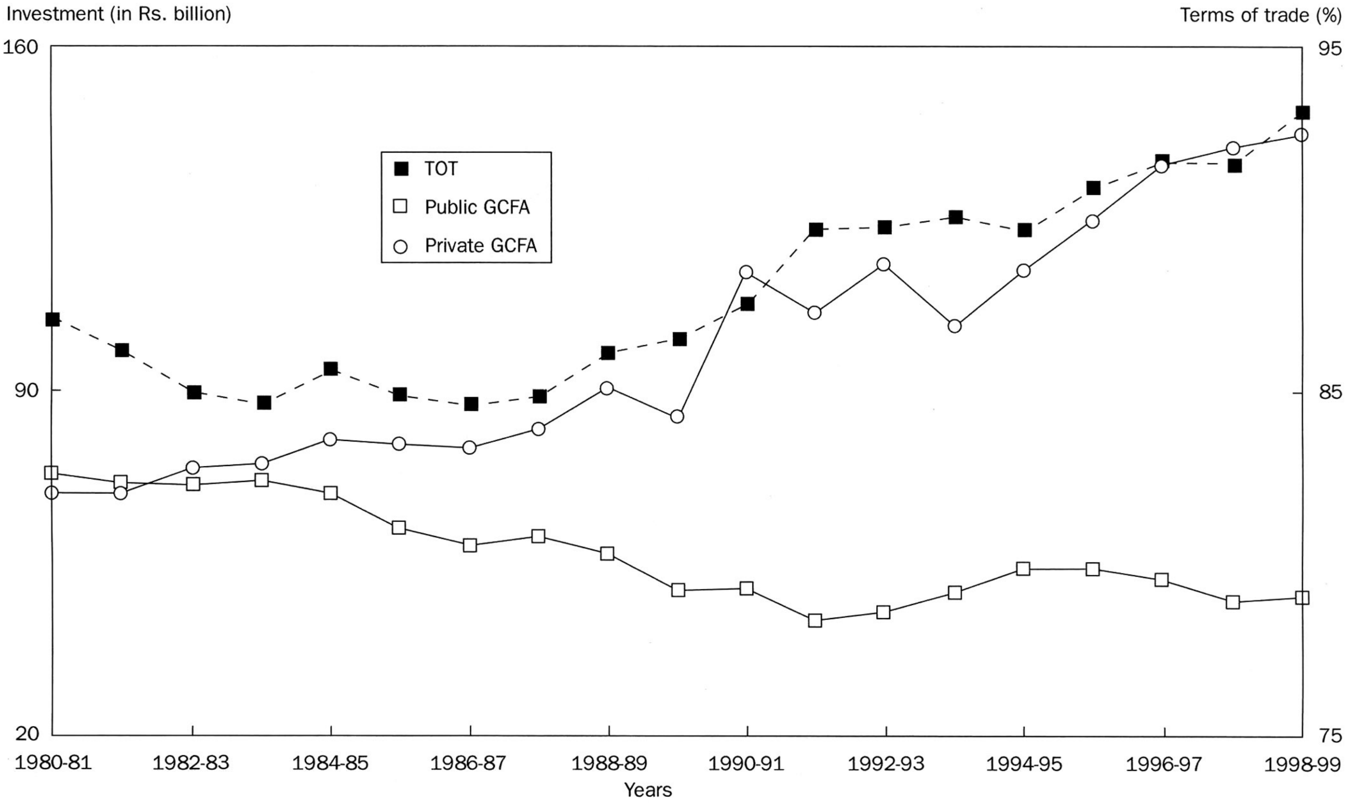


Fig. 5. Terms of trade and investment in agriculture in India, 1980-99. Source: Guiati and Hoda (2002).

by private traders, which contributed significantly to Bangladesh's short-run food security (Dorosh 2001). The legitimate concern that trade liberalization cannot be relied upon for a country's long-run food security needs to be examined not so much through trade policies as it should be through behind-the-border policies such as the provision of safety nets, food stamp systems, and food-for-work programs, thus enhancing productivity and rural economic growth (Dorosh 2001).

Translating potential gains into reality: the hurdles

It seems clear from the literature that rice trade liberalization can help to alleviate poverty in poor developing countries. The fact remains, however, that, despite embarking on a liberalization process in 1995, the current trade environment for rice continues to be highly restrictive. A shift in trade patterns along the lines predicted would require a significant change in policies of both developed and developing countries.

Rice trade liberalization has been slow, but changes are occurring. In exporting countries, the bans and quotas that limited exports are increasingly being lifted as demonstrated in India, Vietnam, Thailand, etc. Given progressive liberalization in the exporting countries, the greatest problems they face are the policies of developed countries—market access, domestic support, and food aid (and other export competition measures).

The experience of the late 1990s in particular suggests that all is not well with rice trade liberalization. The crux of the problem has been the huge price decline starting in 1997. This trend persisted and, by 1999, world prices of rice declined to their lowest level in almost 20 years. This has triggered problems for several rice-producing countries, even efficient producers such as Thailand, Vietnam, and India.

The reason for the price decline is a combination of several factors. International rice prices faced severe downward pressure following the East Asian financial meltdown in June 1997 that weakened demand from Asian importers (Fig. 6; Childs 2001). The crisis affecting Latin America also reduced global agricultural commodity prices, consumption, and trade (Wailes et al 2000). In 1998, however, the drop in prices was almost reversed by a sudden increase in world trade to record levels. This resulted from severe crop damage from El Niño in Southeast Asia and South America. El Niño, for instance, caused Indonesia to become a net importer of about 6 million t, over seven times its 1996 level. By 1999, however, the declining trend in world prices was reinforced, as production in importing countries affected by El Niño recovered. Improvement in domestic rice production meant that net imports declined subsequently to normal levels (Childs 2001).

On the supply side, this was also the time when exporting countries had bumper harvests. Significantly, in 1998, the world rice market saw the entry of China as a major exporter with a supply of more than 3.5 million t. This was largely the result of the Grain Bag Policy that was instituted at the provincial level to ensure self-sufficiency, which augmented supplies and stocks in the country (Childs 2001, Nielsen 2002, Wailes et al 2000).

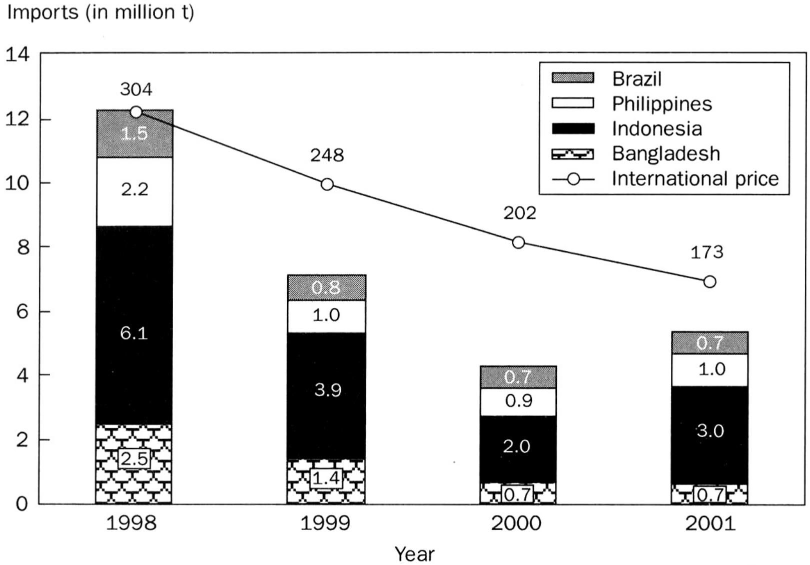


Fig. 6. Declining demand in major rice importers, 1998-2001. Source: FAS/USDA. Figures for 2001 projected. Notes: Rice trade is on milled basis. International prices are f.o.b. Bangkok Thal white milled 5% broken.

However, above all, there has been another important but oft-neglected factor reinforcing the decline in prices, namely, domestic policies in the developed countries. The case of the U.S., a major exporter, is particularly relevant here. The United States uses several instruments to support the rice sector—with three kinds of payments forming the core of domestic rice policy. First, direct payments under the production flexibility contract (PFC) are given to participating farmers. In crop year 2001, payments to rice contract holders totaled US\$41.34 t^{-1}. Second, another program assists farmers when prices are low, as part of the marketing assistance loan or loan deficiency program (LDP) payments. Payments under this program are based on the difference between announced world prices and the national average loan rate for rice, when the former drops below the latter, and called marketing loan gains (MLG). In 2001, this amounted to \$68.90 t^{-1}. Third, over and above this, since 1997, following a decline in actual world prices, the Congress has sanctioned payments termed market loss assistance to enable farmers to tide over periods of low prices. These payments, often equaling the rate under the PFC, have continued for four consecutive years. These payments, accruing to those eligible for PFC payments, were to the tune of \$47.05 t^{-1}. This system of support payments implies that a rice farmer in the U.S. earned as much as \$157.28 t^{-1} in government assistance during 2001, which far exceeded the differential between the higher U.S. domestic prices and lower international prices (Fig. 7).

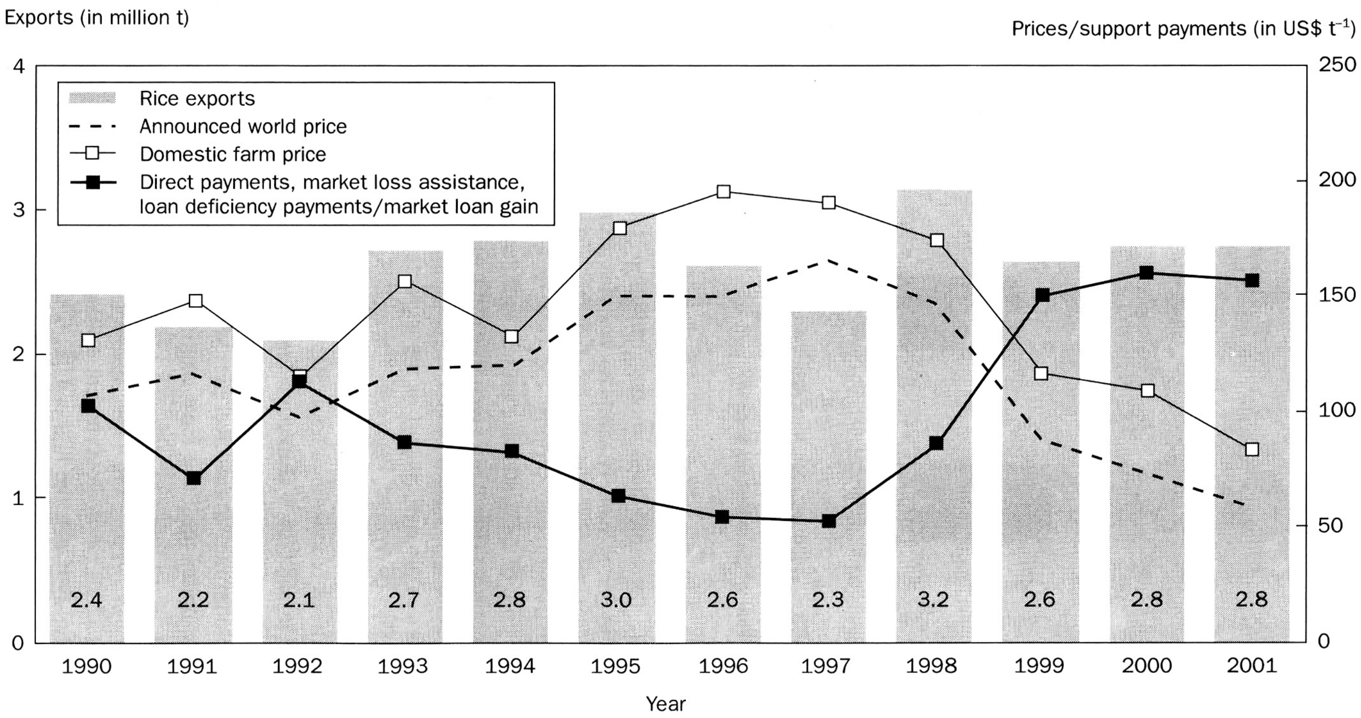


Fig. 7. How United States domestic policy propped up exports. Source: Basic data from ERS/USDA Rice Yearbook (2001). Note: U.S. exports rough brown rice and fully milled rice; figures are for milled rice (including brown rice), calendar years from FAS/USDA. The announced world prices for rice are for its rough form and hence significantly lower than international prices for white milled rice. The direct payments under production flexibility contracts allow farmers to plant any crop on their contract area. Here the assumption is that the farmer who receives a PFC payment for rice also cultivates rice. The announced world price for 2000 has been interpolated.

Such domestic policies have important ramifications for the international market. Given that the U.S. is relatively less competitive in rice than countries such as Thailand, Vietnam, and India, the adjustment to low world prices would ideally have been borne by U.S. farmers. However, direct payments, particularly the market loss assistance payments, which are essentially countercyclical, enable its farmers to sustain or maintain existing levels of production and exports even when prices were declining, and make U.S. farmers artificially competitive. Given that these payments have been disbursed for four consecutive years, farmers in the U.S., rather than fully responding to market conditions, would respond partly to the expected benefits of future payments (USDA 2002). Consequently, U.S. domestic rice policies have the effect of deflecting the shock of low prices back to the international market.

Thus, while the U.S. has succeeded in maintaining its level of exports, the burden of adjustment to low world prices fell on the more competitive countries such as Thailand, Vietnam, and India. These countries had to cope with low demand, blunted competitiveness caused by extraordinarily low prices, and the massive accumulation of foodstocks. In fact, in Thailand, Vietnam, and India, extraordinarily, domestic support prices were higher than world prices (Tabor et al 2002, Poapongsakorn 2002). In Thailand, by February 2002, stocks had built up to more than 4.2 million t under the paddy-pledging scheme. Similarly, in India, rice stocks burgeoned to about 25 million t in 2002 (Tabor et al 2002). This has prompted several of these countries to resort to export competition measures. Vietnam, faced with weak demand, is reported to export rice at a loss of $10-35 t^{-1}, alongside subsidized credit to exporters for the purchase of 1 million t of rice at a minimum price. Similarly, Thailand subsidized export credits worth $487 million under the export support fund specifically for rice (Tabor et al 2002). India has also begun exporting rice from public stocks at a loss.

The current situation illustrates quite clearly that, if rice trade liberalization is to contribute to poverty alleviation in developing countries, there is a need to streamline distortionary agricultural policies, particularly in developed countries such as the U.S., the EU, and Japan. In an integrating world market, a country's competitiveness depends on a range of factors—such as exchange rate and domestic price movements, but importantly also on other countries' domestic policies. A critical factor would therefore be the active participation of developing countries in multilateral trade negotiations aimed at domestic agricultural policy reform in developed countries. With liberalization, one could expect a higher share of production to be traded while the complete integration of large rice producers such as China and India would also bring more stability to world rice markets.

The extent to which rice trade liberalization can be an instrument of poverty alleviation in developing countries, however, is subject to some caveats.

Chief among these is the critical role played by behind-the-border reforms in developing countries. If rice trade liberalization is to be part of a strategy to reduce poverty, there would have to be domestic reform in these poor countries aimed at reducing transaction costs for farmers, ensuring access to risk management institutions and safety nets, and improving access to food. In the long run, rice trade liberalization might have to be coupled with initiatives to enhance agricultural productivity and rural economic growth to be able to make a dent in poverty.

Another important consideration is the environmental costs associated with rice trade. It is often believed that exporting rice is like exporting scarce water resources. Already, the practice of intensive rice monoculture has caused problems of waterlogging, salinity buildup, nutrient depletion, etc., that have in turn resulted in stagnating or declining yields (Pingali et al 1997). Gains from rice trade liberalization in poor developing countries could well be constrained by natural resource degradation.

Similarly, predictions of changes in rice trade flows cannot be considered in isolation of what happens in other crop sectors. Simultaneous liberalization across the board, which is the more likely event, could change the prognosis for rice significantly.[3] Important in this context is the trend in countries such as Vietnam that have recently shifted to policies to limit area under rice in favor of maize by about 0.3 million ha. Such policy shifts in the larger scenario would have to be factored in as well.

Behind-the-border reforms assume greater significance in the context of these two issues. Environmental sustainability of rice systems would require deep reforms in input-pricing policies and also complementary policies pertaining to the environment. It is also important that government intervention in domestic markets ensure that these reforms do not offer perverse incentives to some crops over others in the interests of allocative efficiency.

References

Childs N. 2001. Rice: background and issues for farm legislation. Electronic Outlook Report from the Economic Research Service, United States Department of Agriculture.

Deaton A. 1989. Rice prices and income distribution in Thailand: a non-parametric analysis. Econ. J. 99(Supplement 1989): 1-37.

Delgado C, Hopkins J, Kelly V, with Hazell P, McKenna A, Gruhn P, Hojjati B, Sil J, Courbois C. 1998. Agricultural growth linkages in Sub-Saharan Africa. IFPRI Research Report. Washington, D.C. (USA): International Food Policy Research Institute.

Dorosh P. 2001. Trade liberalization and national food security: rice trade between Bangladesh and India. World Dev. 29(4):673-690.

Elbehri A, Ingco M, Hertel T, Pearson. 1999. Agricultural liberalization in the new millennium. Paper presented at the World Bank/WTO Conference on Agriculture and the New Trade Agenda from a Development Perspective, 1-2 October, Geneva, Switzerland.

FAOSTAT. 2002. http://apps.fao.org.

---

[3] IFPRI's IMPACT 2020 Model, which considers 16 commodities, predicts a scenario quite different from the Arkansas Global Rice Model. The former suggests that, while Southeast and East Asia (13.5 million t) and the United States (2.5 million t) would be the major net exporters of rice, SubSaharan Africa (5.8 million t) and West Asia and North Africa (5.1 million t) would be the major net importers. It is interesting that South Asia is predicted to be a net importer (7.7 million t) along with Latin America, the European Union, and former Soviet Union (Rosegrant et al 2001). In particular, India, which is predicted to be a major net exporter of rice by 2010 by the Arkansas Model, emerged a net importer of 0.3 million t in 2020 (Rosegrant et al 2001).

Gulati A, Hoda A. 2002. Negotiating beyond Doha: Indian agriculture and the WTO. (In mimeo.)

Hazell P, Hojjati B. 1995. Farm-nonfarm growth linkages in Zambia. Discussion Paper No. 8, Environment and Production Technology Division. Washington, D.C. (USA): International Food Policy Research Institute.

Minot N, Goletti F. 1999. Rice market liberalization and poverty in Viet Nam. Research Report No. 1 14. Washington, D.C. (USA): International Food Policy Research Institute.

Nielsen C. 2002. Viet Nam in the international rice market: a review and evaluation of domestic and foreign rice policies. Report 132. Copenhagen (Denmark): Food Research Institute.

Poapongsakorn N. 2002. Trade and domestic policies during the boom and bust periods: a case of Thai agriculture. Paper presented at the International Agriculture Trade Research Consortium (IATRC) Summer Symposium on "The Developing Countries, Agriculture Trade, and WTO' at Whistler, Bristish Columbia (Canada), 15-17 June 2002.

Pingali P, Hossain M, Gerpacio R. 1997. Asian rice bowls: the returning crisis? Manila (Philippines): International Rice Research Institute, and Wallingford (UK): CAB International.

Rashid S. 2002. Dynamics of agricultural wage and rice price in Bangladesh: a re-examination. Discussion Paper No. 44, Markets and Structural Studies Division. Washington, D.C. (USA): International Food Policy Research Institute.

Ravallion M. 1990. Rural welfare effects of food price changes under induced wage responses: theory and evidence for Bangladesh. Oxford Econ. Papers 42:574-585.

Rosegrant M, Paisner M, Meijer S, Witcover J. 2001. Global food projections to 2020: emerging trends and alternative futures. Washington, D.C. (USA): International Food Policy Research Institute.

Tabor SR, Husein Sawit M, Dillon HS. 2002. Indonesian rice policy and the choice of a trade regime for rice in Indonesia. Paper prepared for Roundtable Workshop, Institute for Development Economics and Finance, LPEM-University of Indonesia, March 2002.

United States Department of Agriculture (USDA). 2002. Countercyclical income support payments. ERS Analysis, USDA.

United States Department of Agriculture (USDA). 2001. Rice yearbook 2001, USDA.

Wailes EJ, Cramer G, Chavez E, Hansen J. 2000. Arkansas global rice model: international baseline projections for 2000-2010. Ark. Agric. Exp. Sta. Special Report 2000.

Wan PG. 2001. Welfare and distributional effects of an export tax: Thailand's rice premium. Am. J. Agric. Econ. 83(4):903-920.

Notes

Authors' addresses: A. Gulati is director, Markets and Structural Studies Division, International Food Policy Research Institute (IFPRI), 2033 K Street, NW, Washington, DC 20006, e-mail: a.gulati@cgiar.org; S. Narayanan is senior research assistant, Markets and Structural Studies Division, IFPRI, e-mail: s.narayanan@cgiar.org.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

WTO accession and Chinese agriculture

Justin Yifu Lin

China is poorly endowed with arable land and its agricultural sector is considered to be backward. Many concerns exist about the adverse effects of WTO accession on Chinese agriculture. This paper analyzes the detailed accession agreements on Chinese agriculture and finds that accession will provide a favorable environment for the export of labor-intensive agricultural products, and this is Chinese agriculture's comparative advantage. In addition, the tariff-rate quota system will provide necessary protection for land-intensive grain products, for which China does not have a comparative advantage. If China can overcome its agricultural research, marketing, storage, and other managerial problems, overall, WTO accession will provide a beneficial environment for Chinese agriculture's development.

After 15 years of continuous efforts, China finally became a formal member of the World Trade Organization (WTO) in November 2001. Top Chinese leaders regard WTO accession as the second most important change in China's economic policy regime, following Deng Xiaoping's reform and opening-door policy in the late 1970s. This change will undoubtedly have profound effects on the future course of China's economic development. Many discussions have been held among academic and policy circles in China regarding the possible effects. Some people are very positive about the accession because they believe that any drawbacks to such a move will be overwhelmed by the efficiency gains. As such, new growth impetus will be injected into China's reform and economic development, and China is expected to enter an entirely new development stage. However, other people worry that China's weak economic base, because of the unfinished transition from a planned to a market economy, would not be able to sustain the tremendous external shocks brought about by entry into the WTO. They argue that WTO accession will do more harm than good to the Chinese economy.

My personal judgment is that, before the expiration of the grace periods in the bilateral agreements, most sectors in the Chinese economy will still be protected.

However, in anticipation of the opening up of China's domestic market to foreign firms after the grace period, direct foreign investments from multinational companies will increase substantially immediately after the accession. Therefore, the accession should bring an immediate boost to investments and a spurt in the economic growth rate in the Chinese economy in the short run. In the long run, membership in the WTO will undoubtedly enable the Chinese economy to have a closer integration with the world economy; facilitate better access to foreign technology, capital, and the world market; and be beneficial to China's overall long-run economic growth. The real challenge to the Chinese economy is in the intermediate run after the expiration of the grace period and before the completion of adjustments to the long run. The intermediate-run challenges will certainly be different from one sector to another, depending on the gains and adjustments that the sector needs to make.

Agriculture is the most sensitive issue in the WTO negotiations and it caused the most difficulty in reaching an agreement, as it has with other WTO member countries. Conflicts and disputes on agricultural problems always result in lengthy negotiations among not only the developed countries themselves but also between developing countries and developed nations. China is a developing country with the largest population in the world. Most Chinese people still live in the countryside. Many people are worried that Chinese farmers endowed with small plots of land and backward technology cannot compete with large farmers equipped with modern technology in advanced countries, such as the United States, Canada, and Australia, and that WTO accession will have substantial negative effects on Chinese agriculture. They give as evidence that current prices of grain in Chinese markets are already close to or even exceed world market prices. For example, in March 1999, the price of maize in the domestic market was RMB 1.44 (US$0.17) per kg on average; however, the average price in the Chicago Futures Market was equivalent to RMB 0.72 (US$0.086) per kg. Therefore, some anxiety about the agricultural impact of WTO entry is understandable.

In the bilateral agreement between China and the U.S., agricultural trade occupies a premier position. Since the agricultural agreement with the U.S. is quite comprehensive and has received much public attention, I will base my discussion mainly on the agreement between China and the U.S., supplemented by the agreement between China and the EU only when it is necessary. The main contents of the China-U.S. agreement cover five areas as follows[1]:

1. Elimination of sanitary and phytosanitary barriers on U.S. exports of wheat, citrus, and meat, for example, the bans on importing wheat from smut- affected regions.
2. Elimination of China's subsidies to agricultural exports.
3. Liberalization of state companies' monopoly and allowing private companies to engage in agricultural trade.
4. Adoption of a tariff-rate quota (TRQ) system for grain imports.

---

[1] The US.-China agreement is drawn from the White House Office of Public Liaison, *Summary of U.S.-China Bilateral WTO Agreement,* available on the Web site of the US-China Business Council at www.uschina.org.

5. Reduction in tariffs on agricultural products to well below 20% for major agricultural imports from the U.S.[2]

The first item listed above will not have much effect on China's imports because those trade barriers affect only small amounts of agricultural products and are hard to implement. The second item will not have much effect on China's exports either because there are currently few subsidies for Chinese agricultural exports. The third item is beneficial to Chinese farmers and consumers. The state monopoly on agricultural exports/imports is extremely inefficient. The liberalization of agricultural trade and the consequent competition between private and state traders should be most welcomed by farmers and consumers. Controversy focuses mainly on the fourth and fifth items, namely, agreements on the importation of grain and the lowering of import tariffs.

China is a land-scarce economy. Agricultural production requires land input. However, it does not mean that the agricultural sector in China will be decimated when China enters the WTO. The relatively low price of agricultural products in the U.S. is due to multiple factors. Grain, one of the major agricultural products, is land-intensive and the United States is relatively land-rich, giving it a comparative advantage in grain. In addition, the U.S. government subsidized and protected grain farmers for years, through technology development, export subsidies, and price supports. Such policies deviate from the recent WTO agricultural cooperation agreement. Moreover, the WTO member countries, including the US., are encouraging new negotiations on free trade of agricultural products, including grain. Thus, the U.S. will eventually have to give up almost all of its current protective agricultural policies, leading to a greatly diminished price advantage for U.S. grain. Agricultural production in the European Union is not much threat to Chinese agriculture since, for most agricultural products other than wine, spirits, and milk products, European countries do not have a comparative advantage.

Given that China has limited land but abundant population, it does not have a comparative advantage in grain production. Importing grain is equivalent to importing land, which is not harmful to Chinese economic development. In addition, a considerable portion of the price of grain in the domestic market does not reflect the actual production cost because of the inefficient monopoly operation of the state grain agency. In accordance with China's commitment to allow entry of private traders, this situation will be improved after China enters the WTO. Therefore, the market competitiveness of grain production in China will be enhanced,

Moreover, the China-U.S. agreement on grain is a TRQ system. Within the agreed import quota, low tariffs will be implemented; for imports exceeding quota limits, a

---

[2] According to the agreement with the U.S., China will also eliminate restrictions on soybean imports, the tariff on which will be cut down to 3%. Tariffs on wine will decrease from 65% to 20%. Tariffs on beef will decrease from 45% to 12%. on pork from 20% to 12%, and on poultry from 20% to 10%. Tariffs on oranges will decrease from 40% to 12%. on grapes from 40% to 13%, and on apples from 30% to 10%. Tariffs on apricots will decrease from 30% to 10%. on cheese from 50% to 12%, and on ice cream from 45% to 10%. China made further concessions to the EU and agreed to reduce the tariff on wine to 14%, on all spirits to 10%, on butter to 10%. on milk powder to 10%. on mandarins to 12%, on olives to 10%. on pasta to 15%. on rape oil to 9%, and on wheat gluten to 18% (Lapres 2000).

high protective tariff will be imposed. The TRQ is initially 14.4 million t and will gradually increase to 21.8 million t.[3] In general, imports will not exceed the quota because the high over-quota tariffs are prohibitive. In addition, even if the TRQ of 21.8 million t is fully used, the resulting grain imports will be only 5% of China's average grain output in the 1990s. The effect on domestic prices, and therefore on farmers' income, will be very limited.

Apart from the land-intensive grains, many other agricultural products, such as animal husbandry, horticulture, aquaculture, and processed agricultural products, are labor-intensive. In these commodities, China has a comparative advantage over most other countries.[4] In fact, since reform began in the late 1970s, China's agricultural trade has always been in surplus, soaring from US$57 million in 1980 to $6.8 billion in 1999 (SSB 2000). One of the important reasons for this trend is the increase in exports of labor-intensive agricultural products (Lu Feng 1999). The reduction in China's import tariffs will not hurt China's net exports of those labor-intensive products at all. Moreover, the past growth of agricultural exports was achieved under high protective tariffs and nontariff barriers set by the importing countries. The agricultural trade interventions by WTO countries have been reduced substantially recently, and will diminish further in the near future. After joining the WTO, China will have increased access to foreign agricultural product markets. It is expected that China's exports of labor-intensive agricultural products will increase tremendously.

The agreements on the removal of trade barriers, elimination of export subsidies, reduction of tariffs, and import of grain seem to have given the Chinese general public the impression that China has given in too much to U.S. pressure on a weak sector in the Chinese economy. However, the above analysis shows that accession to the WTO will actually do more good than harm to Chinese agriculture. The agricultural agreement actually is, using a Chinese proverb, *"shu le mian zi, ying le li zi"* (losing face but winning substance).

References

Johnson DG. 2000. WTO and Chinese agriculture. Paper presented at a seminar at the China Center for Economic Research, Peking University, 23 March 2000.

Lapres A. 2000. The E.U.-China WTO deal compared. Available at www.gyoza.com/lapres.

Lu Feng. 1999. The comparative advantage and China's structure of grain trade: the third choice for restructuring China's agricultural policy. In: Lin Yifu, Hai Wen, Ping Xinqiao, editors. China's economics research: the compilation of working papers at the China

---

[3] The TRQ for wheat will increase from 7.3 million t at the time of accession to 9.3 million t after five years, while the share for private traders will be 10%. The TRQ for maize will increase initially from 4.5 million t to 7.2 million t, and the share for private traders will grow from 25% to 40%. The TRQ for rice will increase from 2.6 million t to 5.3 million t, and the share for private traders will reach 50%. No TRQ is set for importing barley and its tariff will drop to 9%.

[4] The exceptions are those commodities that are itemized in the tariff agreements with the U.S. and the EU. However, those commodities are very small in China's production except for soybean (Johnson 2000).

Center for Economic Research at Peking University in 1995-1999. Beijing (China): Beijing University Press. p 456-480.

SSB (State Statistical Bureau). 2000. China statistical abstract 2000. Beijing (China): China Statistics Press.

Notes

Author's address: Peking University.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

The nature of distortions to agricultural incentives in China and implications of WTO accesion

J. Huang and S. Rozelle

China's domestic rice policy has moved toward liberalization over the last 20 years. Setbacks, however, have periodically occurred along the way because of conflicting policy goals. On the one hand, leaders recognize the importance of more efficient market mechanisms. Market outcomes, however, which often go against other important political goals such as holding ample rice reserves, low rice prices (in the 1980s), and higher farm income (in the 1990s), have induced policymakers to intervene in the markets from time to time. Thus, China's economic development has led to market liberalization, but this process is sometimes interrupted by retrenchment policies as a response to grain price fluctuations and other undesirable outcomes. The cyclical nature of grain liberalization has led to debate among scholars over whether China's rice markets are actually liberalizing or not. Some scholars argue that China's markets are not integrated, and rice markets are included among these. Others argue that China's rice markets are becoming remarkably integrated and that policy interventions are increasingly less effective. This paper examines the performance of China's rice markets with attention paid to the period 1995 2000. This period is of particular interest since policy clearly moved to disrupt the independent rice market growth during this time. Using a new set of disaggregated market prices, we analyze market integration using cointegration tests for rice and compare them with those for maize and soybean. In our paper, we find that, despite the periodic interventions into rice markets over this period, market integration remained robust and even increased over this period. In addition, a clear pattern of market activity has emerged for the different regions. Rice markets in North China appear to be more integrated, but that may be because different regions have preferences for certain kinds of local varieties. We also show that, even in poor rice-growing areas, village markets are tied to regional markets.

Although reform has penetrated throughout the economy in China since the early 1980s, most of the successive transformations began with, and in some way depended on, growth in the rural sector (Nyberg and Rozelle 1999). After 1978, decollectivization, price increases, and the relaxation of local trade restrictions on most agricultural products accompanied the takeoff of China's agricultural economy in 1978 to 1984. Grain production increased by 4.7% per year. Even higher growth was enjoyed in horticulture, livestock, and aquatic products. Although agricultural growth decelerated after 1985 after the one-time efficiency gains from the decollectivization, the country still enjoyed agricultural growth rates that have outpaced the rise in population. New opportunities in the off-farm sector have allowed farm families to shift part of their household's labor force out of the agricultural sector into higher-paying off-farm jobs.

Despite the healthy expansion of agriculture, the rural sector still faces several serious challenges. According to the World Bank (2000), more than 100 million people fell below the poverty line in the late 1990s, earning less than US$1 per day in purchasing power parity (PPP) terms. Some regions of the nation are still highly dependent on crop production, such as farmers in some northeast provinces (maize and soybeans) and the North China Plain (wheat and maize—China's Ministry of Agriculture 2001). In the past several years, expanding supplies and increased liberalization have pushed real agricultural prices to their lowest levels in history (Park et al 2002). With the retreat of the state occurring in many sectors of the economy (e.g., rural health care and the provision of welfare services—Nyberg and Rozelle 1999), even though China's record in the rural economy is stellar, large numbers of people are still poor and vulnerable to even relatively minor income shocks.

In part because of the vulnerability of parts of the rural economy, and in part because of its importance in the political economy of several developed nations (with whom China had to negotiate its accession to the World Trade Organization, WTO), agriculture has been at the center of discussion of China's entry into the WTO. However, despite being a central concern for China's policymakers and negotiators from other countries, the likely shifts in China's future agricultural policy and its effects are not well understood. Debates on the future of China's agriculture remain unresolved. Some argue that the effects of China's joining the WTO on its agriculture will be substantial, adversely affecting hundreds of millions of farmers (Carter and Estrin 2001, Li et al 1999). Others believe that, although there will be some effects, including severe ones in some specific areas, overall the effect of accession on agriculture will be modest (Anderson and Peng 1998). In part, the confusion about the ultimate impact of entry into the WTO can be traced to a general lack of understanding of the policy changes that may be induced from China's WTO accession (Martin 2002). However, in another perhaps even greater way, the lack of clarity of the debate can be traced to a lack of understanding of the fundamental facts about the nature of the distortions to China's agricultural sector on the eve of its entry into the WTO.

The overall goal of our paper will be to attempt to contribute to the empirically based literature on the effects on China's agriculture of its entry into the WTO. In general, we seek to answer some of the most basic questions about the expected effects of China's entry.[1] On balance, will the nation's accession to the WTO help or hurt farming households? If farmers lose (gain), who in the agricultural economy will get hurt (benefit)? Will some regions in the country be insulated from the effects of the WTO because of their isolation from domestic markets?

Because of the enormity and complexity of the effects of China's entry into the WTO, we necessarily restrict the scope of our work. First, we realize that the effects on rural households of changes in agricultural commodity prices are only a part of the changes that those in the rural economy will experience. In many cases, even more important effects will occur through changes in off-farm labor markets (e.g., OECD 2001, Zhao and Sicular 2002, Rozelle and Huang 2001). Even within the food economy, the WTO will bring about many complex effects. For example, consumers will also gain from lower prices. Farmers will gain if higher levels of imports lead to lower fertilizer, pesticide, and seed prices. In addition, the nature and magnitude of the effects will also depend on how closely households are integrated into markets (Taylor 1998). Subsistence households in remote areas could escape from being affected at all even though consumers in areas that are linked to international markets enjoy a fall in the price of important commodities in their daily consumption basket.

To meet our objectives, we begin the study with the basic premise that, to assess the effects of the WTO on agriculture, we need to understand two sets of issues. First, we need to understand the magnitude of the current distortions to agriculture—both the main policies behind them and the size of the gap between the world market and China's domestic prices of the nation's important agricultural commodities. Second, once the size of the "shock" at the border is estimated, to understand the crop-specific and regional effects of WTO accession (as well as the effects on certain groups of rural residents, such as the poor), we need to understand how well price shocks are transmitted throughout the economy. Ultimately, with a knowledge of the magnitude of the effects, researchers can work on understanding how the policies that the WTO will impose on China will change the gap between the domestic and international price and affect imports and exports, domestic production and consumption, income, and poverty.

Gradual opening and remaining distortions

Although agriculture has been at the center of China's negotiations over its entry into the WTO, the likely shifts in China's future agricultural policy and its effects are not well understood. Debates on the future of China's food security are growing. We believe that the fundamental confusion about the ultimate effects of the WTO in part

---

[1] Several good analytical papers exist that identify the conditions under which China will enter the WTO, the possible sources of gains and losses, as well as what the effects might be on aggregate trade (see, for example. Johnson 2000, CARD 2001, OECD 2001. Carter and Estrin 2001, Tuan and Cheng 1999). Little of this work, however, tries to track regional, sectoral, or specific effects with empirically based methods.

Table 1. Changes in nominal protection rates (NPRs) over time of China's major agricultural commodities, 1978 to 2000. [a]

Years	NPRs(%)			
	Rice	Wheat	Maize	Soybean
1978-79	10	89	92	40
1980-84	9	58	46	44
1985-89	-4	52	37	39
1990-94	-7	30	12	26
1995-97	-1	19	20	19
1998-2000	-6	26	32	49
1998	-6	22	40	37
1999	-9	30	33	67
2000	-2	26	23	44

[a] NPRs are measured as the difference (in percentage terms) between average border price and average domestic wholesale (market) price.

Source: Huang (2001).

can be traced to a widespread lack of understanding of the policy changes that may be induced from China's WTO accession (Martin 2002). Traditionally, analysts have focused on four sets of trade policies, measures that are most frequently used by other countries to protect their agricultural sector. In examining previous work (e.g., CARD 2001, Tuan and Cheng 1999, OECD 2001), we find that almost all of the discussion is directed at tariffs, quotas and licensing, state trading, and traditional nontariff barriers (NTBs). It is implicitly assumed that the WTO agreement focuses solely on these policies, that these policies are responsible for most, if not all, of the protection that China was enjoying prior to accession, and that accession represents China's initial attack on protection at the border. In fact, although at one time these policies were the source of high distortions, after nearly two decades of reform in the external economy, some of the worst of the distortions caused by these policies have already disappeared.

The experience of China's agricultural tariff policy illustrates the gradual but dramatic changes that China has experienced in the past two decades. In the late 1970s and early '80s, the domestic wholesale prices of China's four major commodities all far exceeded the world price (measured at China's border—Table I). For example, China's rice price was 10% above the world market price (row 1). The nation's wheat and maize prices exceeded the world price by around 90%. However, over the next two decades, the protection rate on rice became negative and that for wheat and maize fell to around 30% (row 4). Although the nominal protection rate (NPR) for soybeans fell similarly from the late 1970s to the mid-l990s, the rate rose in the late '90s before falling to less than 20% in 2001 (column 4 and Xie 2002). During this time period, intervention by state traders and the use of NTBs also gradually decreased (Martin 2002).

Decreasing protection and changes in international trade and domestic marketing policies have resulted in dramatically shifting trade patterns. Disaggregated crop-

Table 2. China's agricultural trade by factor intensity, 1985-97.

Year	Land-intensive products		Labor-intensive products		Labor-/capital-intensive products	
	Value (US$ million)	Share (%)	Value (US$ million)	Share (%)	Value (US$ million)	Share (%)
Agricultural exports						
1985	2,119	36.4	2,199	37.8	1,497	25.7
1990	1,689	17.7	4,971	52.1	2,881	30.2
1995	875	6.0	7,095	48.4	6,704	45.7
1997	2,158	14.1	6,538	42.6	6,642	43.3
Agricultural imports						
1985	1,072	43.8	680	27.8	695	28.4
1990	4,032	71.9	642	11.5	935	16.7
1995	6,575	54.5	3,278	27.2	2,216	18.4
1997	4,644	47.3	2,179	22.2	2,987	30.5

Source: Huang and Chen (1999).

specific trade trends show how exports and imports increasingly are moving in a direction that is more consistent with China's comparative advantage. For example, the proportion of grain exports, which was around 20% of total agricultural exports in the 1990s is less than half of what it was in the early 1980s (Huang and Chen 1999). By the late 1990s, horticultural products and animal and aquatic products accounted for about 80% of agricultural exports. These trends are even more evident when reorganizing the trade data by grouping them on the basis of factor intensity (Table 2). The net exports of land-intensive bulk commodities, such as grains, oilseeds, and sugar crops have fallen (rows 5 to 8), whereas exports of higher-valued, more labor-intensive products, such as horticultural and animal (including aquaculture) products, have risen (rows 1 to 4).

Nontraditional sources of trade liberalization or protection

Based on the preceding discussion, two facts become clear. First, distortions have declined significantly in the past 20 years. Considering this fact, the current episode of policy reform that accompanied China's accession to the WTO should be considered an extension of past efforts. Second, much of the decreasing protection has come from decentralizing authority and relaxing licensing procedures for some crops (e.g., moving oil and oilseed imports away from state trading firms), reducing the scope of NTBs, relaxing real tariff rates at the border, and changing quotas (Huang and Chen 1999). Perhaps for these reasons much research on China's entry into the WTO focuses on the policies that were responsible for much of the earlier progress. In fact, studying these policy tools might be merited. Undoubtedly, changes in China's tariff regimes, the state trading system, and the matrix of NTBs will play a continuing role in creating or eliminating distortions in China's agriculture. However, in part, because many of the gains from traditional trade reforms have already been captured, it may be that there are other policies by which China can further liberalize trade (or engage in more protection if it so desires) as it enters the WTO. Even if traditional policies are still important, the gains from these other policy reforms could be as important as those that can come from traditional trade reform.

For example, China has also used its taxation policy to protect its agriculture, especially in certain sectors, such as soybeans, that have been most liberalized. In the early 1990s, leaders radically revised China's fiscal system, making it much more reliant for obtaining revenue on a value-added tax system (Nyberg and Rozelle 1999). The theory of the tax was that it would be assessed on all goods during their manufacture and sales process from the time the raw material came out of the ground until it reached the consumer. National regulations state that imported goods that are not for immediate reexport are also to be assessed the value-added tax. Although the rates vary, the typical value-added tax ranges from 13% to 17%.

For a variety of political and administrative reasons, in the early stages of the implementation of the tax, authorities decided to exempt farmers from the tax when they sold their products to the market. Traders that purchased grain, for example, from farmers in their home or in a local market would not have to pay the value-added tax. When the good was resold in a downstream wholesale market, the value-added tax was then assessed, but the trader owed the tax on only the amount of the marketing margin, or the difference between the procurement pice and the sales price. Recent fieldwork found that, in China's competitive marketing regime, the marketing margins are from 1% to 10%. Taking an average of 5%, the real tax rate on domestic agricultural goods is only 5% of that on imported goods.

Such a tax system can provide some of China's farmers with significant protection. For example, soybeans have only a 3% tariff on imports. In recent years, however, many traders have been given the right to import soybeans. Theoretically, then, the international price of soybeans (when they arrive at China's borders) should differ by only 3%. However, when soybeans enter the country, importers must also pay a 13% tax to meet their value-added tax obligation. Domestic soybeans, in contrast, are taxed, on average, at less than 1%. Through this means, China's soybean producers have an additional price protection of approximately 10%.[2]

China has also used export subsidies in recent years to increase exports of some commodities and, in that way, to increase protection by raising the price of domestic commodities (Table 3, column 1). Maize and cotton are the two crops that have received the most substantial export subsidies. During interviews in the field during 2001, we found that maize exporters, especially those in northeast China, received subsidies that averaged 34% of the export price (row 3). For example, one trader said that, for each ton of maize that his company exported in 2001, it received back

---

[2] Some scholars in China have also pointed out that, since part of the value of agricultural commodity production uses inputs on which the value-added tax has been assessed, the "real" tax rate on agricultural commodities is actually higher. Although certainly this is the case, the maximum that could be added would only be an additional 2 to 4 percentage points (15% times the share of the inputs that were taxed—about 10% to 30%—depending on the commodity, the technology, and the region of production).

Table 3. Subsidies and tax rebates for exports of selected agricultural commodities in China, 2001.

Commodity	Export subsidies (%)	Rebate of value-added tax for exported agricultural commodities (%)
Rice	<1	0
Cotton	10	0
Maize	34	0
Pork	0	5.2
Beef	0	5.2
Chicken	0	13

Source: Authors' survey.

378 yuan per ton (or US$45.70 per ton) after it produced an export bill of sale with the export sales price. With a sales price of $104 per ton, the trading company received a subsidy of 44%, a level 10 percentage points above the average. In other words, the total payment it received (export earnings plus subsidy) was 1,240 yuan per ton, which was even 90 yuan higher than the company could have earned in the domestic market (1,150 yuan). We also discovered that cotton exporters received fairly large subsidies when they exported raw cotton, up to 10% or more (row 2). Finally, in several isolated cases, rice exporters reported that they received small subsidies (though no more than 5% for any single trade) from municipal and prefectural governments, a subsidy that we documented only in South China (although it should be noted that we did not have a chance to interview many rice traders in North China—that is, ones that might be exporting japonica varieties into Japan and Korea). Of rice traders we did talk to, most received no subsidy for their exports, meaning that the average subsidy almost certainly was less than 1% (row 1).

Although no subsidies were provided to meat exporters (this is a more difficult transaction to make fiscally since there are many more meat exporters and most of them are private or commercialized public firms, unlike maize and cotton traders that are mostly associated with formal, public state trading firms), tax policies favor exporters. Based on the trade ministry's estimate of the average value-added tax paid on the products exported by meat traders, when a meat exporter executes a contract, the company can receive a rebate equal to the estimated value of the value-added tax (Table 4, column 2). For example, pork and beef exporters receive a rebate equal to 5.2% of the value of their transaction (rows 4 and 5). Poultry exporters receive 13% rebates (row 6). Since rebates are not provided to domestic wholesalers, such policies give the trading system an incentive to export, since the demand will be higher as the ultimate user outside of China actually sees a relatively lower price than the domestic user.

In summary, as China enters the WTO, those officials interested in liberalizing China's trade will still face several challenges. Alternatively, China also has several instruments that it has been using and may continue to use (legally or not) in managing its domestic economy. In addition to traditional trade policies, tariffs, quotas and

Table 4. Disaggregated nominal protection rate (NPR) for selected grains in China, October 2001.

Variety or quality	Comparable domestic price (estimated at official exchange rate)[a]		Border prices (US$ t^{-1})		NPR (%)
	Yuan t^{-1}	US$ t^{-1}	CIF	FOB	
Rice					
Weighted average					–3
Thai jasmine rice	3,690	446	380		17
High-quality japonica	2,930	354		398	–11
Medium-quality indica	1,519	184		185	–0.5
Wheat					
Weighted average					12
U.S. DNS[b]	2,350	284	190		49
Canadian #3	1,800	218	181		20
Australian soft	1,625	196	175		12
U.S. hard red	1,550	187	169		11
UK	1,350	163	145		12
China—high quality	1,350	163	145		12
China—medium quality	1,250	151	140		8
China—low quality	1,100	133	133		–0.1
Soybean					
Common variety	1,950	236	205		15
Maize					
Common variety	1,150	139		105	32

[a] The estimated official exchange rate is US$1 = 8.28 yuan. [b] DNS = dark northern spring.
Data source: Authors' survey.

licensing, state trading and NTBs, we have shown that China has protected and/or has the potential of protecting its agriculture with several other policy measures. In particular, our analysis has shown that taxation policy may still be a tool that China could try to use to protect or further open its agricultural sector. It has also used export subsidies and rebates to create wedges between the domestic and international prices of importable commodities and to decrease the domestic price relative to the world price of exportable goods.

New estimates of China's nominal protection rates

In this section, we estimate a new set of NPRs on the eve of China's accession to the WTO. These estimates will attempt to overcome some of the previous problems of researchers. In particular, we try to understand in a more disaggregated way the part of certain markets (in terms of varieties or commodity type) that China is protecting. Such an analysis should help us more accurately assess what the effects will be after China implements its WTO obligations. To do this, we first explain how we collected our data. Next, we look at the disaggregated results. Finally, to make the information more useful to policymakers and other researchers, we create a series of more aggregate NPRs. The aggregation of our disaggregated NPRs into a single crop-specific figure allows us to assess how different our estimates are from those calculated using traditional methods of estimating NPRs. Appendix A summarizes some of the difficulties that practitioners face when trying to measure NPRs for China's agriculture.

To overcome previous shortcomings of NPR studies, we conducted a set of interviews and surveys with the stated goal of precisely identifying the differences in prices at a precise time and a particular location between an imported good on one side of the border (outside China) and a domestic good of identical quality on the other side (inside China). Likewise, we also wanted to identify the same price gap between exportable domestic goods as they leave the country and the same goods from other countries that are being traded in international markets. For the interviews conducted in 2001, the enumeration team was in the field from August to November. The team visited seven port cities—Guangzhou, Shenzhen, Ningbo, Shanghai, Lianyungang, Qinghuangdao, and Dalian—and two other more inland cities, Beijing and Changchun. In each port, several "sampling frames" were used to select a sample of domestic traders, importers and exporters, wholesalers, grain and oilseed users, trade regulators, agents, and other grain and fiber officials. In total, more than 100 people were interviewed.[3] Only a small fraction (less than 10%) of those contacted refused to be interviewed.[4]

Disaggregated NPRs for selected agricultural commodities in China

The results of our analysis clearly illustrate the problems with a strategy of NPR estimation that attempts to come up with a single rate of protection for a commodity. For example, it is difficult to provide one single NPR of wheat in China, one of the world's largest importers of wheat (Table 4, rows 5 to 13). Traders reported that the price of very high quality wheat from North America was 20% to 50% higher in the

---

[3] Because of the absence of a single central authority that manages grain flows, the enumeration team chose its sample in several ways. In each location, we first visited the local grain bureau and obtained access to a list of all grain bureaus, the firms that they were running on a commercial basis, and their subsidiaries. We interviewed an official in the grain marketing division and transportation division. We also chose three firms that were owned directly by the grain bureau and three that were affiliated with it. In several cities, the grain bureau had a list of large grain-trading and grain-using firms (e.g., mills and feed lots). In others, this list was obtained from the market administration bureau. Five firms were chosen because they were private and had yearly sales that exceeded one million yuan. We interviewed at least two flour or rice mills and feed mills in each location. Finally, we visited the wholesale market and randomly chose five stalls to interview. The team also visited several other entities, such as the grain reserve, the local state import agency, and supermarket chains. In some cases, the managers of these entities knew the grain trade business well enough to answer our questions, in other cases they did not.

[4] During the interviews, a survey was filled out documenting the scope of the interviewee's participation in China's domestic and international food and fiber trade. We were particularly concerned about understanding the transactions that the interviewees were involved with or knew about that concerned imported or exported grains, fiber, meat, and other goods. The survey recorded the characteristics of the commodities that were involved in trade in the immediate marketing area during autumn of 2001. Enumerators then asked the interviewee a series of questions about commodities about which the traders were most familiar. For imported commodities, interviewees first told the enumerators the international CIF price of the good. Second, interviewees then told enumerators what the good would sell for if auctioned off in a competitive auction. In other words, we elicited a series of price gaps for a carefully defined set of goods. Since, on average, each interviewee had information about several commodities, we had several hundred observations, A similar set of questions was asked about exportable goods, including maize, rice, cotton, and meat products.

domestic markets of China's major ports than when it was sitting on a ship in China's port ready to be brought into the country (rows 6 and 7). More precisely, the average trader told US that, if a ton of Canadian Number 3 hard white wheat were brought in and auctioned off in October 2001, the competitive bid price would have been 20.5% higher than the international price on a CIF basis. Hence, based on this price gap, one would have to assume that China's protection price is high and, if it were to open its markets completely, wheat prices would plummet and the import volume would soar.

However, traders were quick to point out that they thought that, even with open markets, China's wheat price would fall much less than 50% (even if there was no effect on the world price—i.e., they were not considering the effect of China's imports on the world price). According to our interviews, the market for baking-quality wheat, the main use for hard white wheat from North America, is actually relatively small in China, at most only several million metric tons (MMTs). We were also told that few users in China outside of those who required flour for making cakes, pastries, and high-quality breads would use this type of wheat, and that only a small group of farmers and processors inside China could supply this type of wheat. If this is in fact the case, this would mean that, even in a world free of any trade restrictions, imports would come into China up until demand was fulfilled and the domestic price for that variety fell to international levels. Alternatively, it could be that all production of that particular variety shifted to outside of China if all of China's domestic farmers who were producing these varieties abandoned them because they could not make a profit at such low prices. In such an extreme case, with few domestic supplies and with little or no use of the baking-quality wheat for other domestic uses, there would be only a small price effect on most domestic producers. Growers of the high-quality wheat would lose; they would have to keep growing it at a lower price, switch to another wheat variety, or change cropping patterns. Since the quantities of such grain are so small, however, the overall effect would be minimal.

While other cases are not as extreme as the case for North American baking-quality wheat, traders reported that there were arbitrage possibilities in other markets (Table 4, rows 8 to 10). In a remarkable degree of consistency, the CIF price of medium-quality wheat imports from Australia, England, and the Pacific Northwest of the United States (hard red) was reported to be 10% lower than the price that traders believed the same wheat would command in China's domestic market. This medium-quality wheat is used for common bread, cheaper pastries, industry, and high-quality noodles. The interviewees believed that this market accounted for around 10% to 15% of China's wheat demand. However, unlike the case of the highest-quality baking wheat, there was more production in China. In fact, in 2001, domestic producers supplied most of the wheat of this quality into this segment of China's wheat market. In China's domestic market, however, this wheat was considered to be high-quality Chinese wheat. Interestingly, evidence that medium-quality wheat on international markets is the same as high-quality wheat supplied by China's farmers is found in the answer to the question that we asked our interviewees: If China's high-quality wheat were sold on international markets, how much loss would a trader incur? Our survey found that this 10% loss was almost exactly the same as the premium importers would make from bringing in medium-quality grain from the international market.

Finally, although there have been no imports of low- (or lower-medium) quality wheat from international markets, it appears as if China's medium-quality wheat, by far the biggest part of China's production (estimated to be more than 60%), is only marginally protected (Table 4, row 12). Our survey found that traders believed that, if China's medium-quality wheat were sold on the international market in late 2001, it would sell at a discount of about 8%. Another way to interpret this result is that, if international traders could ship this quality of wheat to China, it would command a premium of 8%. With medium-quality wheat being the largest part of China's wheat crop, imports of wheat will be likely after China's entry into the WTO because of the persistent price gap. The effect, however, appears to be less than 10%. China's lowest quality of wheat (about 10% to 15% of its harvest) is at the world's feed-wheat price (row 13). China did export some feed wheat into international markets in 2001 (mostly to Asia, according to an interview). Similar differences in the size of the price gap among varieties of a single grain are found for rice (rows 1 to 4), though not for soybean and maize, which are more homogeneous products (rows 14 and 15).

New NPRs for China

Although there are differences among major types of any individual agricultural commodity, by weighting them by their sown area (for crops) and production (for meats) shares, a set of crop aggregate NPRs can be created (Table 5). Wheat, for example, has an NPR of 12% (row 1) when the individual NPRs from Table 4 are weighted by their area shares. On average, the price of all varieties of domestically produced wheat that are sold in the domestic markets of China's major port (and inland) cities is 12% above the average CIF price of all types of imported wheat varieties. Rice, on the other hand, is implicitly taxed 3%. The aggregate figures, although helpful (and perhaps needed for analysis that is disaggregated only to the crop level), are less interesting and provide much less insight into which groups of farmers in which areas that are producing which varieties will be hurt or helped if trade liberalization reduces distortions.

However, to the extent that certain commodities have less intracrop quality differences, the aggregate measures have more inherent interest. For example, maize and soybeans (and cotton and sugar) have far fewer quality differences among varieties than rice and wheat. In part, this is because maize and soybeans are rarely consumed directly (as are rice and wheat, which make them more sensitive to human tastes and preferences). Instead, maize and soybeans are mostly used as a feed (and animals have fewer taste preferences) or are processed. As a consequence, in our analysis we examine only aggregate crop NPRs for maize, soybeans, cotton, and sugar.[5]

---

[5] We should stress, however, that our survey was conducted the same way. In most cases, interviewees told us that there were not a lot of quality differences among maize varieties. Moreover, when asked if both imported and domestic soybeans were available on the market, what the price difference would be, there was only a slight difference (around 2% to 3%).

Table 5. Average nominal protection rate (NPR) for major imports and exports in China, October 2001.

Major imports and exports	Domestic price (yuan t^{-1})	NPR (%)
imports		
Wheat[a]	1,250	12
Maize	1,150	32
Soybeans	1,950	15
Cotton	9,500	17
Sugar	2,612	40
Exports		
Rice[a]	1,954	-3
Pork[a]	11,442	-30
Beef[a]	13,743	-10
Poultry[a]	9,904	-17
Fresh fruits	5,472	-4

[a] Average NPRs are created by summing the NPRs of individual varieties weighted by the sown area (production) share.
Source: Authors' survey.

Our findings show not only that significantly positive rates of protection exist for several of China's major field crops but also that they vary over the nation and according to the position in which China finds itself (as a net importer or as a net exporter). Maize prices, according to exporters, were more than 30%, on average, above world prices. In other words, exporters would have lost more than 30% of the value of their shipment had the government not paid them a subsidy. Protection rates, when considering maize as an import, differed. For example, traders in the northeast told our survey team that, if they were not exporting and foreign maize were to come into China, importers could make 21%. Our interviews in South China, however, found that the price gap between imported maize (CIF) and maize being traded in the domestic market in and around Guangzhou was more than 30-40%. By aggregating these maize NPRs across regions on the basis of relative shares of national meat consumption, we estimate that China's maize NPR was 32% in 2001 (Table 5, row 2).

Interviewees also reported that, despite the large volume of increase in soybean imports in recent years, there is still a difference between the CIF and domestic price in the port (Table 5, row 3). The average difference between the domestic price and the international price was 15%. On the one hand, the fact that there is a remaining price gap is remarkable given that China imported almost 15 MMTs of soybeans in 2001, the official tariff is only 3%, and the commodity is freely traded without a license or quota allocation. On the other hand, the remaining price gap reminds us that there may be other reasons for distortions beyond tariffs and state trading, a point to which we will return shortly.

Our results also found that cotton and sugar were fairly highly protected in October 2001 (Table 5, rows 4 and 5). The case of cotton, however, is an example of how fast the NPR can change across time. The NPR was measured at 17% in October 2001.

When our team went back to do follow-up work at the end of November, however, the domestic price of cotton had fallen from 9,500 yuan per ton in October to less than 8,000 yuan per ton. With this fall, the NPR dropped to less than zero. However, later in the year, the international price of cotton also dipped, which led to a higher NPR. Being less variable in 2001 in both China's and international markets, the NPR of sugar remained at about 40% throughout the year.

Assessing the new methodology

Since one of our objectives was to use a new data source and method for aggregating NPR data to calculate crop-specific NPRs, it is interesting to analyze what would have happened had we not used this time- and data-intensive survey methodology. To conduct such an "experiment," we used the same methodology, data sources, and assumptions that many people use for calculating NPRs to calculate an NPR for China in 2001.[6] Although the two approaches give almost the same answers for some commodities, such as soybeans and maize (though the NPR for soybeans was still overstated, in part because of the difference in price over the entire year-China's domestic prices fell sharply over the year, suggesting that the NPR in late 2001 was lower than it was in early 2001), the answers vary considerably for other commodities. For example, the national average price for wheat in 2001 reported from the Ministry of Agriculture's reporting system was 1,113 yuan per ton. The average price of imports calculated by dividing total import value by total import quantity was 1,393 yuan per ton. In other words, the domestic price of wheat using these sources of data on prices is 21% below the CIF price of imports. From this standard methodology, one would conclude that wheat, rather than being protected (by 12%—see Table 4), was actually being taxed by trading policies. Yet, as we have seen, China is importing almost exclusively very high grade, baking-quality wheat, while its domestic consumers use mostly medium- and lower-quality wheat. The wrong conclusion is reached when one uses the specialty prices for imports as an international reference price for types of wheat that are of much lower quality and are lower priced.

The same problem is found for rice. Because China imports only high-quality jasmine rice from Thailand, the international price of rice (3,908 yuan per ton—calculated by total import value divided by total import quantity) appears to be more than 167% higher than the average domestic price (1,464 yuan per ton). In fact, as shown in Table 4, China's average price protection (tax) rate, calculated on a variety-by-variety basis, is almost zero (–3).

Thus, according to this illustrative example, we can see the necessity of approaching the estimation of NPRs in a more careful way for some commodities. Using the traditional approaches works fairly well for commodities that are fairly homogeneous in their quality characteristics (such as maize and soybeans). We have seen for the case of wheat and rice for China in 2001, however, that comparing

---

[6] These are computed by comparing the domestic wholesale price with the average implicit price of trade; for the importable (exportable), it is the total value of import (export) divided by the total volume of import (export).

average prices inside and outside of the nation can lead to misleading results. Based on this example, one might conjecture that traditional estimates of NPRs for some products, such as sugar and edible oils, may be fairly reliable. Those for meat products, cotton, and horticulture crops, however, could be misleading.

WTO effects away from the border

Although important in determining the size of the shock at the border, the broader magnitude of the effect of the WTO agreement on China's farmers depends not only on the size of the distortion but also on the size of the area across which it will be felt. This second factor, in turn, is a function of the size and nature of China's market. In fact, at least three factors—policy safeguards (which prevent market forces from fully equilibrating domestic and international prices), household responses (e.g., changing cropping patterns in response to changing prices), and high transaction costs—may limit the effects of WTO entry on farm profitability. In this section, we focus on the nature of markets. The policy safeguards and the effects of household responses are discussed in Taylor (1998) and Huang and Rozelle (2002).

Ultimately, the distributional effects of the WTO will depend on the nature of China's markets. If large areas of the country are isolated from coastal markets where imports land, the effects of the WTO may be circumscribed to restricted parts of the country and should not be expected to have highly adverse effects on the poor, who are largely located in inland areas far from major urban centers. Although being isolated from negative shocks is a plus, there is also a cost. Those living in poor, isolated areas would not benefit from price rises and opportunities to export. However, if markets exist that link distant regions with the coast and price changes in one part of the economy quickly ripple through the economy, even though imports are infused into (and exports flow out of) areas concentrated around a few large coastal cities, they could have ramifications for poor households thousands of kilometers away.

To the extent that transaction costs are high inside China and to the extent that certain domestic markets are isolated from others in the country—especially those inland areas that are isolated from port regions where imports land—it could be that the effects of WTO policies are not evenly distributed. In previous work done on China's agricultural markets (e.g., Park et al 2002), it was found that, in general, China's markets were becoming fairly integrated by the mid-1990s. However, this conclusion should be qualified. First, although markets improved greatly during the early 1990s, the analysis still found that large parts of the country, especially poorer areas, were not completely integrated into national markets in all years. Second, the study's data set is dated. Since the final year of the available data, more than seven years have passed. It is unclear whether markets have matured since that time or whether the actions taken by leaders have led to greater fragmentation (Nyberg and Rozelle 1999). Surprisingly, given the fragile nature of reforming China's agricultural markets, almost no recent work examines these questions.

Assessing the determination of price and market integration in China

To assess how integrated and developed markets in rural China were in the late 1990s and 2000, we first describe the data. Second, we test for integration and conduct direct tests of how well prices in different markets move together and if prices are integrated between market towns and China's villages. Finally, we measure the degree of price transmission.

Data. The data come from a unique price data set collected by China's State Market Administration Bureau (SMAB). Nearly 50 sample sites from 15 of China's provinces report the prices of agricultural commodities every 10 days. These prices are the average prices of transactions that day in the local rural market. The Ministry of Agriculture assembles the data in Beijing, making them available to researchers and policymakers.

We examined rice, maize, and soybean prices from 1996 to 2000. These three crops are produced and consumed in nearly every province in China. Rice price data are available for 31 markets. Because of quality differences among rice varieties in different regions of China, we looked at price integration between markets within four regions: South China (South), the Yangtze Valley (YV), the North China Plain and northwest China (NCP), and northeast China (NE). For the provinces included in the sample, rice prices were available for more than 90% of the time periods. The prices for maize and soybean were available for 13 and 20 markets, respectively.[7] Product homogeneity made it possible to include a broader geographic range of buyers and sellers in a single analysis, and we were able to assess the integration of markets spread out over thousands of kilometers. We compared these results with results from 1988 to 1995 that were produced with the same data and published in Park et al (2002).

Integration tests. In this section, we used more formal tests of market integration. Cointegration statistics measure the proportion of movement in one price that is transmitted to another price during the period of observation. The coefficient on the "causing" price is bounded from 0 to 1, where 0 indicates that there is no effect on the "affected" price variable (and markets are not integrated), and where 1 indicates that markets completely adjust within the analysis period. A coefficient inside the 0–1 interval indicates that prices adjust only partially within the period of observation (or that markets are integrated, but that frictions slow down price transmission). Two markets are cointegrated if the coefficient is not different from 1 at a 5% level of significance.

In the middle part of the reform era (1988 to 1995), a time when markets were starting to emerge, Park et al (2002) show that from 20% to 25% of the markets showed signs that prices were moving together during the study periods and subperiods. According to their findings, although there were many market pairs in

---

[7] Since we use data over time, we need to convert prices to a real basis. Nominal prices from our data set are deflated using the monthly consumer price index calculated and reported by the China National Statistical Bureau. Deflation facilitates transaction cost comparisons across time and allows us to disregard transaction cost increases within periods associated with inflation.

Table 6. Percentage of market pairs that test positive for being integrated based on the Dickey-Fuller test in rural China, 1988 to 2000. [a]

Commodity	1989-95	1996-2000
	(% of market pairs)	
Maize	28	89
Soybeans	28	68
Japonica rice (Yellow River Valley)	25	60
Indica rice (Yangtze Valley and South China)	25	47

[a] Results for two periods from the same data set. For results from 1989 to 1995 for maize and rice, see Rozelle et al(2000). Rice results are for the whole country in 1989-95. Results for soybeans for 1989-95 and all results for 1996 to 2000 are by authors.

which prices did not move together, there was evidence of rising integration from the late 1980s to mid-1990s.

Using the results from the early 1990s as a baseline, our current analysis shows that, during the late 1990s, China's markets continued along their previous path of maturation and that markets in China, especially those for maize, are remarkably integrated (Table 6). In the late 1990s, examining the co-movement of prices between pairs of markets in our sample, we saw a large increase in the number of integrated markets. For maize, for example, the prices in one market moved at the same time as in another in 89% of the cases (Table 6, column 2). This is up from only 28% of the time in the early 1990s. Soybeans and japonica and indica rice also showed large increases (rows 2 to 4). The integration of these markets is notable because, in many cases, the pairs of markets are separated by more than 1,000 kilometers. For example, we find that prices in almost all years are integrated between markets in Shaanxi and Guangdong provinces and between those in Sichuan Province and southern Jiangsu.

Despite the significant progress in integration, our results also show that some pairs of markets are not fully integrated. For example, in one-third of the cases, japonica rice prices changed in one market but not in another. The case of indica rice trade is even more notable. In more than half the cases, prices did not move together in China's indica rice-producing and -consuming regions. One explanation for such a result is that some kind of policy or infrastructure breakdown is creating China's fragmentation, as shown in Park et al (2002). Also, because every province in China has rice production and consumption, if, during a certain year in a certain area, supply in one region is just equal to demand, moderate price movements in another area may not necessarily induce a flow into or out of the region that is in equilibrium.

Even with the nontrivial number of cases in the late 1990s in which market prices in pairs of markets do not move together, based on each of the market performance analyses, one must conclude that the effects of the WTO on China's agriculture will be experienced across wide regions of the nation from coastal to inland areas. However, this is only half of the story. Although there is a remarkable degree of integration between markets on the coast and those inland, such an analysis is still not sufficient to show that China's inland villages will be affected by shocks that hit the coast.

To investigate this possibility, we examine the extent to which villages are integrated into regional markets. Our test of integration will essentially test whether farmers in China's villages are price takers integrated with larger markets or live in isolated villages, where prices are determined by local supply and demand. In briefest terms, if variables that affect local supply significantly affect prices, we will assume that villages are isolated and markets are not integrated to the village level; in contrast, if the local supply shock does not affect prices, villagers are price takers and markets will be thought to be integrated.[8] Our regression analysis clearly shows that markets in China are integrated down to the village level (Table 7). The signs and level of significance of the coefficients on variables, such as the distance that a village is from the market, demonstrate that, the further a village is from a market, the lower the price the farmer receives, which is the expected result. More importantly for our purposes, the t-ratios of the coefficients of the village supply shock variables are all less in absolute value than 1.35, signifying that the output of the local village's crops does not affect the local price. One implication of this result is that it is factors outside the village that are affecting the price that farmers receive, making them price takers. In other words, farmers, even in China's remote villages, are linked to the markets of its main commodities.

Price transmission coefficients

Although integrated markets mean that inland markets will experience price changes in the direction of the price movements at the ports (for those crops that are imported and exported), frictions in the marketing system may shield inland producers from some of the effects. Moreover, as we have seen, despite the rise in price integration in China's domestic markets during the reform period, a significant number of market pairs during certain years still did not move together. Hence, when assessing the

---

[8] The data for this study were collected in a randomly selected, nearly nationally representative sample of 60 villages in six provinces of rural China (henceforth, the China National Rural Survey, CNRS). To accurately reflect varying income distributions within each province, one county was randomly selected from within each income quintile for the province, as measured by the gross value of industrial output. Two villages were randomly selected within each county. The survey teams used village rosters and our own counts to randomly choose 20 households, both those with their residency permits *(hukou)* in the village and those without. A total of 1,199 households were surveyed. The CNRS project team gathered detailed information on both the production and marketing behavior of all the farmers in the sample and the characteristics of each village and its relationship to the nearest regional market. From each individual respondent in the survey in each village, we know the price and timing of the sale for each commodity. From these data, we construct an average village price for each month in yuan per kilogram. In a community questionnaire, we know how far the village's center is from the nearest paved road and the distance to the county market (both in kilometers). Finally, for each crop that the farmer cultivated, we know whether the farmer's crop suffered a shock, recording both the incidence and the percentage by which the yield fell. We do not include any variable that controls for the presence of a community buffer stock system, primarily because such an institution is almost never observed in modern China. In addition, sales among farmers within a village are rare (according to our data, less than 5% of sales).

Table 7. Soybean, maize, and wheat village price regression, 2000.[a]

Explanatory variable	Soybean price[b]	Maize price	Wheat price
Distance to the nearest county market	–0.029 (2.37)**	–0.00064 (–1.63)*	–0.0095 (3.24)**
Village-level shock to production	–0.04 (–0.17)	0.12 (–1.34)	0.081 (–1.02)

[a] Coefficients for timing of sales and net purchase position are not shown.
[b] Numbers in parentheses indicate t-statistics. * = significance at P = 0.05, ** = significance at *P*=0.01.

effects of WTO-induced price shocks at the border on farmers inland, we need to examine the degree of transmission of these effects.

To examine the proportion of the price changes that would be experienced at the port, we conducted a series of analyses to try to measure the extent of the change in prices inland for a percentage change at the port. We did the analysis for the two major crops for which we had complete data series, rice and maize. In the first analysis, we stacked the price data from various markets for the last three years (1998 to 2000) and regressed the price of the inland market (in logs in time period t) on the price at the port market (in logs in time periods t, t-1, t-2, and t-3—Table 8, row 1). The sum of the coefficients on the port variables provided an intuitive measure for the total transmission of price shocks in percentage terms. The price transmission coefficients ranged from 42% to 51% for rice (column 2).[9] According to these measures, about half of the price change at the port was transmitted to the inland market. The transmission coefficients for maize ranged from 51% to 57% (column 1). This means that, if maize prices fell 10% at the border because of the import of an amount up to China's TRQ limit, the price of maize inland would fall around 5%.

The analysis in the above paragraph, however, does not account for the fact that the error term in the equation could be subject to autocorrelation. The corrected transmission coefficients fell only modestly for maize, declining to 49% (Table 8, row 2, column 1). In other words, even after accounting for autocorrelation, if the price at the border (or port) changed by 10%, the inland price fell by nearly 5%. After the same treatment in the rice equations, however, the price transmission coefficient fell sharply (to around only 10%—column 2). According to this result, we found that rice markets are subject to much more friction than maize markets, perhaps a result of the inherent differences between rice (a commodity with a wide range of qualities) and maize (a more homogeneous commodity). In other words, when we observe a price shock in the port market, it may be being caused by the new inflow (or shortage) of a particular type of rice. For example, when a certain type of rice in Guangzhou suffers a shock (e.g., the harvest in one of the production bases is greatly reduced), although the price may move in another production base that also produces that variety, the price in an area that does not produce that variety may not

---

[9] The lower range is a measure of the price effect not including coefficients with t-ratios under 1.58.

Table 8. Transmission coefficients for rice and maize measuring the percentage of price shock at port that is transmitted to inland markets in China, 1996 to 2000. [a]

Technique	Maize	Rice
Standard vector autoregression model (VAR)[b]	51 to 57	42 to 51
VAR with corrections for autocorrelation	49	10 to 13
VAR with impulse response simulation [c]	20 to 35	12 to 25

[a] The transmission coefficient is interpreted at the average proportion of a price shock in the port market that is experienced by the markets inland. [b] Standard vector autoregression analysis stacks the price data from various markets for the last three years (1998 to 2000) and regresses the price of the inland market (in logs in time period t) on the price at the port market (in logs in time periods t, t – 1, t – 2, and t – 3). The sum of the coefficients on the port variables is a measure of the total transmission of price shocks in terms of proportions. [c] This uses the same model as in row 1, but also includes lags of the dependent variable for t – 1, t – 2, and t – 3. Simulation analysis proceeds by shocking the price at the border and following the price from port to inland, holding the own market's price constant.

change. For maize, however, its homogeneous nature means that most of the price shock in one market is passed on by traders.

A third analysis confirmed the finding of the more traditional price transmission model (Table 8, row 3). Using an impulse response analysis (which basically uses the price transmission model and adds a set of lagged own prices—the price in the inland market in periods t – 1, t – 2, and t – 3), we find that a 10% price change in the port price of maize changes the inland price by up to 3.5% and up to 2.8% for rice.

Conclusions

The purpose of this paper was to study the effects of China's accession to the WTO on the agricultural sector. Although other effects on the rural economy from other subsectors may be equally large or even larger, this study's focus on the agricultural sector showed that there will be an impact. However, like other effects, those in the agricultural sector may not all be negative. Our findings, based on new methods to collect data and create NPRs, showed that indeed for some crops entry into the WTO will likely lead to a decline in prices and an increase in imports. Maize and cotton may be most affected. Soybeans and sugar could be significantly affected in the longer run. For some commodities for which China has a considerable comparative advantage, such as rice, meats, and horticulture products, the WTO could provide benefits to those engaged in these activities. The prospect of increased imports of feed grains (e.g., maize and soybeans) at lower prices means that livestock producers could become even more competitive.

The extent to which prices fall from rising imports or rise from increasing exports in part depends on how China executes its WTO obligations. Although there may be room for footdragging (which could delay the negative effects), the nature of the agreement also provides many means to limit the downside effects. Likewise, China's benefits are going to depend on how well its trading partners honor their commitments and provide China with better access to global markets. We suggest that, rather than footdragging, China would be better off to use some of its capital and goodwill to fight measures of its trading partners, such as Japan's safeguards against mushrooms. Here, China already has had a huge, unheralded win by getting Japan to move from its original proposal for using sanitary and phyto-sanitary measures to block imports to safeguards that are transparent and temporary. Complainants against foreign trade barriers in the WTO tend to have a high success rate. In general, to gain the most in the long run from this agricultural agreement, both China and its partners need to endeavor to try to live up to their agreements.

Our paper also found that, unlike the case of Mexico, it appears that most of China's markets may be well integrated into the economy. This is good news and bad news for poor farmers. The good news is that they can benefit from falling input prices and rising export opportunities. The bad news is that, unlike a large number of maize farmers in Mexico who were not affected by NAFTA's reduction in maize import restrictions, if our results are correct for large parts of China, its farmers will be affected. The problem, although it is a short-run one, may be that it is this group of rural households that is most dependent on agriculture and least able to be flexible. As a consequence, our findings should be taken as a warning to government leaders that they need to begin to be concerned about the welfare of these susceptible groups.

References

Anderson K, Peng CY. 1998. Feeding and fueling China in the 21st century. World Dev. 26(8):1413-1429.

CARD. 2001. Effect of WTO on agriculture. Paper presented at the 2001 annual meetings of the American Agricultural Economics Association. Chicago, IL. 5 to 8 August.

Carter CA, Estrin A. 2001. China's trade integration and impacts on factor markets. University of California, Davis. (In mimeo.)

Huang J. 2001. Agricultural policy and food security. Working Paper. Center for Chinese Agricultural Policy, Chinese Academy of Sciences. Beijing.

Huang J, Chen C. 1999. Effects of trade liberalization on agriculture in China: institutional and structural aspects. United Nations ESCAP CGPRT Centre, Bogor, Indonesia.

Huang J, Rozelle S. 2002. Market distortions and the impact of WTO on China's rural economy. Working Paper. University of California, Davis, Calif.

Johnson D, Gale. 2000. WTO and China's agriculture. Can. J. Agric. Econ. 48(4):473-478.

Li S, Zhai F, Wang Z. 1999. The global and domestic impact of China joining the World Trade Organization. A Project Report. State Council (China): Development Research Center.

Martin W. 2002. Implication of reform and WTO accession for China's agricultural policies. Econ. Trans. (Forthcoming.)

Ministry of Agriculture. 2001. China statistical yearbook. Beijing (China): China Agricultural Press.

Nyberg A, Rozelle S. 1999. Accelerating China's rural transformation. Washington, D.C. (USA): World Bank.

OECD (Organization for Economic Cooperation and Development). 2001. Implications of trade and investment liberalization for China's agriculture. Working Paper. Paris (France): OECD.

Park A, Jin H, Rozelle S, Huang J. 2002. Market emergence and transition: arbitrage, transaction costs, and autarky in China's grain markets. Am. J. Agric. Econ. 84:67-82.

Rozelle S, Huang J. 2001. Implications of trade liberalization on China's rural economy. Working Paper. University of California, Davis, Calif.

Rozelle S, Park A, Huang J, Hehui Jin. 2000. Bureaucrat to entrepreneur: the changing role of the state in China's transitional commodity economy. Econ. Dev. Cult. Change 48(2):227-252.

Taylor JE. 1998. Trade liberalization and the impact on smallholders in rural Mexico. Working Paper. Department of Agricultural and Resource Economics, University of California, Davis, Calif.

Tuan FC, Cheng G. 1999. A review of China's agricultural trade policy. Paper prepared for the IATRC Summer Meeting, China's Agricultural Trade and Policy: Issues, Analysis, and Global Consequences, San Francisco, Calif., USA, 25-26 June 1999.

Xie Yuping. 2002. WTO and China's agricultural trade and impact on domestic markets. Unpublished Masters thesis. Center for Chinese Agricultural Policy, Chinese Academy of Sciences, Beijing, China.

World Bank. 2000. An assessment of China's poverty policy. World Bank Working Paper. Washington, D.C. (USA): World Bank.

ZhaoYaohui, Terry Sicular. 2002. Affects of WTO accession on China: labor market responses. Working Paper. Center for Chinese Economic Reform, Peking University, Beijing, China.

Notes

Authors'addresses: J. Huang, director and professor, Center for Chinese Agricultural Policy, Institute for Geographical Sciences and Natural Resource Research, Chinese Academy of Sciences, China; S. Rozelle, professor, Department of Agricultural and Resource Economics, University of California, Davis, USA.

Acknowledgments: The authors are grateful for the research assistance of Yuping Xie. This work could not have been done without him. We also acknowledge the helpful comments and suggestions of Kym Anderson, Fred Crook, Tom Hertel, Ilena Ivanochina, Will Martin, Francis Tuan, and participants at the World Bank-sponsored meeting on the "Impact of Accession into WTO on China." We acknowledge the financial support of the World Bank's Trade and Rural Development divisions.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Appendix A. Challenges and issues in measuring nominal protection rates

The wide range of estimates of NPRs that exist for China demonstrates that it is not a straightforward process to measure the difference between an economy's domestic price and the international price. Several issues complicate NPR measurement. First, confusion may result because policymakers and researchers have sought to summarize the effect of various commodities with a single number. Trade modelers need a single number to make their analytical frameworks tractable. People want to know what is the price of wheat in China and compare that with the world price of wheat. With this information, the NPR of a commodity is simply the ratio of these two numbers.

However, more careful observation shows that the search for a *single* number may be one of the main reasons different analysts can come to *so many different* conclusions. In fact, there are many prices for wheat in China. Prices vary across time within a year. Prices vary across regions within a time period. When calculating the NPR, does one look at the price of maize in a Guangzhou feedlot or the price of maize sitting in storage in a farmer's homemade silo in northeast China? Moreover, rice in particular presents problems because it is a heterogeneous commodity. There are many different varieties and types, all of which command different prices at different places at different times during the year. In fact, for some commodities, such as rice, China is exporting one type at the same time it is importing another. The same sets of issues face analysts when they attempt to choose a price series (or more difficult yet, the single price) to represent the international price. Which price should an analyst choose? Should it be FOB or CIF? Should it be the average annual price or a price during one particular period? And, if there are many different types of imported varieties, which type should be chosen?

In part, because previous studies have not dealt with these issues (at least explicitly), it is unsurprising that different research efforts have produced different estimates of NPR. For example, Tuan and Cheng (1999) estimated quite high and variable NPRs for agricultural commodities. Their estimates for wheat, maize, and soybeans in 1997 were 62%, 15%, and 140%, respectively. On the other hand, Carter and Estrin (2001) found generally negative price distortions. Huang (2001) provided sets of estimates that showed that some products were highly protected and others had negative rates of protection.

U.S. rice policy and support to U.S. farmers: implications for WTO domestic support commitments

D.-S. Lee, L.A. Hoffman, and G.L. Cramer

U.S. government programs and support for rice farmers have been important to rice production and crop income for more than 70 years. The 1996 farm bill focused on producing for the domestic and international market. Government support was minimal until 1998, even though farmers had available the marketing loan program, decoupled production flexibility contracts, crop and revenue insurance subsidies, ad hoc market loss assistance payments, and export assistance programs. Because of high prices and increased farm output, production and stocks reached high levels and prices plunged very low. Therefore, the 2002 farm bill continued most of the provisions of the 1996 bill but provided higher direct payments, countercyclical payments, and target prices to maintain a reasonable farm safety net. The US. provides less agricultural support than some other countries. The URAA ceiling for current aggregate measurement of support for U.S. farmers is $19.1 billion compared with $60 billion for the EU and $30 billion for Japan. The impacts of the URAA on the global rice market have been profound. However, the global rice market continues to be characterized by high levels of trade intervention such as state trading enterprises, high-bound tariff rates, and limited market access gains from tariffication. As a result, WTO member countries submitted proposals on how they intend to further liberalize agricultural trade, which includes the elimination of export subsidies and a further reduction in tariffs and domestic support.

U.S. rice farming has been highly influenced by federal legislation since the enactment of the Agricultural Adjustment Act of 1933. One main objective of US. rice policy has been to support farm price and income, thus providing a safety net for the rice sector. U.S. rice policy and its support to the rice sector have long been a domestic issue, but, since the Uruguay Round Agreement on Agriculture (URAA), they have also become a global issue because of the U.S. obligations encountered under the URAA. The US. agreed to reduce its rice tariffs, export subsidies, and domestic support programs that were distorting trade.

The U.S. is the third-largest exporter of all rice and its global export market share averages 11%,[1] a share that has steadily declined since the early 1980s when the U.S. was the largest exporter. However, the U.S. remains the largest exporter of rough rice. The U.S. is a net exporter of rice, shipping about two-fifths of its production and importing about 5% of the supply. Rice imports have been increasing steadily for the past two decades, accounting for about 9% of total consumption (Wailes 2000). The U.S. exports both indica and japonica rice, in contrast to most countries producing and exporting only one type of rice (Song and Carter 1996). The largest markets for U.S. rice are currently Latin America, the EU, Japan, Saudi Arabia, the Philippines, and Canada.

A major effect of the URAA has been increased global rice trade, especially japonica (Sumner and Lee 2000, Childs and Hoffman 1999, Cramer et al 1999). However, the global rice market continues to be characterized by high levels of trade intervention such as government control through state trading enterprises (STEs), high-bound tariff rates, tariff escalation, limited market access gains from tariffication, and, to a lesser degree, continued use of trade-distorting domestic support programs and export subsidies. The opening of the Doha Development Agenda offers a chance to reduce intervention as it calls for substantial improvement in market access, a phasing out of all forms of export subsidies, and substantial reductions in trade-distorting domestic support.

Since enactment of the URAA, most of the support provided to the U.S. rice sector has been through domestic support, in contrast to border policies or export subsidies.[2] The World Trade Organization (WTO) is interested in a country's domestic support programs because policies that support prices or subsidize production may encourage excess production and distort trade flows by causing a decline in imports in some markets and/or increasing the use of export subsidies. On 13 May 2002, a new U.S. farm bill titled Farm Security and Rural Investment Act of 2002 was signed into law covering a period of 6 years. This new farm bill caused great concern globally. Many wondered whether the U.S. could continue to meet its current or future WTO commitments.

This paper provides an overview of recent U.S. rice policy and support levels for U.S. rice producers. Next, it presents the U.S. domestic support obligations committed to under the URAA and it provides a review of how the URAA categorizes different domestic support policies for rice. Provisions of the new 2002 U.S. farm bill are presented to determine major changes in domestic support from the 1996 farm bill and whether there are any likely problems for maintaining URAA commitments. Lastly, issues that will be important for the U.S. rice sector during the upcoming negotiations of the Doha Development Agenda are identified.

---

[1] Global rice trade averaged 24.1 million metric tons for the past three years (1999-2001), about 6% of global rice production, compared to 18% for wheat, 26% for soybeans, and 11% for coarse grains.

[2] Developed countries, such as the U.S., rely on domestic support policies to provide their producers with a safety net. U.S. tariff rates on rice are very low and export subsidies have not been used since 1995.

Domestic support and the URAA

First, we specify the U.S. domestic support commitments for the URAA and then we explain how the URAA classifies its domestic support between trade- and nontrade-distorting policies. Based on data from 1998, the last U.S. notification to the WTO, we determine the level of contribution of rice to the U.S. "aggregate measurement of support" (AMS).

The URAA distinguishes between domestic support policies that are considered production distorting ("amber box") and nondistorting ("green box") and requires WTO member countries to annually report amber-box support provided to domestic agricultural producers. The total value of support related to policies in the amber box is referred to as the AMS. Countries agree to keep their AMS from exceeding limits specified by the URAA. The domestic support commitment level for the U.S. in 1995 was $23.1 billion, which declined to $19.1 billion in 2000. These limits declined by 20% from the 1986-88 base support level over the implementation period of 1995-2000 for developed countries (13% from the base over the implementation period of 1995-2004 for developing countries) (Hoffman and Dohlman 2001).

Amber-box policies subject to reduction include price supports, marketing loans, direct payments based on current production or price levels, input subsidies, and certain subsidized loan programs. If support for a specific crop is equal to or less than 5% of its production value (10% for developing countries), it is not counted toward the AMS limits. This *de minimis* exemption provides some flexibility to a country in the design of its domestic support policies for specific commodities. Individual commodity support receives much more flexibility from the concept of AMs since the reduction commitments do not apply to specific commodities but to the total value of support for a country.

The marketing loan program benefits for rice were included under the URAA amber-box category. This program's producer benefits depend on the level of current rice production and the announced world price for rice relative to the commodity loan rate. Recent research shows that levels of realized per-unit rice revenues facilitated by marketing loans exceed commodity loan rates when crop prices are relatively low (Westcott and Price 2001). This finding is likely caused by producers receiving program benefits when prices are seasonally low (and benefits high) and selling their crop later in the marketing year when prices have risen. The historical above-loan-rate level of realized per-unit revenues provides a level of expectations of per-unit revenues in subsequent years. This policy effect raises producers' expected net returns and can lead to increased production and exports, depending on the cross-commodity effects.

Market loss assistance (MLA) payments for rice mandated by recent emergency legislation have been notified to the WTO as noncommodity-specific amber-box payments. Each producer's MLA payment is determined by past program participation, not by current production, and in response to market price experiences. Consequently, it does not meet green-box criteria.

The benefits received by rice producers from the crop and revenue insurance programs are considered to be production-distorting amber-box policies under the URAA. Since these programs are administered using noncommodity-specific (generic) provisions, they count toward the U.S.'s AMS only if total benefits from all noncommodity-specific amber-box policies exceed 5% of the total value of U.S. agricultural production.

Direct producer payments under certain production-limiting programs (referred to as "blue-box'' policies) are exempt from reduction (not included in the current AMS) as long as they satisfy specific criteria. Specifically, the program must be production-limiting, with payments based on fixed area and yield, or on 85% or less of the base level of production or fixed number of livestock. The deficiency payments paid to rice producers in crop year 1995 totaled $471 million and were categorized as blue-box because of the area reduction program in effect for that year.

Support from policies with minimal effects on trade or production (green-box policies) is also excluded from the AMS. Examples of these policies include public stockholding, natural disaster relief, marketing and promotion, inspection, extension services, pest and disease control, food aid, and research. They also include producer payments that are minimally distorting to production, such as certain forms of decoupled income support not tied to production, assistance to help producers make structural adjustments, and direct payments under environmental, conservation, and resource retirement programs.

Rice production flexibility contract (PFC) payments are considered green-box because they are decoupled payments. The amount of the producer's PFC payments depends on past program participation and does not depend on current market prices, production, or resources, U.S. rice food aid is currently listed in the "green box" of domestic support.

For 1998, the last year that the U.S. made an official notification to the WTO, U.S. rice support did not contribute to its AMS because of the *de minimis* exemption. The total value of amber-box support was less than 5% of the value of U.S. rice production. Ad hoc MLA payments are reported as non-commodity-specific "amber box" and the sum of these non-commodity-specific expenditures is subject to a *de minimis* exemption equal to 5% of the total U.S. production of all commodities (Tables 1 and 2).[3] Upon checking Figure 1, it should be remembered that few marketing loan benefits were received in 1998-99 and both PFC and MLA payments did not count toward amber-box expenditures because of the aforementioned reasons. However, for the crop years of 1999-2000, 2000-01, and 2001-02, it appears that rice will contribute to the U.S. AMS because of declining market value but increasing marketing loan benefits. Proportionally, rice's expected contribution to the AMS will be small compared with that of the other major grains or dairy and sugar.

Countries with amber-box expenditures on rice for 1998 included Brazil, Colombia, the EU, Mexico, the Philippines, South Korea, Thailand, Turkey, the United States,

---

[3] Items that contributed most to the U.S. AMS in 1998 were price supports for dairy, sugar, and peanuts and marketing loan benefits from cotton, oilseeds, and other grains.

Table 1. U.S. amber-box support for rice and the aggregate measurement of support (AMS), 1995 98.

Crop year	Amber-box support	Value of U.S. rice production (million US$)	5% of production value (million US$)	Rice contribution to U.S. total AMS	U.S. total AMS commitment (billion US$)
1995	11.6	1,514.3	75.7	0	23.1
1996	5.8	1,687.4	84.4	0	22.3
1997	6.4	1,756.1	87.8	0	21.5
1998 [a]	20.8	1,686.6	84.3	0	20.7

[a] 1998 is the latest WTO notification.
Source: WTO country notifications.

Table 2. U.S. domestic support and support reduction commitments, 1995-98.

Policy category	1995	1996	1997	1998
		(million US$)		
1. Market price support using fixed reference prices [a]	6,213.342	5,919.287	5,815.879	5,775.597
Dairy	4,693.182	4,673.964	4,455.156	4,32.299
Sugar	1,107.815	937.187	1,045.454	1,093.254
Peanuts	412.345	308.136	315.269	350.044
2. Asessments paid by producers [b]	(109.479)	(66.607)	(84.335)	(112.268)
3. Nonexempt direct payments [c]	7,118.680	6.629	578.385	4,465.050
Deficiency payments (using fixed reference prices)	7,030.417	0.000	0.000	0.000
Diversion payments	0.000	0.000	0.000	0.000
Certificate payments	0.000	0.000	0.000	0.000
Marketing loan gains (CCC loan-related)	0.000	0.006	161.259	1,038.656
Certificate exchange gains	0.000	0.000	0.000	5.563
Loan deficiency payments (CCC loan-related)	0.001	0.000	2.780	2,779.641
Forfeit subsidy (CCC loan-related)	(0.038)	(0.035)	(2.331)	1.764
ELS cotton payments	0.000	0.000	0.000	0.000
Cotton first-handler payments	0.000	0.000	0.000	0.000
User marketing payments (cotton)	35.000	6.401	416.260	280.072
Rice marketing payments	0.000	0.000	0.000	0.000
Dairy indemnities	0.208	0.257	0.417	0.126
Dairy market loss	0.000	0.000	0.000	200.012
Dairy NE compact	0.000	0.000	0.000	28.000
State subsidies	0.000	0.000	0.000	7.995
Mohair payments	15.087	0.000	0.000	0.000
Wool payments	38.005	0.000	0.000	0.000

continued on next page

Table 2. continued

Hogs and pigs payments (SHOP)	0.000	0.000	0.000	123.221
4. Other commodity-specific support[d]	119.081	78.144	164.739	421.822
Storage payments (cotton and farmer-owned reserves)	4.052		23.663	78.051
Interest subsidy (loan-related)	115.029	78.144	141.076	343.771
5. Commodity-specific totals (1+2+3+4)	13,341.624	5,937.453	6,474.668	10,550.201
6. Noncommodity-specific policies[e]	1,543.451	1,113.407	567.602	4,583.883
Water subsidies	543.300	381.400	348.459	348.459
Grazing program outlays	44.997	50.449	50.808	50.996
Insurance indemnities, less producer premiums paid	906.348	632.752	119.529	746.966
Credit program benefits from state programs	48.806	48.806	48.806	48.806
Crop market loss	0.000	0.000	0.000	2,811.307
Crop multiyear disaster	0.000	0.000	0.000	577.349
Value of production	190,109.694	205,701.345	203,883.653	190,885.951
5% of value of production[f]	9,505.485	10,285.067	10,194.183	9,544.298
7. Total before exemptions and adjustments (5 + 6)	14,885.075	7,050.860	7,042.270	15,134.084
8. Exemptions and adjustments	8,671.216	1,153.202	803.863	4,742.232
Deficiency (bluebox) payments[g]	7,030.417	0.000	0.000	0.000
Noncommodity-specific *de minimis*[f]	1,543.451	1,113.407	567.602	4,583.883
Commodity-specific *de minimis*[f]	97.348	39.795	236.261	158.349
9. Current total AMS (7 - 8)	6,213.859	5,897.658	6,238.407	10,391.852
10. WTO ceiling commitment	23,083.142	22,287.173	21,491.203	20,695.234

[a] Support is total eligible production times the difference between the current administered price and the 1986-88 world reference price. [b] Fees paid by producers to help offset the cost of the commodity programs. [c] Commodity-specific payments, including deficiency payments that are deducted in row 8. With a method similar to that used for market price support, deficiency payments were recalculated using the amount of eligible production times the difference between the administered target price and the 1986-88 reference price (the higher of the loan rate or market price). [d] These are generally input subsidies or other forms of support. [e] Benefits from policies implemented using generic rather than commodity-specific provisions. [f] If the calculated commodity support or noncommodity-specific total is not larger than 5% of its respective total value of production, the support did not have to be included in the current total AMS. [g] These payments are included here because they are exempt "bluebox" payments under Article 6, paragraph 5, of the Agriculture Agreement (payments under production-limiting programs).

Source: World Trade Organization and Economic Research Service (www.ers.usd.gov/briefing/Farm Policy).

Note: This table was updated 11 Sept. 2001.

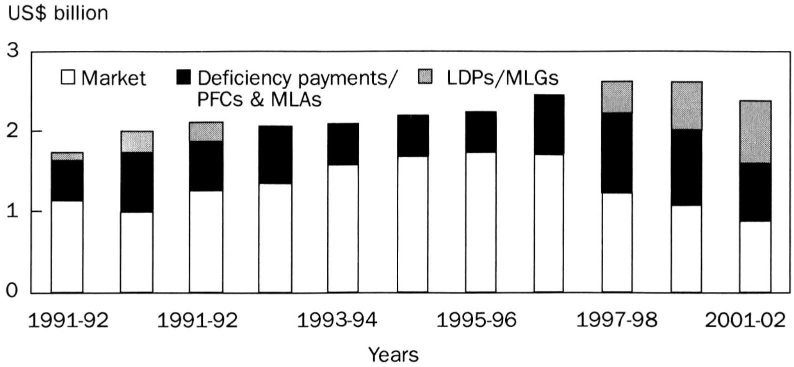


Fig. 1. U.S. rice sector: sources of revenue, 1991-92–2001-02. PFCs = production flexibility contracts, MLAs = market loss assistance, LDPs = loan deficiency payments, MLGs = marketing loan gains. August-July market year. 2001-02 projected. Source: Economic Research Service and Farm Service Agency, USDA.

and Venezuela (Table 3).[4] It is interesting to note that countries such as Brazil, the EU, South Korea, and Thailand have amber-box expenditures that exceed U.S. levels for 1998. Countries with amber-box expenditures on rice in excess of their de *minimus* and thus included in their AMS were Colombia, the EU, Mexico, South Korea, and Thailand (Table 3). Rice constituted a large portion of the AMS for South Korea and Thailand, nearly 80%, but the AMS is small or nonexistent for the EU, Japan, or the U.S. Further reductions in domestic support could eventually reduce support to rice producers, likely causing area and exports to drop. However, since the AMS is not commodity-specific, the new negotiations may want to consider a domestic support reduction mechanism that is commodity-specific. Unless this mechanism becomes commodity-specific, a further reduction in a country's AMS may or may not have an effect on a specific country's rice production.

Domestic support for U.S. rice

National legislation has affected and shaped the U.S. rice sector over the past 69 years, 1933-2002. Price support, income support, and supply control programs made major contributions to the safety-net programs for the U.S. rice sector. A more complete history of U.S. rice support can be found in Setia et al (1994) and Schnepf and Just (1995). To provide a more current understanding of domestic support for the U.S. rice sector, we review the support provided by the 1996 farm bill, crop and revenue insurance, and export assistance and promotional programs for rice.

During 1995, the first year of the URAA implementation period, the U.S. rice sector received most of its support from the provisions of the 1990 farm bill. A bulk of the support came from target price deficiency payments, as no marketing loan

---

[4] Japan converted its rice support from amber-box to blue-box in 1998.

Table 3. Amber-box and blue-box expenditures for rice by WTO member countries, 1998.

Country or region	Amber-box expenditures (million US$)	Amber-box expenditures counted toward AMS[a] (million US$)	Country's rice AMS as a proportion of total AMS (%)	Blue-box expenditures (million US$)	Total amber- and blue box expenditures (million US$)
Brazil	26.4	0.0	0.0	0.0	26.4
Chile	0.0	0.0	0.0	0.0	0.0
Colombia	4.7	4.7	1.2	0.0	4.7
European Union	478.0	478.0	0.1	89.0	567.0
Japan[b]	0.0	0.0	0.0	392.0	392.0
Mexico	5.0	5.0	0.0	0.0	5.0
Philippines	8.0	0.0	0.0	0.0	8.0
South Korea	1,077.0	1,077.0	77.4	0.0	1,077.0
Thailand	394.0	394.0	78.9	0.0	394.0
Turkey	13.3	0.0	0.0	0.0	13.3
United States	20.8	0.0	0.0	0.0	20.8
Venezuela	0.0	0.0	0.0	0.0	0.0
Total	2,027.2			481.0	2,508.2

[a] AMS = aggregate measurement of support. Changed support policies in 1998. They are now counted as blue box instead of amber-box.

benefits were made that year (Fig. 1). During the remainder of the implementation period, 1996-2001, the rice sector received support primarily from PFC payments and marketing loan benefits as provided by the 1996 Farm Act, emergency and supplemental assistance provided by Congress, subsidized crop and revenue insurance, and trade promotion programs such as export credit guarantees.

1996 farm bill

The 1996 FAIR Act significantly changed the price and income support mechanisms for rice and other grains. It established a seven-year payment contract for eligible farmers and ranchers. Under this system, rice producers were provided nearly complete flexibility in planting decisions. Owners of rice base area received a contract payment whether they produced rice or not. Thus, production decisions were determined primarily by relative market returns (Cramer et al 2000a).

Program participants were eligible for PFC payments. The income support program of target price deficiency payments was eliminated along with the Acreage Reduction Program (ARP), 50/85-92, and Normal Flex Acreage/Optional Flex Acreage (NFA/OFA) programs (Table 4). In 2000-01, the PFC payment rate was $2.60 per cwt. Participants received payments on 85% of their contract area based on their program yield (frozen at mid-1980s levels).

In addition to annual PFC payments, a marketing loan program was provided to U.S. rice producers. Producer support under the marketing loan program included both loan deficiency payments (LDPs) and marketing loan gains (MLGs). Payment

Table 4. Farm program base areas, program areas idled, and participation, 1982-83-2001-02.

Crop year	Contract area (000 acres)		Participation rate (%)	ARP as a percent	Area idled/diverted/flexed[b] (000 acres)				
	Total	Enrolled[a]			ARP	CRP	50/8592	NFA/OFA	Total
1982-83	3,969	3,093	77.9	15	422	na	na	na	422
1983-84	3,946	3,857	97.7	15	547	na	na	na	739
1984-85	4,183	3,517	84.6	25	785	na	na	na	785
1985-86	4,234	3,814	90.1	20	682	na	na	na	1,241
1986-87	4,249	3,978	93.6	35	1,305	1	174	na	1,480
1987-88	4,160	3,998	96.1	35	1,325	3	241	na	1,569
1988-89	4,155	3,918	94.3	25	950	4	138	na	1,092
1989-90	4,168	3,906	93.7	25	939	9	245	na	1,193
1990-91	4,154	3,890	93.7	20	735	13	287	na	1,035
1991-92	4,155	3,947	95.0	5	196	13	654	454	1,143
1992-93	4,139	3,989	96.4	0	0	13	446	448	907
1993-94	4,143	4,000	96.5	5	199	13	481	469	1,162
1994-95	4,158	3,969	95.4	0	0	13	258	433	703
1995-96	4,182	3,962	94.7	5	197	13	279	427	916
1996-97	4,176	4,158	99.6	na[c]	na[c]	6	na[c]	na[c]	6
1997-98	–	4,157	–	na[c]	na[c]	4	na[c]	na[c]	4
1998-99	–	4,166	–	na[c]	na[c]	4	na[c]	na[c]	4
1999-40	–	4,153	–	na[c]	na[c]	3	na[c]	na[c]	3
2000-01	–	4,151	–	na[c]	na[c]	3	na[c]	na[c]	3
2001-02	–	4.151	–	na[c]	na[c]	3	na[c]	na[c]	3

[a] Enrolled for area reduction or contract payments. [b] 1983-84 and 1985-86 diverted areas (in 000 acres) are excluded, 192 and 559, respectively. [c] Eliminated under the 1996 farm act. na = not applicable.

Source: USDA, Rice Yearbook, various years, and USDA, Farm Service Agency, Rice Fact Sheet, March 2002.

rates were based on the difference between the announced world price and the established loan rate, with payments resulting when the announced world rice price was less than the loan rate.

Payments received by farmers from the marketing loan program vary from year to year. From 1995-96 through 1997-98, the announced world price exceeded the loan rate, so no marketing loan payments were made. However, in early 1999, when world prices began to fall, marketing loan payments were available. A steady decline in world rice prices pushed these payments to more than $1 per cwt. in August 1999 and, by the end of the 1999-2000 crop year, they exceeded $3 per cwt. For 1999, government payments for the marketing loan program totaled $395 million (Farm Service Agency, etc.).

High rice prices in the mid-1990s increased world production and caused world prices to fall and stocks to rise (Fig. 2). Because of low commodity prices and other problems such as weather-related disasters, the U.S. Congress provided supplemental emergency assistance payments to recipients of PFC payments in 1998, 1999,2000, and 2001. Emergency rice payments for 1998 equaled approximately 50% of that year's PFC payment or $1.45 per cwt. In 1999 and 2000, contract owners received supplemental payments equal to the 1999 PFC payment rate of $2.82 per cwt. The payment rate for 2001 was $2.39 per cwt.

Government payments rose substantially after 1997-98, a result of declining world prices triggering LDPs, MLGs, and MLA payments authorized by Congress. For example, in 1997-98, only PFC payments of $448 million were made to the sector. By 1999-2000, direct payments exceeded $1.3 billion, consisting of $466 million in PFCs, $401 million in LDPs and MLGs, and $465 million in MLAs. Interestingly, government support represented about 22% of total sector revenue in crop years 1995 and 1996, but this proportion rose substantially beginning in 1998 and continuing through 2001-02 to 62%. However, not all of this support is considered significantly trade-distorting by the URAA and is exempt from reductions. Classification of domestic support into trade-distorting and nondistorting policies is discussed in the next major section.

Crop yield and revenue insurance

Producers of specific crops can purchase insurance policies at a subsidized rate, under federal crop insurance programs. These insurance policies make indemnity payments to rice producers based on current losses related to either below-average yields (crop yield insurance) or below-average revenue (revenue insurance) (Table 5). From 1995 to 2001, 55% to 97% of the area planted used some form of crop insurance. Member countries report the indemnity minus producer premium or net indemnity to the WTO as an insurance subsidy. Based on these criteria, domestic support for rice crop insurance has ranged from -$1.1 million to $41.1 million from 1995 to 2001.

Policies are sold through private insurance companies, but the USDA's Risk Management Agency (RMA) subsidizes the insurance premiums, subsidizes a portion of the companies' administrative and operating expenses, and shares underwriting gains

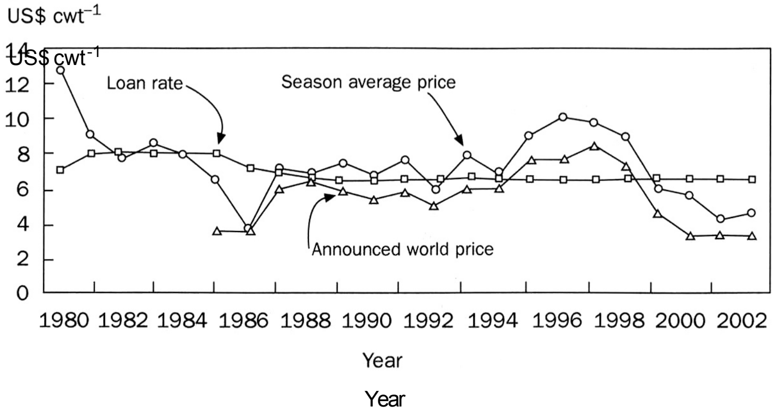


Fig. 2. Price received by U.S. producers, loan rate, and announced world price. 2001 = estimate, 2002 = projection as of 23 Aug. 2002. Source: Economic Research Service, USDA.

Table 5. Federal crop insurance experience for U.S. rice, 1995-2001.

Year	Planted area (million acres)	Insured area (million acres)	Participation (%)	Total premium (million US$)	Premium subsidy (million US$)	Producer premium (million US$)	Indemnity payments (million US$)	Net indemnity (million US$)
1995	3.1	3.0	96.8	11.9	8.9	3.1	5.4	2.3
1996	2.8	1.9	67.9	10.1	7.4	2.7	1.6	-1.1
1997	3.1	1.7	54.8	12.2	8.5	3.7	8.5	4.8
1998	3.3	2.0	60.6	16.5	11.7	4.7	14.1	9.4
1999	3.5	2.6	74.3	32.1	19.4	12.6	53.7	41.1
2000	3.1	2.3	74.2	20.4	11.9	8.4	11.7	3.3
2001	3.3	2.5	75.8	19.8	13.4	6.4	13.8	7.4

and losses with the companies under the Standard Reinsurance Agreement. Premium subsidy rates were raised under the Agricultural Risk Protection Act of 2000, so that most farmers pay around 40% to 50% of the premiums. Insurance is widely available, though coverage is not available for all crops in all areas, and all types of insurance are not available for all crops. Farmers sign up for insurance prior to planting, but usually pay premiums after harvest. Rice can be covered by both yield and revenue insurance (www.ers.usda.gov/briefing/FarmPolicy/insure.htm).

Crop insurance influences production decisions and therefore prices. Government crop insurance subsidies are likely to alter producer behavior because they lower the cost of purchasing coverage. The cost reduction represents a benefit to producers that raises expected returns per area and provides an incentive to expand area in crop production. Research results suggest that area effects of subsidized crop insurance are small. Area planted to rice was expected to rise by 1% and prices were expected to decline by 3% (Young et al 2001).

Export assistance and promotional programs

Although U.S. rice exports receive some assistance, such assistance is not listed under the URAA's export subsidy category. The U.S. donates rice to needy countries either bilaterally or through the World Food Program and sells rice on concessional credit terms. USDA currently provides food aid abroad through three channels: the Public Law 480 (P.L. 480) program, the Section 416(b) program, and the Food for Progress program (Childs 2001). U.S. rice exports under the food aid programs totaled about 400,000 tons in fiscal 2000, about 18% of U.S. rice exports.

USDA provides export credit guarantees for commercial financing of U.S. agricultural exports. The Commodity Credit Corporation (CCC) administers export credit guarantee programs for commercial financing of U.S. agricultural exports to buyers in countries where financing may not be available without CCC guarantees. The Export Credit Guarantee Program (GSM-102) covers credit terms for up to 3 years. The Intermediate Export Credit Guarantee Program (GSM-103) covers longer-term credit for up to 10 years. In addition, under the Supplier Credit Guarantee Program, the CCC guarantees a portion of payments due from importers under short-term financing (up to 180 days) that exporters have extended directly to the importers for the purchase of U.S. agricultural commodities and products. For fiscal 1999 and 2000, annual U.S. rice exports shipped under credit guarantees averaged more than 200,000 tons. Some countries would like to treat these guaranteed export credits as export subsidies and would like to eliminate them.

Lastly, USDA funds the creation, expansion, and maintenance of foreign markets for U.S. agricultural products through marketing programs that help U.S. agricultural exporters finance the marketing and distribution of their products abroad. These marketing promotion programs provide exporters greater access to credit and credit risk protection. Included in this category are the Market Access Program (MAP) and Foreign Market Development (FMD) program (Childs 2001).

2002 farm bill

Next, the provisions for the new 2002 farm bill are examined to gain an understanding of its income support mechanisms and assess changes from the 1996 farm bill. Globally, there is much concern that the U.S. may not be able to meet its current or even future WTO commitments.

Selected rice provisions of the 2002 farm bill

The 2002 farm bill[5] continues the marketing loan program,[6] planting flexibility, and direct payments but creates a new countercyclical payment.[7] Direct payments replace the PFC payments from the 1996 Act and countercyclical payments replace ad

---

[5] Farm Security and Rural Investment Act of 2002.

[6] Compared to the 1996 Farm Act, additional commodities are eligible for marketing loan benefits: peanuts, wool and mohair, honey, small chickpeas, lentils, and dry peas.

[7] Compared to the 1996 Farm Act, additional commodities, such as soybeans, minor oilseeds, and peanuts, are eligible for direct and countercyclical payments.

hoc MLA payments provided by Congress on an annual basis since 1998. Provisions for subsidized crop and revenue insurance and export assistance have been extended with the new bill.

Nonrecourse marketing assistance loans. The new law calls for a continuation of nonrecourse marketing assistance loans and their use is intended to minimize potential loan forfeitures and subsequent government accumulation of stocks. Under the 1996 Farm Act, the loan rate for the 1996 through 2002 crops of rice was $6.50 per hundredweight, with this rate being differentiated for long-, medium-, and short-grain rice. Under the new law, this loan rate remains at $6.50 per hundredweight, with differentiation for grain length. Since the rice loan rate remained the same but loan rates for competing crops such as soybeans and soft red winter wheat declined, there could be an incentive to produce more rice during periods of low prices.

This loan program allows rice producers to receive a loan from the government at a commodity-specific loan rate using the crop as collateral. A producer may obtain a loan for all or part of the new rice production after harvest. Producers may repay this 9-month marketing assistance loan in one of three different ways: (1) at the loan rate plus interest, (2) forfeit the loan collateral crop to the Commodity Credit Corporation at loan maturity or (3) at the prevailing world market price (adjusted for U.S. quality and location).

If market prices are below the loan rate, producers are given the option to repay the loan at a lower loan repayment rate. For rice, this is the adjusted world market price computed on a weekly basis. If the producer repays the loan at an adjusted world market price, the difference between the loan rate and loan repayment rate is referred to as an MLA and is considered a benefit to a producer. Any accrued interest on the loan is waived.

Furthermore, an eligible producer may choose to receive marketing loan benefits through an LDP when market prices are lower than commodity loan rates. The LDP option allows the producer to receive the benefits of the marketing loan program without taking out the commodity loan. The LDP rate is the amount the loan rate exceeds the adjusted world market price.

Direct payments. Direct payments are available to eligible producers of rice. An annual agreement must be signed to receive these payments. Direct payments for rice are $2.35 per cwt. and remain the same from 2002 to 2007 (see Box 1). For crop years 2003-07, payments are to be made no sooner than 1 October of the year the crop is harvested. An advance payment of up to 50% can be made beginning 1 December of the calendar year before the year when the rice crop is harvested.

These payments are considered decoupled from current production and are made based on 85% of the base area. Although direct payments are likely to be classified as green-box payments, they do lead to increased wealth and greater investment. Some WTO member countries are calling for elimination of all green-box payments.

Box 1. Estimates of average annual PFC payments for 1996-2002 and maximum annual direct payments for 2002-07.

Payment rate Payment acres Payment yield

PFC payments

(1996 Farm Act \$2.57 cwt.$^{-1}$ × 3.532 million × 4,816 lbs acre^{-1}) = \$437.2 million

Direct payments

(2002 Farm Act \$2.35 cwt.$^{-1}$ × 3.528 million × 4,815 lbs acre^{-1}) = \$399.2 million

Countercyclical payments. These payments are made to owners of a rice base when the effective price is less than the rice target price of \$10.50 per cwt. (Table 6). The effective price is equal to the sum of (1) the higher of the national average farm price for the marketing year or the national loan rate for the commodity and (2) the direct payment rate for the commodity. The countercyclical payment for a farmer equals the product of the payment rate, the payment area, and the payment yield. These payments could be viewed as a risk-reducing income hedge when electing to produce.

The maximum countercyclical payment rate per year is \$1.65 per cwt. for 2002-07 compared with the ad hoc average MLA payment rate of \$2.37 per cwt. for 1998-2001. The payment acres are expected to remain virtually unchanged at 3.528 million. The payment yield is expected to increase by about 872 lbs acre^{-1} or 18% to 5,687 Ibs acre^{-1}. Based on these aggregate calculations, it is estimated that annual countercyclical payments could be about \$72.2 million less than previous ad hoc MLA payments. This would represent less amber-box non-commodity-specific support than under the 1996 Farm Act. If domestic U.S. prices rise above the loan rate, estimates of countercyclical payments would decline (see Box 2).

Box 2. Estimates of average ad hoc MLA payments for 1998-2001 and maximum annual countercyclical payments for 2002-07.

Payment rate Payment acres Payment yield

PFC payments

(1996 Farm Act \$2.37 cwt.$^{-1}$ × 3.533 million × 4,816 lbs acre^{-1}) = \$403.3 million

Direct payments

(2002 Farm Act \$1.65 cwt.$^{-1}$ × 3.528 million × 5,687 lbs acre^{-1}) = \$331.1 million

Countercyclical payments for rice are made as soon as practicable after the end of the crop year. The timing of these payments occurs in the following manner: up to 35% of the payment shall be made in October of the year the crop is harvested, a second payment of up to 70% minus the first payment shall be made after 1 February, and the final payment shall be made as soon as possible after the end of the crop year.

Base area. Landowners will be able to update base area if so desired. One of two choices must be made: (1) update the rice base area to capture a 4-year average of planted area plus "prevented from planting" for the crop years 1998-2001; (2) use

Table 6. Maximum countercyclical rates for 2002-07 and selected policy parameters for the 2002 farm act.

Commodity	Maximum [a] countercyclical payment rate		Target price		Direct payment		Loan rate		Minimum[b] effective price	
Rice ($ cwt^{-1})	1.65	1.65	10.50	10.50	2.35	2.35	6.50	6.50	8.85	8.85
Wheat ($ bu^{-1})	0.54	0.65	3.86	3.92	0.52	0.52	2.80	2.75	3.32	3.27
Maize ($ bu^{-1})	0.34	0.40	2.60	2.63	0.28	0.28	1.98	1.95	2.26	2.23
Sorghum ($ bu^{-1})	0.21	0.27	2.54	2.57	0.35	0.35	1.98	1.95	2.33	2.30
Barley ($ bu^{-1})	0.09	0.15	2.21	2.24	0.24	0.24	1.88	1.85	2.12	2.09
Oats ($ bu^{-1})	0.03	0.09	1.40	1.44	0.02	0.02	1.35	1.33	1.37	1.35
Soybeans ($ bu^{-1})	0.36	0.36	5.80	5.80	0.44	0.44	5.00	5.00	5.44	5.44
Peanuts ($ t^{-1})	104	10	495	495	36	36	355	355	391	391

[a] The first column reflects 2002-03 payment rates and the second column represents 200407 payment rates. [b] Minimum effective price equals loan rate plus direct payments.
Source: USDA, 2002; www.ers.usda.gov/features/farmbill/.

2002 PFC payment area as the new base for rice and add oilseed bases using a 4-year average of planted area plus "prevented from planting" for individual oilseeds during crop year 1998-2001. In general, oilseed base area cannot exceed the difference between total area for covered crops for the crop year and the sum of 2002 contract area.

Landowners have a one-time opportunity to select a method for determining base area. Anyone not making a decision will be assigned option 2. Lastly, base area cannot exceed available cropland. Adjustments to base area can be made when a conservation reserve program contract expires or is voluntarily terminated.

This update can affect calculations for both direct and countercyclical payments and can create an incentive to build a base area and also protect existing base areas. However, in the aggregate, it is not expected to affect rice because the current base areas for rice in the aggregate are larger than the more recent area planted to rice.

Payment areas. Payment areas for either direct payments or countercyclical payments are equal to 85% of the newly updated base areas.

Program yield. Payment yields for direct payments are not changed from those used in the 1996 Act except for soybeans and other oilseeds, which were added to the program. Yields for oilseed payments will be determined by the farm's 1998-2001 average yield multiplied by the national average yield for 1981-85, divided by national average yield for 1998-2001.

Payment yields for countercyclical payments may be updated during the signup period with one of the following two choices: (1) add 70% of the difference between program yields for the 2002 crop and the farm's average yields for 1998-2001 to program yields or (2) use 93.5% of the 1998-2001 average yields. If there is a year when the actual yield is less than the county average yield, yield will be 75% of county average yield. Updating yields creates an incentive for increasing yields.

Commodity certificates. A rice producer may purchase commodity certificates in exchange for the outstanding loan collateral at or before loan maturity. The comodity certificate can be purchased at the repayment rate in effect on the date of the request. Any market gain realized from a commodity certificate exchange is not applied to payment limitations but is considered income to the producer. These provisions enable producers who are facing payment limits an opportunity to benefit from the lower repayment rates.

Payment limits. MLGs and LDPs are $75,000 per person per crop year, $40,000 per person for direct payments, and $65,000 for countercyclical payments. The three-entity rule is retained. Under the three-entity rule, an individual may receive a full payment directly and up to a half payment for each of two additional entities. Producers having an adjusted gross income over $2.5 million, and averaged over 3 years, are not eligible for payments, unless more than 75% of the adjusted gross income comes from agriculture.

Uruguay Round compliance. If the U.S. AMS ceiling is expected to be exceeded, the Secretary of Agriculture is required to adjust expenditures to avoid exceeding allowable levels. Before these adjustments are made, the Secretary must report to Congress on the proposed changes. This provision assures that the United States will not exceed its WTO limits. Although domestic spending levels may appear high with the 2002 farm bill, some analysts think that they should not be higher than what has been provided to U.S. farmers over the past few years when ad hoc MLA payments were added to annual farm program costs. Much of the new support will be minimally trade-distorting (www.ers.usda.gov/features/farmbill).

Income support provisions of the 2002 farm bill

The 2002 farm bill provides income support to the rice sector from three sources: marketing loans, direct payments, and countercyclical payments. This compares with sources of income support from the 1996 farm bill such as marketing loans, PFC payments, and ad hoc MLA payments provided by Congress. In general, it is not certain, but income support payments under the new legislation should not be that much greater than in the later period covered by the 1996 farm bill, especially for rice.

However, it is still uncertain how the new income support policies will be categorized by the URAA. For example, there probably will be little debate over marketing loan benefits, but direct and countercyclical payments should receive more discussion because of base and yield updating potential and selected blue-box characteristics. Since the reduction commitments do not apply to specific commodities but to the total value of support for a country, it is difficult to say that increased amber-box expenditures for one commodity will violate a country's URAA domestic support commitment. However, since the AMS is not commodity-specific, the new negotiations may want to consider a domestic support reduction mechanism that is commodity-specific.

Trade barriers and issues for further trade liberalization

In November 2001, more than 140 WTO member nations agreed to launch a new round of multilateral trade negotiations. These negotiations, called the Doha Development Agenda, seek to reduce and possibly phase out all forms of export subsidies, improve market access, and reduce trade-distorting domestic support. These upcoming negotiations could expand global markets and reduce trade barriers.[8] The US. proposal, as of 25 July 2002, is calling for a two-phase process. The first phase eliminates export subsidies and reduces worldwide tariffs and trade-distorting domestic support over a five-year period. The second phase is the eventual elimination of all tariffs and trade-distorting domestic support (www.fas.usda.gov/itp/wto/proposal.htm).

Market access

In the area of market access, U.S. tariffs on agricultural imports average 12% compared with more than 60% for all WTO members, more than 50% for Japan, and more than 30% for the EU and Cairns group of 17 agricultural-exporting nations. Base-

---

[8] Trade liberalization issues regarding rice trade can be found in "Upcoming World Trade Organization Negotiations: Issues for the US. Rice Sector" in *Rice Situation and Outlook Yearbook,* RCS-1999, US. Department of Agriculture, November 1999.

period rice tariffs in the U.S. were already low at $22 per metric ton for milled rice. The U.S. reduced milled rice tariffs to $14 per metric ton by 2000. Rice imports have been increasing steadily for the past two decades. Although the URAA provided for some increased market access, there is potential for additional and more stable access if high-bound tariff rates are reduced, tariff quotas are increased, or out-of-quota duties are substantially reduced. Trade barriers in the global rice market continue to exist, most noticeably in the areas of tariff and nontariff barriers, unfair trading practices, and preferential trading arrangements in key markets.

Lowering tariffs and expanding tariff-rate quotas (TRQs) will focus primarily on increasing Japan and South Korea's minimum access imports from the URAA. These two markets are critical for expanding global trade in japonica rice. Without a new agreement, Japan's TRQ will remain at 7.2% of base-period (1986-88) consumption after 2000. Recent tariffication by Japan has slowed the increase in minimum access imports and placed a prohibitively high tariff on above-quota imports. South Korea's imports will be 4% of base-period (1986-88) consumption in 2004.

A big reduction in Japan's tariff rate on over-quota imports would expand trade further. In addition, China's accession to the WTO would open a potential large market to foreign rice and possibly allow the U.S. to capture a niche market for high-quality rice. The U.S. may capture a large share of Taiwan's minimum access imports, mostly japonica rice.

The EU still maintains high tariffs on imported rice, especially for milled rice, limiting imports mostly to brown rice that is fully milled in the EU. A reduction in EU tariffs on milled rice could boost imports, although intervention buying is currently the primary means of domestic support in the EU. The EU is considering adoption of a new rice regime that would rely more on tariffs and end intervention buying to support domestic prices. This would make tariff reduction more important. Developing-country exports to the EU appear very likely because of the "everything but arms" arrangement that extends duty-free access to the EU.

Regional trading agreements hinder U.S. rice exports in much of Latin America by applying higher tariffs on U.S. rice. Greater trade liberalization would end this tariff differentiation. Tariff rates for U.S. rice are already low and further reductions would have little effect on imports, mostly Asian aromatics not grown in the U.S.

Domestic support

The new round of negotiations has brought attention to the trade-distorting policies of developed countries, such as the EU, Japan, and the U.S. Developed countries account for virtually all domestic support and export subsidies, which distort agricultural markets worldwide. However, the U.S. subsidizes its agricultural products less than other countries. Currently, the U.S. AMS ceiling is $19.1 billion, as mentioned earlier, compared with the EU's AMS ceiling of about $60 billion and Japan's ceiling with respect to trade-distorting policies of $30 billion.

Reducing trade-distorting domestic support programs for agriculture has had a limited effect on rice production in developed or developing countries-which account for the bulk of global rice production. Several reasons account for this noneffect. First, the URAA allowed developing countries "special and differential" exemptions for certain input and investment subsidies, which cover most programs used to support rice production in these countries. Second, trade-distorting price support measures are not subject to reduction if in total they do not exceed 10% of the value of production, the developing-country *de minimis* provision, or 5% for developed countries, as mentioned earlier. Third, some countries, such as Japan, have reinstrumented their rice policy. As of 1998, what had been amber-box has been converted into a blue-box policy. Lastly, limiting a country's AMS is not commodity-specific and individual commodity support receives much more flexibility.

Countries that reported amber-box expenditures on rice include Brazil, Chile, Colombia, the EU, Japan, Mexico, the Philippines, South Korea, Thailand, Turkey, the United States, and Venezuela. For the 1998 WTO notification, rice was included in the AMS for the following countries: Colombia, the EU, Mexico, South Korea, and Thailand, as mentioned previously (Table 6). The United States' new proposal calls for a limit to all countries' use of trade-distorting support to 5% of the value of agricultural production, with reductions made from current caps over a five-year period. Further reductions to the AMS could eventually reduce support to rice producers, likely causing area and exports to decline (www.fas.usda,gov/itp/wto/proposal.htm).

Export subsidies

The EU is the only region currently using export subsidies for rice. The U.S. discontinued its use of these rice subsidies in 1995. Developing countries rarely use export subsidies.

EU rice export subsidies totaled $28.2 million in 1999, 65% of their value commitment, and their volume totaled 140,000 metric tons, 101% of their quantity commitment. Elimination of EU rice export subsidies would lower EU rice exports and potentially open some markets for the U.S. in the eastern Mediterranean and Eastern Europe. However, there may not be much potential here because the EU is a small exporter and many of its exports involve special trading arrangements.

State trading enterprises (STEs)

The upcoming negotiations will look to further discipline activities of state trading enterprises (STEs). Of major concern is the lack of transparency in pricing by STEs and the possibility that some countries are using STEs to circumvent URAA rules. Price discovery is complicated by STEs as they segregate markets by price. Countries that use STEs account for about one-half of global rice exports and about one-third of rice imports. STEs account for much of the rice trade for several WTO member countries: Indonesia, Malaysia, Australia, the Philippines, South Korea, and China. Several countries seeking WTO accession—Vietnam and Russia—use STEs to conduct rice trade.

Conclusions

U.S. government programs and support to rice farmers figure prominently in rice production, with a major part of crop income derived from direct government payments (Cramer et al 2000b). The government also supported exports with credit assistance and market access and development. The 1996 farm bill focused on producing for the market with a reduced safety net. Government support was in the form of marketing loan benefits, decoupled PFC payments, crop and revenue insurance subsidies, ad hoc MLA payments, and export assistance programs, The 2002 farm bill continues programs from the 1996 bill, with direct payments replacing PFC payments and countercyclical payments replacing ad hoc MLA payments.

The U.S. provides less agricultural support than other countries. The current AMs for the U.S. is $19.1 billion and it will remain at this level until a new WTO agreement is reached. Under the new farm bill, government support for rice is not expected to exceed the later years of the 1996 farm bill. A new WTO agreement is expected to further reduce domestic support levels. Unless future reductions in domestic support are made commodity-specific, it is unclear that further reductions in the AMs will necessarily translate into domestic support reductions for each commodity. With less government support, production could decline not only for the U.S. but also for Brazil, the EU, South Korea, and Thailand. However, some countries have reinstrumented their policies, such as Japan, and can therefore bypass reductions in amber-box support. However, the effects of increased market access could offset any changes caused by reduced domestic support.

In the meantime, in 2000, WTO member countries submitted proposals on how they intend to further liberalize agricultural trade. Issues raised by various proposals that will affect rice trade liberalization in the current negotiation round include market access, domestic support, export competition, state trading enterprises, and special and differential treatment for developing countries. In addition, the WTO accession of China will be important for agricultural trade liberalization for rice. China has agreed to reduce all agricultural tariffs to an average of 17%. Rice will have a low in-quota tariff and set-quota levels for 2002 through 2004. Nonstate trading companies will be given a share of the imports. Although China is not required to purchase the entire TRQ, imports will be based on market conditions rather than policy or economic planning considerations (USDA 2002a,b).

Rice remains one of the most protected global agricultural commodities. Reforms of the Uruguay Round resulted in a significant increase in global rice trade. Completion of the ongoing negotiations holds promise that additional reforms will expand rice trade and improve the welfare of both producers and consumers. Moving toward greater market orientation and an orderly international agricultural trading system is important for rice producers in the U.S. and the rest of the world.

References

Childs NW. 2001. Rice: background and issues for farm legislation. Electronic Outlook Report from the Economic Research Service. www.ers.usda.gov. RCS-0601-01, July 2001.

Childs NW, Hoffman L. 1999. Upcoming World Trade Organization negotiations: issues for the U.S. rice sector. Rice Situation and Outlook Yearbook. USDAIERS.

Cramer GL, Hansen JM, Young KB. 2000a. The United States and world rice industries. In: Competition in agriculture: the United States in the world market. Binghamton, N.Y. (USA): Haworth Press.

Cramer GL, Young KB, Wailes EJ. 2000b. Rice marketing. In: The U.S. rice industry. John Wiley and Sons.

Cramer GL, Wailes EJ, Hansen JM. 1999. Impact of rice tariffication on Japan and the world rice market. Am. J. Agric. Econ. 81:1149-1156.

Hoffman LA, Dohlman E. 2001. The new agricultural trade negotiations: background and issues for the coarse grain sector. Feed Situation and Outlook Yearbook. p 25-45.

Schnepf RD, Just B. 1995. Rice: background for 1995 farm legislation. Agric. Econ. Rpt. No. 713. USDAERS.

Setia P, Childs N, Wailes E, Livezey J. 1994. The U.S. rice industry. Agric. Econ. Rpt. No. 700. USDAERS.

Song JH, Carter CA. 1996. Rice trade liberalization and implications for U.S. policy. Am. J. Agric. Econ. 78:891-905.

Sumner DA, Lee H. 2000. Assessing the effects of the WTO agreement on rice markets: What can we learn from the first five years? A paper presented at the Allied Social Sciences Association Conference, Boston, Massachusetts, January 2000.

USDA (U.S. Department of Agriculture). Economic Research Service. Rice Situation & Outlook. Various issues.

USDA (U.S. Department of Agriculture). 2002a. Farm Services Agency. Fact sheet: rice—summary of 1996-2001 program and related information. March. www.fsa.usda.gov/pas/publications/factslhtml/rice02.htm.

USDA (U.S. Department of Agriculture). 2002b. USDA agricultural baseline projections to 201 1. Staff Report WAOB-2002-1, February. p 96-97.

Wailes E. 2000. Trade liberalization in rice. A paper presented at the Global Agricultural Trade in the New Millennium Conference, New Orleans, Louisiana, USA.

Westcott P, Price JM. 2001. Analysis of the U.S. commodity loan program with marketing loan provisions. Agric. Econ. Rpt. No. 801. USDAERS.

Young CE, Vandeveer ML, Schnepf RD. 2001. Production and price impacts of U.S. crop insurance programs. Am. J. Agric. Econ. 83(5):1196-1203.

www.ers.usda.gov/briefing/FarmPolicy/insure.htm

www.ers.usda.gov/featuresffarmbill/

www.fas.usda.gov/itp/wto/proposal.htm

Notes

Authors' addresses: D.-S. Lee and G.L. Cramer are assistant professor of research and professor and department head, respectively, at Louisiana State University, Baton Rouge, LA. L.A. Hoffman is an agricultural economist at the Economic Research Service, USDA, Washington, D.C.

The authors' views do not necessarily represent those of the U.S. Department of Agriculture.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.

Equity effects of rice trade liberalization in the Philippines

D. Dawe

Although many developing countries have a history of taxing the agricultural sector, domestic rice prices in the Philippines are substantially above current world price levels, resulting in high effective rates of protection. This has been a chronic situation for the past 15 years. This paper takes a preliminary look at the effects that trade liberalization might have on (1) the rural landless and (2) land-owning rice farmers using various disaggregated data on incomes, expenditures, and production costs and returns. The rural landless are the poorest of the poor in the Philippines and they constitute a large percentage of the population. Higher prices have two effects on this group. First, the landless are net rice consumers, so higher prices reduce their effective purchasing power. Second, high rice prices might raise the demand for unskilled labor, thus increasing the wages of unskilled labor. These two effects have opposite implications for welfare, but various evidence suggests that the first effect dominates the second, so that the rural landless would benefit from liberalization. Rice farmers benefit from current policies and would be hurt by liberalization, but the brunt of liberalization would fall on large farmers with higher incomes. Small farmers would be less affected because they have smaller marketable surpluses. However, it cannot be denied that many small rice farmers are also poor and would be hurt by liberalization.

Trade liberalization would likely lead to substantial reductions in dry-season area planted to rice, whereas wet-season rice would be less affected. A reduction in dry-season rice area would facilitate crop diversification into vegetables and would likely lead to increased demand for rural labor, which would help the rural landless. Substantial reductions in domestic rice prices in the Philippines would thus simultaneously increase economic efficiency, improve the welfare of those at the bottom of the income distribution, facilitate crop diversification, and accelerate the transition of the labor force to higher-productivity industrial and service sectors. The Philippines has not made substantial commitments to rice trade liberalization under GATT/WTO, but, if high trade barriers remain in place, conflicts with commitments under the ASEAN Free Trade Area (AFTA) might occur.

As is true throughout developing Asia, rice is the single most important commodity in the Philippines, where it accounts for about 40% of caloric intake and 30% of protein consumption, and more than 20% of expenditures for the bottom one-fourth of the income distribution. It is also the most widely planted crop in the Philippines, currently accounting for more than 30% of total agricultural area harvested. Finally, it is an important source of income for many farmers: for rice farm households, income from rice accounts for about half of household income on average.

For the past 15 years, domestic rice prices in the Philippines have been much higher than prices in other countries or on world markets, with domestic retail prices often reaching levels 100% higher than would be the case if unrestricted imports were allowed. Furthermore, the Philippines has entered into various international trade agreements that could reduce this protection for rice in the next decade. Because of rice's importance in consumption, production, and rural livelihoods, as well as the large degree of protection currently afforded the rice sector, rice trade liberalization is an important and controversial subject.

The goal of this paper is to contribute to an improved understanding of the effects of the current high price policy. More specifically, the major objective of this paper is to examine the equity effects of this policy by comparing effects on nonrice farmers, rural landless laborers, and different classes of rice farmers. Before achieving this objective, I will first briefly describe the history of Philippine rice policy and explain why the Philippines is a net rice importer. Next, I will outline the main effects of the high price policy, followed by a more detailed discussion of the equity effects on different groups in society. I conclude with some policy implications.

A brief history of rice prices in the Philippines

In the Philippines, the rice sector has a long history of protection from import competition, with domestic prices typically being above world market prices for comparable grain quality (Bouis 1982, Dawe 1993). Figure 1 shows a graph of domestic prices in Manila compared with world market prices in Bangkok from 1950 to the present, with Bangkok prices adjusted for transport costs and quality to reflect the landed price at the Philippine border. These prices are in real terms, that is, they are adjusted for inflation into 2001 Philippine pesos. The graph shows that domestic prices have been consistently above world market prices for most of the past half-century, although there have also been periods when domestic prices were more or less in line with world prices.

Timmer (1993) shows that Asian countries try to keep their domestic prices stable over time. He argues that deviations of domestic prices from world prices are not determined by explicit policy decisions influenced by the relative bargaining power of farmers and consumers, but rather are endogenous given the goal of domestic price stability, exogenous changes in world market rice prices in U.S. dollar terms, and exogenous changes in the exchange rate. This pattern can be seen clearly for the Philippines in Figure 1. During the 1950s, domestic prices were substantially above world prices. When world prices increased in the early 1960s (in constant peso terms),

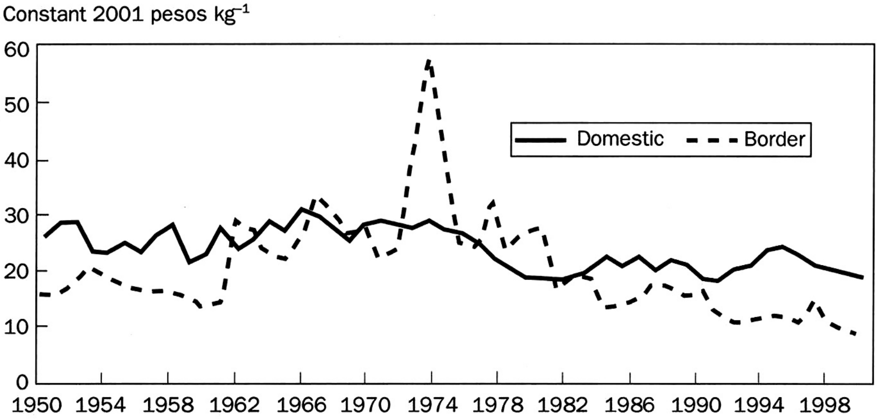


Fig. 1. Domestic and border prices for rice, Manila, 1950-2001.

domestic prices remained constant, erasing the previous nominal protection. Thus, while domestic prices were relatively constant from 1950 to the early ’70s, the degree of nominal protection changed substantially as world price equivalents changed. In the early 1970s, there appeared to be an exception to this trend, as domestic prices declined substantially. This may suggest some policy flexibility on the part of the government, but in reality there was little choice for Philippine policymakers. As the Green Revolution technologies gathered steam, there was a pronounced outward shift of the domestic supply curve. This put downward pressure on domestic prices. At the same time, world prices were also declining in constant peso terms. Thus, it was not possible to keep domestic prices constant by exporting at world market prices. In this environment, the only way to keep domestic prices constant would have been through export subsidies or continual accumulation of domestic stocks. Both of these alternatives would have required large government financial support that was not feasible at the time.

Since the domestic price decline of the late 1970s, prices have remained approximately constant in real terms since 1980. However, as world prices have continued to decline in the past 20 years, the gap between domestic and world prices has widened once again, and there is now substantial protection afforded the domestic rice sector. A farm survey of several “rice bowls” in Asia conducted every year from 1994 to 1999 showed that farm prices for paddy in the Philippines were on average \$0.28 kg^{-1} compared to a range of \$0.12 to \$0.16 kg^{-1} in Indonesia, Thailand, Vietnam, India, and China (Moya et al, n.d.). These data refer to prices received by farmers, so they do not indicate that trading margins are higher in the Philippines than in neighboring countries.

It is not clear how long this protection will last. As part of the Uruguay Round Agreement on Agriculture (URAA), the Philippines agreed to certain minimal levels of annual imports, but this is not an effective constraint on policy, as current imports exceed this level every year in any event. The URAA reached no binding agreements on the import privileges of state trading enterprises (STEs), so there are no effective constraints in that agreement on the import monopoly of the National Food Authority (NFA). Under the guidance of the Association of Southeast Asian Nations (ASEAN), however, the Philippines has made more extensive commitments under the ASEAN Free Trade Agreement (AFTA). Under AFTA, the Philippines has agreed to eliminate all nontariff barriers on rice by 2010 for intra-ASEAN trade; however, the Philippines has not yet agreed to a maximum tariff for such trade.

Why does the Philippines import rice?

Despite the price protection afforded the rice sector, the Philippines remains a rice importer, as it has been for more than 130 years (with the exception of a few years in the late 1970s and early 1980s). In recent years (1996-2000), imports have accounted for 14% of total supplies.

Why does the Philippines appear to have a comparative disadvantage in rice production relative to the major world exporters? Many observers point to a variety of agricultural policy problems in the Philippines (e.g., irrigation, credit, postharvest losses), but such problems are common in developing countries and are not restricted to the Philippines. Thus, they are not good candidates for an explanation of comparative disadvantage unless it can be shown that they are substantially worse in the Philippines. There is little evidence for this latter assertion. Instead, more fundamental forces of land quantity and quality are likely at work (Dawe and Castillo 2001).

First, the quantity of arable land per person is much lower in the Philippines than in most other Asian countries (Table 1). The traditional rice exporters of the 20th century (Thailand, Myanmar, Cambodia), on the other hand, all have relatively large quantities of arable land per person (by Asian standards). Vietnam is an exception to this pattern, as its level of arable land per person is similar to that of the Philippines. However, Vietnam is different in that nearly two-thirds of its agricultural crop area is planted to rice, compared with just 30% in the Philippines (Table 1). The share of crop area devoted to rice is lower in the Philippines than in all other Asian countries where rice is the dominant staple food, with the exception of Malaysia (another rice importer). Bangladesh has a lower level of arable land per capita than the Philippines, but it plants 74% of its agricultural area to rice. The Philippines, Indonesia, Malaysia, and Sri Lanka are the only four countries in South and Southeast Asia that have less than 10 hectares of arable land per hundred people and plant less than half of their agricultural crop area to rice. These are precisely the countries that are traditional net importers of rice.

It is true that the share of land devoted to rice is not determined entirely by biophysical land characteristics, but also by price policies. However, in the Philippines, rice receives more protection than other agricultural crops, not less. Thus, if anything, policy has led to an excessive proportion of land devoted to rice (current price policy in Thailand and Vietnam is relatively neutral toward rice). Along with the fact that

Table 1. Arable land per person and share of rice area in agricultural crop area for selected Asian countries. [a]

Country	Arable land per person (ha per 100 people)	Share of rice in agricultural crop area (%)
Cambodia	28.2	85
Thailand	23.4	57
Myanmar	20.7	52
Lao PDR	16.6	75
Indonesia	9.7	38
Malaysia	8.2	13
Vietnam	7.4	63
Philippines	7.3	32
Bangladesh	5.9	74
Sri Lanka	4.7	40

[a] Raw data are from FAO (2002). India and China are not included because wheat and other grains are the staple food for a large percentage of their population. Data on arable land per person are for 2000. Data for share of rice area are for 1999.

the Philippines has been a net rice importer for more than 130 years, this suggests that the Philippines is a rice importer primarily because of a low quantity of arable land per person and the relatively large proportion of land suitable for nonrice crops.

The effects of price protection for rice

One major effect of price protection for rice in excess of that afforded to other crops is that farmers are encouraged to plant relatively more rice and relatively less of other crops. These are "deadweight" losses to the economy because more valuable crops could be produced in the absence of the price distortion.

A second important effect of price protection for rice is that it transfers income away from rice consumers in favor of rice producers. Whether this helps or hurts the poor on balance is an important question, and several authors have examined this question on either a theoretical level or empirically in the context of individual countries (Sah and Stiglitz 1984, 1987, Ravallion 1990, Minot and Goletti 1998, Warr 2001, Rashid 2002).

A third effect of higher rice prices is reduced employment. Because rice is such an important part of consumption for the poor, higher rice prices lead to upward pressure on wages, especially since unions in the Philippines have an important role in the wage-setting process. This is only natural—workers need to eat and, if rice prices are high, they will demand higher wages to cover the higher food costs. However, the quantity of employment is determined by the willingness of entrepreneurs (both domestic and foreign) to invest in the Philippines. These entrepreneurs create jobs and provide capital that make workers more productive, but in their investment decisions they are guided by the prevailing wages in the Philippines relative to those in other countries. High food prices in the Philippines force these wage rates higher and investors are discouraged from creating jobs. It is crucial to realize that the higher nominal wages in the Philippines ultimately do not benefit workers-they merely function as compensation for the higher food prices faced by these workers compared to other countries. The higher wages do reduce employment, however, creating a larger pool of unemployment than would exist if food prices were lower.

Finally, because rice is the dominant crop in the Philippines, very high prices for rice may substantially raise the value of land, since the higher value of rice output is capitalized into land values. Higher values of land arguably make it more difficult to implement land reform, as landowners are more reluctant to give up a very valuable asset. If rice prices were to fall substantially, the government would probably have to pay less to purchase the land and transfer it to someone with less or no land.

A thorough discussion of all of these effects would be very ambitious and is beyond the scope of this paper. Thus. beginning in the next section, I will focus on the equity effects of Philippine rice price policy.

The equity effects of higher rice prices

The literature

Although there is much discussion in the popular press of the poverty faced by Asian farmers, many papers in the literature have noted that the poorest people in Asia are often net consumers of rice, even in rural areas. For example, Mellor (1978) found that the two poorest deciles of the income distribution in India were net buyers of food, while each of the top eight deciles were net sellers of food. Sahn (1988) showed that 84% of rural households in Sri Lanka were net consumers of rice (and, of course, all urban households). The data he presented also show that two-thirds of all farmers with marketable surpluses of rice are in the top half of the expenditure distribution. In Madagascar, Barrett and Dorosh (1 996) found that “the roughly one-third of rice farmers who fall below the poverty line have substantial net purchases of rice, suggesting important negative effects of increases in rice prices on household welfare.” This finding only concerns rice farmers with land and ignores the rural landless, who are even poorer and are also net purchasers of rice. The authors go on to state that “the poorest rice farmers are quite vulnerable to an increase in the price of their principal crop.... Conversely, the largest, wealthiest 10% or so of farmers stand to benefit significantly from rice price increases.”

Not all countries follow a similar pattern. For example, Minot and Goletti (1998) showed that an increase in rice prices because of export liberalization would (slightly) reduce the incidence and depth of poverty in Vietnam. This result is different from those discussed above because a period of Communist rule provided for a comprehensive land reform that left very few landless laborers. The small number of landless laborers in Vietnam contrasts with the situation in countries such as India, Indonesia, Bangladesh, Sri Lanka, and the Philippines, where there are large pools of landless or nearly landless laborers in the countryside.

But the fact that the poorest of the poor are net consumers of rice does not necessarily imply that they will be helped by lower rice prices. There is a literature, surveyed briefly by Ravallion (1990), that correctly points out that many of these poor consumers earn wages from working as laborers on farms. Because higher rice prices increase the demand for labor, there will be resulting upward pressure on wages. Thus, the net effect on the welfare of these poor households will depend on both their net consumption position in rice and the effect of rice prices on wages, which is often their main source of income.

Using a dynamic econometric model of agricultural wage determination and data from the 1950s to '70s, Ravallion (1990) finds that, in the short run of one to two years, the induced wage response from higher rice prices in Bangladesh will be inadequate to compensate the poor for the adverse effects of higher rice prices. In the longer run of three to four years, the effect of higher rice prices is more neutral as wages eventually rise with a lag. Nevertheless, the initial short-run negative effect of higher rice prices on a temporally aggregated measure of welfare would remain. In the context of Thailand, Warr (2001) uses a computable general equilibrium (CGE) model to assess the impact of a hypothetical increase in the rice export tax. An export tax would lower domestic rice prices, and he finds that these lower prices would hurt both the urban and rural poor by depressing the real wages of unskilled labor. The different result in Thailand may be because of the larger land endowment in Thailand, which leads to fewer landless laborers than in Bangladesh. Rashid (2002), using co-integration techniques and updating the data used by Ravallion (1990), found that since the mid-1970s, rice prices in Bangladesh no longer have a significant effect on agricultural wages.

Effects in the Philippines

Net rice consumption of the poor. In the Philippines, rice constitutes an important share of expenditures for the poor. For the poorest three deciles of the income distribution, rice constitutes more than 20% of total expenditures. This consumption is measured in gross terms, however, not net, and gives no insight into the net consumption position of the poor. Using data from the 1997 Family Income and Expenditures Survey (FIES), Balisacan (2000) estimated net rice consumption as a percentage of total consumption, and found that it was highest for the bottom two deciles of the expenditure distribution. For the bottom decile (decile 1), the share was approximately +7.5%, while for the second decile, it was about +2%. Net consumption was estimated to be negative (i.e., production exceeds consumption) for the middle of the distribution, that is, deciles 4 to 8. These data show that the poorest of the poor in the Philippines are net consumers of rice, not net producers.

Who are these poor net rice consumers? There are at least four major categories, listed here in no particular order. First, perhaps the most obvious category, is the urban poor—they produce no rice and must be net consumers. Approximately 24% of urban dwellers are below the poverty line in the Philippines, accounting for 30% of the poor in the country (NSCB 2002).

The second group is the rural landless, who are often overlooked in many popular discussions of the rural sector. According to unpublished data from the ongoing PhilRice/BAS project on "Effects of potential rice trade liberalization," a recent survey of more than 300 agricultural laborer households throughout the Philippines showed that these poor landless people living in rural areas must purchase rice on markets to satisfy their consumption needs, and are net rice consumers. The 2000 FIES shows that the number of agricultural household heads classified as "agricultural, forestry, fishery, and related workers" accounts for 13% of agricultural households. Clearly, they are not as numerous as farmers, but they still constitute a substantial minority of the agricultural population.

More important, the rural landless are poor. Data from the 2000 FIES show that the average income of households where the household head is an agricultural laborer is 22% lower than in households where the head is a farmer. Unfortunately, these data do not pertain to the income of *rice* farm households relative to laborer households. Hayami et al (1990) show that rice farm households are wealthier than most other farm households and that average family income for rice farmers in 1980 was 47% higher than that for agricultural wage and salaried workers, compared to a gap between all farmers and agricultural wage workers of just 32%. Thus, the income gap of 22% between farm households and agricultural laborer households in 2000 probably understates the actual gap between rice farm households and agricultural laborer households.

The third main group is nonrice farmers, who are obviously net rice consumers. The most recent agricultural census (1991) shows that 49% of all farmers grow no rice at all. Other than rice, the most common crops in the Philippines are maize and coconut. Using national data from the early 1980s, Hayami et al (1990) found that maize and coconut farmers had 41% and 19% less income, respectively, than rice farmers. Poverty incidence was also higher, at 61 % and 49% for maize and coconut farmers, compared with 35% for rice farmers.

The fourth and final group is small rice producers who do not produce enough rice to meet family consumption demand. As is shown below, wealthier rice farm households tend to have higher levels of rice area, and thus tend to have higher levels of marketed surplus. Nevertheless, the poorest decile of rice farm households still markets on average 40% of its production (even after subtracting the amount of rice that is sold immediately after harvest and repurchased later in the year because of inadequate on-farm storage facilities). Ultimately, this derives from the fact that it takes much less land than is commonly realized to provide rice for the average family. To feed a family of six in the Philippines, just 0.3 ha of single-cropped rice land is required (at the national average yield level of 3 t ha^{-1}) compared with an average farm size in the Philippines of almost 2 ha. If the land is double-cropped to rice, as is the case for a majority of Philippine rice farmers, then only 0.15 ha is needed. As a result, it is estimated that in any given year only 7% of Philippine rice farmers are net rice consumers (estimates are constructed from the 1996-97 BAS/PhilRice project "Monitoring of rice-based farm households in strategic rice areas").

How would these different groups be affected by a trade liberalization policy that allowed more imports and reduced the high level of rice prices in the Philippines? In the absence of an induced wage response, the answer is clear: net rice consumers will benefit from lower prices and net rice producers will be hurt. In this situation, trade liberalization will clearly help the poor, since the bottom two deciles of the income distribution are net rice consumers (Balisacan 2000). But what might the induced wage response be if rice prices were to fall substantially? Would agricultural wages decline so much that the income of the poor would be eroded, more than offsetting the benefit of lower rice prices?

Induced wage response and the effects of lower rice prices on landless laborers. In his work on Bangladesh, Ravallion (1990) derived a theoretical minimum elasticity of agricultural wages to rice prices above which the poor would benefit from high rice prices even though they are net consumers of rice. In other words, if real agricultural wages rise sufficiently because of the increased demand for unskilled labor brought on by high rice prices, then the poor, who earn much of their income from wages, will benefit. He then empirically estimated this elasticity of wages to rice prices using more than 30 years of time-series data. Long time series of data are necessary for the estimation of dynamic wage determination models, but an important drawback to this approach is that it must be assumed that the structure of the rural economy has not changed during the estimation period, or else there will ultimately be inadequate degrees of freedom for the estimation. In fact, Rashid (2002) confirms this problem and finds that parameter estimates for this elasticity are very different depending on which time period is used. This problem will plague any approach that relies on econometric estimation, including CGE models (e.g., Warr 2001) that rely on empirical estimates of necessary parameters.

This paper takes a different approach by examining the current structure of the Philippine rural economy and using standard economic reasoning to determine the sign of the induced wage response. An important drawback of this approach is that it is not possible to come up with a quantitative estimate of the net effect of lower rice prices. However, in this particular case, the problem is not severe. Given the structure of the Philippine rural economy, it is argued below that lower rice prices will put *upward* pressure on the wages of unskilled labor. If true, then trade liberalization clearly benefits the poor because they will benefit from both lower prices and higher wages. While it would be helpful to have a quantitative estimate of the net benefits to the poor from trade liberalization, it seems more important in the first instance to clearly establish the correct "sign" of the effects. Subsequent research will focus on obtaining better estimates of the magnitude of the effects.

The effect of lower rice prices on the wages of unslulled labor will depend on several factors, including the functioning of land markets, the labor intensity of alternative crops to rice, and the influence of urban-sector wages on agricultural wages. With lower rice prices, rice farming must remain profitable for those farmers who continue to grow rice. For farmers who cannot restore profitability in the face of lower rice prices, they must necessarily give up rice farming and use the land for some other purpose.

If output prices are lower, then profitability can be restored only through a lower use of inputs and/or lower input prices. For inputs that are traded on international markets, such as fertilizers and pesticides, trade liberalization for rice in the Philippines would unlikely affect these prices. Thus, as far as tradable inputs are concerned, the only possible response for farmers is to reduce the use of these inputs to some extent.

A reduction in pesticide use would probably be helpful to the environment and would likely have little effect on rice yields. However, pesticides account for a very small share of total costs, so even complete elimination of pesticide use will have little effect on profitability. Some reduction in fertilizer use and thus yield might occur, but this is not likely to be large, since the economically optimal yield is very close to the maximum yield for a wide range of prices.[1] Thus, cost savings in fertilizer are also likely to be small.

Because there will be little adjustment in tradable inputs, nontradable inputs such as labor and land must absorb most of the necessary adjustments. If nothing else changes, lower rice prices will reduce the demand for both land and labor in rice production. Because land supply is more inelastic than labor supply, land rents are likely to be affected more than wages. According to the most recent agricultural census (1991), about one-third of rice parcels in the Philippines are either tenanted or leased. For these parcels, the rental that tenants are willing to pay will decline with lower rice prices, and, to the extent that this happens, the effect of lower rice prices on wages will be muted.

In addition to these land-market effects, the effect of lower rice prices on the demand for labor will also depend on the labor intensity of the crops that are grown as alternatives to rice. It is difficult to know which alternative crops farmers will plant as a result of lower rice prices, but it is important to keep several facts in mind. First, as is well known, much land that is planted to rice has little alternative use. In the wet season, when much land is flooded, farmers often have only two choices: grow rice or leave the land fallow. Because the opportunity cost of land is so low in the wet season, most of this land will likely remain in rice production even with a substantial fall in prices. Rice will be the dominant wet-season crop in the Philippines for many years to come, regardless of the trade policy adopted.

In the dry season, however, more choices are available. In recent years (1999-2001), rice area harvested in the first semester of the year (January to June, which is the dry season in most of the country) has accounted for 43% of the total annual harvested area. This is a much larger percentage than was the case in the early 1970s, when the first-semester share of area was about 32%.

Were rice prices to fall substantially, what alternative crops might be grown in the dry season instead of rice, and would they be profitable for farmers? Alviola et al (2002) conducted surveys in several Philippine provinces of rice-based farming systems where rice was grown in the wet season in conjunction with any of a wide range of vegetable crops, Almost without exception, they found that these alternative crops are profitable without tariff protection, that is, the Philippines has a comparative advantage in vegetable production. Furthermore, nearly all of these crops are substantially more labor-intensive than rice. Thus, if lower rice prices induced farmers to plant more vegetables in the dry season, this would place upward pressure on the

---

[1] This statement is based on an analysis of thousands of nitrogen-response experiments at IRRI. Although the economically optimal yield is always below the maximum yield, the difference between these two yields is very small, usually on the order of 2-3%.

demand for unskilled labor. In fact, many farmers who grow rice in the dry season state that labor shortages are one reason for not diversifying into vegetables, which suggests that lower rice prices will increase demand for unskilled labor. Of course, the other reason why farmers do not diversify is that farm-gate prices for rice are very high in the Philippines, although this fact is not widely appreciated.

Farmers might also diversify into other crops besides vegetables. The most likely alternative is maize, for which demand continues to increase more rapidly than for rice. Large parts of Mindanao and the Cagayan Valley already grow both maize and rice, and a fall in rice prices would encourage a more pronounced shift to maize in these areas. In fact, in each of the ten years from 1983 to 1992, maize, not rice, was the dominant crop in the Philippines in terms of area planted. Thus, a large shift into maize would not be unprecedented. Maize and rice use similar quantities of labor per hectare (BAS 2001b), so there is unlikely to be a reduction in labor demand with such a shift in cropping patterns. The only important crop in the Philippines that is less labor-intensive than rice is coconut, but it is highly unlikely that major rice-growing areas will shift into coconut as a result of lower rice prices.

In summary, it seems unlikely that lower rice prices would lead to a decline in wages because of a lower demand for unskilled labor. First, land markets will absorb some of the impact through lower land rents. Second, the main alternative crops to rice in the dry season are vegetables, which are more labor-intensive than rice, and maize, which is of equal labor intensity. Third, to the extent that labor markets are integrated between urban and rural areas, agricultural wages will be less likely to change because of events in the agricultural sector (i.e., lower rice prices). If there is little induced wage response caused by lower rice prices, or if lower rice prices lead to diversification in the dry season into vegetables and higher wages for unskilled labor, then landless laborers, the poorest of the poor, will unambiguously benefit from lower rice prices. They will benefit directly from lower rice prices because they are net consumers of rice, and, if anything, it appears that lower rice prices would exert upward pressure on real wages, which would raise their incomes.

The effects of lower rice prices on different types of rice farmers. Although lower rice prices are likely to help landless laborers, it is almost certain that they will hurt the half of the nations' farmers who grow rice. As mentioned earlier, rice farmers tend to be wealthier than the nonrice farmers who will benefit from lower rice prices, but rice farmers are still an important group as they are poorer than the average Filipino. To understand the effects of lower rice prices on rice farmers, it is important to realize that rice farmers in the Philippines are not a homogeneous group. Some rice farmers are indeed poor but, perhaps surprisingly, many others are quite well-to-do.

The analysis in this section uses data from a survey of 2,500 rice farm households conducted jointly by the Bureau of Agricultural Statistics (BAS) and the Philippine Rice Research Institute (PhilRice). This survey was conducted in 1997 and covered rice farmers in 30 major rice-producing provinces that account for more than 70% of rice production in the Philippines. Thus, the sample is nationally representative. The survey collected information on household demographics and characteristics, rice production practices and labor use, marketed surplus, and household income by source. Analysis of these data reveals many important facts.

First, the annual per capita income of the wealthiest rice farmers is much greater than that of the poorest. The average income of the top 20% of rice farm households (ranked according to per capita income) is 15 times as large as the average income of the bottom 20%! This indicates great disparities in income among different rice farm households. This top fifth of rice farm households is located in the top half of the national income distribution: they are not poor.

Second, the richest rice farm households tend to have larger landholdings of higher quality (i.e., irrigated as opposed to rainfed) than the poor. The top fifth of rice farm households plants on average 4.2 ha of rice per year (including double cropping), while the poorest fifth plants just 1.3 ha (again, including double cropping).

Third, the richest rice farm households have much higher levels of nonfarm income than the poor. In per capita terms, the top fifth of rice farm households has nonfarm income that is more than 30 times as large as that of the bottom fifth.

Fourth, the richest rice farms are more specialized in rice than are poor households. While the poorest fifth of rice farm households obtains 25% of its agricultural income from nonrice crops, the richest fifth obtains just 11 %. Thus, while lower rice prices will force rice farmers to diversify their cropping patterns, it appears that poor farmers have already made this adjustment to some extent. The burden of learning how to manage new crops will fall disproportionately on the rich.

Fifth, the richest rice farm households (the top quintile) hire in nearly all of their labor. On average, 90% of the labor used on their rice farms is hired (this does not include reciprocal exchange labor). For the poorest fifth of rice farm households, just 51% of labor is hired, with the remainder coming from their own family. Thus, the richest rice farm households operate like businesses, not family farms. Interestingly, though, even the poorest rice farm households hire in more than half their labor: to a large extent, they are not family farms either. This preference for hired labor, even among poor farmers, reflects the large pool of landless laborers in the countryside.

Rice farmers themselves occasionally work on other farms, but this is rare and accounts for just 5% of total income even for the poorest quintile of rice farmers. In fact, the average rice farm household in the Philippines works just about 36 days in rice farming per year. If each household has two working members who share responsibility for the farm, that amounts to just 18 days per adult per year, or 1.5 days per month on average! Rice farming is clearly not a full-time occupation for either rich or poor farm households.

Sixth, nearly half (44%) of the rice marketed surplus in the Philippines comes from the top quintile of rice farm households. A further 23% comes from the second quintile. Since the benefits of the current high rice price policy are allocated among farmers in direct proportion to their share of marketed surplus, this means that the wealthiest 40% of rice farm households receive two-thirds of the benefits of this policy, with relatively little accruing to poor rice farm households.

Were rice prices to fall, the benefits from lower rice prices would also be skewed toward higher income households because rich households eat more rice than poor households. However, the skew would be much less than in the case of marketed surplus. Using data from the most recent Bureau of Agricultural Statistics (2001a) survey on consumption of selected agricultural food commodities, it is estimated that the wealthiest quintile of the population in the Philippines eats about 21.5% of all rice in the country. This is not much different from the 20% that would result if all people ate the same amount of rice, regardless of income. Thus, the benefits from lower rice prices, in absolute terms, would be distributed relatively evenly across all income classes. Because the poor have lower incomes, however, the benefits in terms of a percentage increase in income would be skewed in favor of the poor.

Conclusions

Because rice is the most important agricultural commodity in the Philippines and is an important user of unskilled labor, the changes that would accompany a large fall in its price would be profound and controversial. The main beneficiaries of the current high price policy are, of course, rice farmers. However, the wealthiest rice farm households, that have large amounts of nonfarm income and hire in nearly all the labor necessary to grow the crop, receive most of the benefits. Poor rice farmers do benefit, but they receive very little.

Many groups are harmed by high rice prices, especially since it appears that lower rice prices would not affect the wage rate for unskilled labor, and might even raise it. These groups include the urban poor, rural landless laborers, maize and coconut farmers, and small rice farmers who produce no marketed surplus. All of these groups tend to be poorer than rice farmers who produce a surplus for sale.

If there were substantial rice trade liberalization leading to more rice imports, would the lower prices from imports be passed on to poor consumers? Contrary to popular belief, most of the reason for high rice retail prices in the Philippines is not because of a poor marketing system dominated by private traders who restrict trade for their own benefit. For example, Hayami et al (1999) show that, in a small village in Laguna, rice trading is very competitive: a sample of 45 farmers sold their crop to 37 different buyers. Millers came from hundreds of miles away to purchase these farmers' crops to keep their mills operating at close to full capacity. Competition among mills with such a wide spatial distribution makes it difficult for traders to collude with one another. Furthermore, simple arithmetic shows that most of the reason for higher rice retail prices in the Philippines than in Thailand (as one example) is not differences in marketing costs, but rather the higher prices received by Philippine farmers compared with Thai farmers.

If the Philippines chooses to substantially liberalize trade in rice, it appears that there will be three main effects. First, lower rice prices will tend to redistribute income within society. Although there will be some redistribution among various poor families, there will also be a substantial transfer from the nonpoor to the poor, which will help to reduce poverty incidence. The exact magnitude of the poverty reduction needs to be quantified, but, given the extremely high level of rice prices in the Philippines and the importance of rice in the budget share of the poor, the effect will probably be substantial. A study in Indonesia, where the protection afforded to rice at the time was much less than is the case in the Philippines, concluded that allowing more rice imports by setting a zero tariff would move 14 million people (about 30% of the poor) above the poverty line (Bappenas 2001).

Second, lower rice prices will also result in less domestic rice production, especially in the dry season. However, other crops will be grown in place of rice. Such cropping shifts are not unprecedented in recent Philippine history: in the 1980s, maize was planted to a larger area than rice. And, dry-season rice is not a "traditional" crop: the share of dry-season rice in the early 1970s, when Philippine rice farming was not protected, was much lower than it is today. More area planted to vegetables would be new, but this would be welcome for consumers, who will benefit from improved nutrition (Block, this volume). More diversified cropping is also necessary for diversification of the rural economy so that farmers can escape from poverty.

Third, the quantity of rice imports will increase, probably substantially. In the past, increased reliance on the world rice market may have caused legitimate concern, since it has historically been much less stable than other world grain markets (Falcon and Monke 1979-80, Siamwalla and Haykin 1983, Monke and Pearson 1991). Recent research has shown, however, that the world rice market has become much more stable since the mid-1980s because of increased stability of production and more active participation of commercially oriented rice exporters (Dawe 2002). As a specific example, when Indonesia suddenly entered the world market for 6 million tons of imports in 1998 because of the effects of El Niño (Naylor et al 2002), world prices barely increased.

It is unlikely, even with complete liberalization and a zero tariff, that the Philippines would need to import 6 million tons of milled rice in a single year. Furthermore, the impact of larger quantities of imports on world prices will be much less if these imports are made consistently from year to year because consistent demand will encourage exporters to increase rice production beyond current levels. Malaysia has adopted such a strategy of increased reliance on imports, and during the past few years has routinely imported at least 30% of its domestic consumption. Thus, if the Philippines does substantially liberalize its domestic rice market to allow more imports, it will be able to source those supplies reliably without endangering its food security. With more imports, domestic prices will decline substantially, and these lower prices will reduce poverty by allowing many poor households to afford food security.

References

Alviola P, Cataquiz G, Francisco S. 2002. The global competitiveness of rice-vegetable farming systems: implications for Philippine food security. Paper presented at the International Rice Research Conference, 16-20 September 2002, Beijing, China.

Balisacan A. 2000. Growth, inequality and poverty reduction in the Philippines: a re-examination of evidence. University of the Philippines. Quezon City.

Bappenas/USAID/DAI Food Policy Advisory Team. 2001. An approach to macro food policy. Working Paper No. 4. http://www.macrofoodpolicy.com/htm/pubwp.htm. 45 p.

Barrett CB, Dorosh PA. 1996. Farmers' welfare and changing food prices: nonparametric evidence from rice in Madagascar. Am. J. Agric. Econ. 78(3):656-669.

BAS (Bureau of Agricultural Statistics). 2001a. Consumption of selected agricultural food commodities (by socio-economic class of households), Volume 3. Quezon City (Philippines): Bureau of Agricultural Statistics/Department of Agriculture. 47 p.

BAS (Bureau of Agricultural Statistics). 2001b. Trends in agricultural wages 1998-2000. Quezon City (Philippines): Bureau of Agricultural Statistics. 64 p.

Bouis HE. 1982. Rice policy in the Philippines. PhD dissertation. Stanford University. 392 P.

Dawe D. 1993. Essays on price stabilization and the macroeconomy in low income countries. PhD dissertation. Harvard University, Cambridge, Massachusetts. 147 p.

Dawe D. 2002. The changing structure of the world rice market, 1950-2000. Food Policy 27(4):355-370.

Dawe D, Castillo G. 2001. The Philippines' iron rice bowl: import controls and subsidies on rice are hurting the island nation's poorest people. Asian Wall Street Journal. 19 June.

Falcon WC, Monke E. 1979-80. International trade in rice. Food Research Institute Studies. 17(3):271-306.

FAO (Food and Agriculture Organization). 2002. FAOStat on-line electronic database. www.fao.org.

Hayami Y, Quisumbing MA, Adriano LS. 1990. Toward an alternative land reform paradigm: a Philippine perspective. Manila (Philippines): Ateneo de Manila University Press. 209 p.

Hayami Y, Kikuchi M, Marciano EB. 1999. Middlemen and peasants in rice marketing in the Philippines. Agric. Econ. 20:79-93.

Mellor JW. 1978. Food price policy and income distribution in low-income countries. Econ. Dev. Cult. Change 26(1):1-26.

Minot N, Goletti F. 1998. Export liberalization and household welfare: the case of rice in Vietnam. Am. J. Agric. Econ. 80(4):738-749.

Monke E, Pearson S. 1991. The international rice market. In: Pearson S, Falcon W, Heytens P. Monke E, Naylor R, editors. Rice policy in Indonesia. Ithaca (New York): Cornell University Press.

Moya PF. Dawe D, Pabale D, Tiongco M, Chien NV, Devarajan S, Djatiharti A, Lai NX, Niyomvit L, Ping HX, Redondo G, Wardana P. n.d. The economics of intensively irrigated rice in Asia. In: Dobermann A, Witt C, Dawe D, editors. Increasing the productivity of intensive rice systems through site-specific nutrient management. International Rice Research Institute (IRRI), Los Baños, Philippines, and Science Publishers, Inc., New Delhi, India. (Forthcoming.)

Naylor RL, Falcon WP, Wada N, Rochberg D. 2002. Using El Niño/Southern Oscillation climate data to improve food policy planning in Indonesia. Bull. Indonesian Econ. Stud, 38(1):75-92.

NSCB (National Statistical Coordination Board). 2002. 33.7% of Filipino families are poor. Makati City (Philippines): NSCB. 20 p.

NSO (National Statistics Office). 1994. Census of agriculture, 1991: final report. Manila (Philippines). Vol. 1 and 2.

Ravallion M. 1990. Rural welfare effects of food price changes under induced wage responses: theory and evidence for Bangladesh. Oxford Econ. Papers 42:574-585.

Rashid S. 2002. Dynamics of agricultural wage and rice price in Bangladesh: a re-examination. Markets and Structural Studies Division Discussion Paper No. 44. Washington, D.C. (USA): International Food Policy Research Institute. 40 p.

Sah RK, Stiglitz JE. 1984. The economics of price scissors. Am. Econ. Rev. 74:125-138.

Sah RK, Stiglitz JE. 1987. Price scissors and structure of the economy. Quarterly J. Econ.. 102:109-134.

Sahn DE. 1988. The effect of price and income changes on food energy intake in Sri Lanka. Econ. Dev. Cult. Change 36(2):315-340.

Siamwalla A, Haykin S. 1983. The world rice market: structure, conduct, and performance. International Food Policy Research Institute Research Report 39. Washington, D.C. (USA): IFPRI. 79 p.

Timmer CP. 1993. Rural bias in the East and South-East Asian rice economy: Indonesia in comparative perspective. J. Dev. Studies 29(4):149-176.

Warr PG. 2001. Welfare effects of an export tax: Thailand's rice premium. Am. J. Agric. Econ. 83(4):903-920.

Notes

Author's address: Social Sciences Division, IRRI, DAPO Box 7777, Metro Manila, Philippines.

Citation: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, editors. 2003. Rice science: innovations and impact for livelihood. Proceedings of the International Rice Research Conference, 16-19 September 2002, Beijing, China. Beijing (China): International Rice Research Institute, Chinese Academy of Engineering, and Chinese Academy of Agricultural Sciences. 1,022 p.