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Edited by P.K. Aggarwal, J.K. Ladha, R.K. Singh, C. Devakumar, and B. Hardy

ICAR

IRRI

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Foreword

Foreword

The demand for rice worldwide has increased dramatically over the last 50 years because of increases in population. In many regions, the supply of rice has generally kept pace with the increase in demand, largely due to the introduction of modern high-yielding varieties, expansion of irrigation, and the use of synthetic nitrogen fertilizers. Rice is now grown globally on about 150 million hectares, with an annual production of about 600 million tons. It is the staple food for more than half of the world population, and its production is a source of income and livelihood for millions of people across the world. In Asia alone, where nearly 90% of the world's rice is produced and consumed, more than 2 billion people obtain 60% to 70% of their energy intake from rice and its products.

As the population of rice-growing regions of the world increases, demand for rice becomes higher. It is estimated that the rice grain requirement by 2020 in the region will be almost 30–50% more than now. The additional quantities will have to be produced from the same land resources, or less, because of the increase in competition for land and other resources by nonagricultural sectors. There is growing evidence of a gradual deterioration in natural resources, a decline in soil fertility, changes in water-table depth, deterioration in the quality of irrigation water, and rising salinity. This situation is further complicated by global climate change, which is likely to lead to reduced yields and increased production instability. As these proceedings were going to press, the climatic calamities of drought and cyclones were taking their toll on global rice supplies. The world faces sharply rising rice prices and global stocks are plummeting to levels not seen for nearly 30 years.

Many nations today thus face the second-generation challenge of producing more rice at less cost in a deteriorating environment. Rice research and development therefore need to address the Millennium Development Goals on poverty alleviation, food and nutritional security, and environmental conservation. Opportunities are emerging from recent technological developments in space, information, communication, and biotechnology for tackling these goals. The 2nd International Rice Congress, IRC2006, was organized to discuss these developments and to provide a common platform for sharing knowledge and expertise on research, extension, production, processing, trade, consumption, and related activities with all stakeholders of rice. The Congress was organized by the Indian Council of Agricultural Research and the National Academy of Agricultural Sciences (India) and sponsored by the International Rice Research Institute, Philippines, and Government of India. A comprehensive event for the world's most important crop, this Rice Congress had simultaneous conferences, symposia, workshops, and exhibitions based on the theme "*Science, technology, and trade for peace and prosperity.*" The main events of the Congress were the 26th International Rice Research Conference, 2nd International Rice Commerce Conference, 2nd International Rice Technology and Cultural Exhibition, and 2nd International Ministerial Round-Table Meeting. The deliberations of the Asian Ministers led to a *Delhi Declaration* that highlighted the need to establish a comprehensive partnership among the participants through strengthened dialogue on a regular basis for the development of rice research and trade with greater emphasis on the social, cultural, and human dimension.

The International Rice Research Conference (IRRC), organized every two years by the International Rice Research Institute, is the world's premier rice research event. This 26th Conference in 2006 focused on "*Innovations for efficiency enhancement*" in view of the increasing need to conserve resource use in rice. All important aspects of rice research and related environmental and economic impacts were covered in several sessions by plenary lectures, invited lead papers, poster papers, and workshops by the experts. These proceedings provide a summary of the key plenary and invited papers presented during the IRRC on various themes. We hope the knowledge base in these proceedings will help address the challenge of producing more rice with greater ecological efficiency and profitability in a changing global environment.

M.S. Swaminathan	Mangala Rai	Robert S. Zeigler
Chair	Co-Chair	Co-Chair

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Science and Shaping the Future of Rice

M.S. Swaminathan

According to the Food and Agriculture Organization (FAO) of the United Nations, the global rice requirement in 2025 will be on the order of 800 million tons. Now, production is less than 600 million tons. The additional 200 million tons needed will have to be produced by increasing productivity per hectare. The average productivity may have to go up to 8 tons per hectare from the present near 5 t ha^{-1} (yield figures relate to paddy or brown rice). Land is a shrinking resource for agriculture and rice cultivation is also becoming uneconomical. Therefore, a three-pronged strategy will have to be promoted for ensuring the security of adequate rice availability.

1. Enhancement of the productivity, profitability, and sustainability of rice yields. This will call for new technological developments, including higher-yielding hybrids, super rice, and rice varieties possessing resistance to/tolerance of a wide range of biotic and abiotic stresses. The use of new technologies, including biotechnology and genetic engineering, becomes important in this context.
2. Promotion of rice farming systems based on the principles of economics, ecology, and nutrition. Rice farming systems involving crop-livestock-fish integration would help to enhance not only household nutrition, but also income and work security. At the same time, they will help to promote integrated nutrient supply systems.
3. Adding value to every part of the rice biomass such as the straw, husk, and bran through the establishment of Rice BioParks, so as to enhance the income of rice farming families.

The pathways to improving productivity should be both environmentally and economically sound. Breeding for high yield and feeding for higher productivity should go together. It is important that crop feeding practices do not lead to the pollution of groundwater as well as soil. The goal should be to achieve an “ever-green revolution” in rice that could help to improve productivity in perpetuity without associated ecological harm. We could then witness a situation in which there is not only adequate rice in the market but also happiness on the faces of both farmers and consumers. In the case of new technologies, farming families should be fully involved in both participatory research and knowledge management. Sustainable rice farming needs location-specific varieties and economical water management procedures. Farmer-scientist partnership is essential for mainstreaming environmental concerns in the ever-green revolution strategy for rice.

The importance of rice will grow in the coming decades because of potential changes in temperature, precipitation, and sea-level rise, as a result of global warming. Rice grows under a wide range of latitudes and altitudes and can become the anchor *of* food security in a world confronted with the challenge of climate change.

THE POWER OF INTERDISCIPLINARY SCIENCE

The power of interdisciplinary science and of a clear vision on goals and objectives is exemplified by the history and achievements of the International Rice Research Institute. Within 6 years of its establishment, IRRI helped to change the history of rice in Asia. Robert Chandler has described in his book “An Adventure in Applied Science” how, with single-minded devotion to the cause of achieving a yield breakthrough in indica rice, IRRI scientists raised the yield ceiling in indica rice from about 3 t ha^{-1} to 9 t ha^{-1}. Scientists involved in developing priorities and strategies in agricultural research should read this book.

The seeds of progress in yield improvement in indica rice were sown soon after World War II, by Dr. K. Ramaiah, who proposed the transfer of genes for fertilizer response from japonic rice to indica rice through a well-designed indica-japonica hybridization program. FAO and the Indian Council of Agricultural Research organized this program at the Central Rice Research Institute in Cuttack in the early 1950s. The advent of the Dee-gee-woo-gen dwarfing gene from China hastened the process of breeding rice varieties that could respond well to good soil fertility and water management. Chinese scientists, led by Dr. Yuan Long Ping, showed that the commercial exploitation of hybrid vigor was possible even in a self-pollinated crop such as rice.

In India, rice is grown below sea level in Kuttanad in Kerala and at above 3,000 meters in Kashmir and Himachal Pradesh. The importance of rice as the mainstay of a sustainable food security system will grow during this century because of climate change. No other cereal has the resilience of rice to grow under a wide range of growing conditions. Both cultural and agro-climatic diversity have helped to introduce rich genetic diversity in rice. The first reference to Basmati rice was in the famous poem “Heer Ranjha” by poet Wazir Shah. There is a beautiful portrait of a woman credited with first introducing rice into cultivation in a temple in Arunachal Pradesh. In recognition of the pivotal role played by women in rice culture, IRRI started (more than 20 years ago) the Women in Rice Farming Network. The social

Table 1: The Green Revolution and ever-green revolution: pathways.

Green Revolution: commodity-centered increase in productivity	**Ever-green revolution:** increasing productivity in perpetuity without associated ecological harm
Change in plant architecture and harvest index	**Organic agriculture:** cultivation without any use of chemical inputs such as mineral fertilizers and chemical pesticides
Change in physiological rhythm—insensitive to photoperiodism	**Green agriculture:** cultivation with the help of integrated pest management, integrated nutrient supply, and integrated natural resource management systems
Lodging resistance	**Eco-agriculture:** based on conservation of soil, water, and biodiversity and the application of traditional knowledge and ecological prudence
	EM agriculture: a system of farming using effective microorganisms (EM)
	White agriculture: a system of agriculture based on the substantial use of microorganisms, particularly fungi
	One-straw revolution: a system of natural farming without plowing, chemical fertilizers, weeding, and chemical pesticides and herbicides

dimensions of rice farming should receive as much attention as the scientific dimensions in any strategy to improve the productivity, profitability, and sustainability of rice farming systems.

PATHWAYS TO AN EVER-GREEN REVOLUTION IN RICE

An ever-green revolution implies the enhancement of productivity in perpetuity without associated ecological harm (Swaminathan 1996). If farm ecology and economics go wrong, nothing else will go right in agriculture. The pathways to an ever-green revolution are indicated in Table 1. The major threats to an ever-green revolution are

- Invasive alien species
- Abiotic and biotic stresses
- Market factors
- Climate change
- Constraints in the exchange of genetic resources
- Intellectual property rights and access to technologies
- Diminishing support to research on public goods

Impact of Climate Change on Rice

- The results of recent international modeling exercises suggest a mixed future of doubled CO_2 for rice production in Asia, with some countries benefiting and others losing production.
- Overall Asian rice production, based on present varieties and systems, could decline by about 4% in the climates of this century.

Indirect Effects of Global Climate Change on Rice

- Altered timing and magnitude of precipitation can induce drought or flood injury.
- Increased temperatures, and/or changes in precipitation, could have dramatic effects on rice diseases and insects.
- Enhanced UV-B, enriched CO_2, and increased temperature may all alter competition between rice and major weeds, and the contribution of other organisms to nitrogen fixation in rice fields.

Effects of CO_2 and Temperature on the Rice Ecosystem

- Increasing atmospheric CO_2 stimulates plant growth; the beneficial effects on rice growth have been observed for amounts only up to 500 ppm. Some plant species respond positively to CO_2 amounts up to 1,000 ppm.
- The benefits of increased CO_2 would be lost if temperatures also rise because increased temperature shortens the period over which rice grows.

Organic agriculture precludes the use of mineral fertilizers, chemical pesticides, and genetically modified varieties of crops. In contrast, green agriculture permits the use of the minimum needed mineral fertilizers and chemical pesticides in integrated pest management (IPM) and integrated nutrient supply (INS) schedules. Green agriculture also permits the use of genetically modified crop varieties, if these have been cleared by the prescribed regulatory authority from the viewpoints of biosafety and environmental safety. Green agriculture is the more feasible pathway for achieving an ever-green revolution under conditions in which small and marginal farmers without cattle wealth constitute the dominant segment of the farming community. It would be useful to introduce separate certification procedures for products from organic and green agriculture.

Raising the Yield Ceiling

During the 20th century, the following technological innovations helped to enhance considerably the productivity of rice varieties:

- Indica × japonica crosses
- Introduction of semidwarf plant stature, accompanied by relative photo-insensitivity
- Indica × indica hybrids
- Indica × javanica × japonica crosses resulting in super rice strains
- *Oryza sativa* × *O. glaberrima* crosses followed by farmer participatory breeding, resulting in the New Rice for Africa (NERICA)

Superfine aromatic rice hybrids such as RH10 developed at the Indian Agricultural Research Institute, New Delhi, have helped to combine high yield with highly prized quality characters. The use of thermosensitive genetic male sterility (TGMS) helps to achieve a rapid improvement in grain quality. Molecular tests are also now available to ensure the genetic purity of the hybrids.

Increasingly, specialty rice is being developed. It includes medicinal rice and rice that can grow well in coastal areas. This includes rice with medicinal properties.

Rice Varieties of Medicinal Importance

Ancient Indian scriptures Susrutha Samhita (circa 400 BC), Charakasamhita, Astangahri-dayam, and Indian *Materia Medica* (15th-16th century) mention the curative value of certain rice varieties for various ailments:

● Njavara	Arthritis and body rejuvenation
● Aalcha	Pimples and skin ailments
● Baisoor	Epilepsy
● Laicha	For healthy child delivery
● Maharaji	For postdelivery recovery
● Kulikulichan	To increase milk flow in lactating mothers
● Bhejri	To clear hoarseness of voice and throat problems
● Pitchavari	For treating cattle diarrhea

There are also several efforts to improve the nutritive quality of rice, with particular reference to the content of beta-carotene (Paine et al 2005) and iron (Sivaprakash et al 2006) through recombinant DNA techniques. Transgenic rice plants containing the superoxide dismutase gene from the mangrove species *Avicennia marina* have been developed for imparting tolerance of salinity (Prashanth et al 2007). This work is significant in the context of potential changes in sea level as a result of global warming.

Finally, there is a need for scientific and public policy steps for bridging the gap between potential and actual yields in rice. The National Commission on Farmers (NCF) investigated this question in detail and some of its recommendations are summarized in this paper.

SHAPING OUR AGRICULTURAL FUTURE—A THREE-PRONGED STRATEGY

India will remain during most of the 21st century a predominantly agricultural country, particularly with reference to livelihood opportunities. Therefore, there is a need for both vision and appropriate action to shape our agricultural destiny. Our major agricultural strengths are our large population of hard-working farm women and men, our varied climatic and soil resources, abundant sunshine throughout the year, reasonable rainfall and water resources, a long coast line, and rich agro-biodiversity. Converting these into jobs and income is the challenge.

We should look upon agriculture not just as a food-producing machine for the urban population, but as the major source of skilled and remunerative employment and a hub for global outsourcing.

Just as IT industries have specialized in handling outsourcing assignments efficiently, we must enable our farm graduates and farmers to take up outsourcing jobs in areas where we have a comparative advantage. Some examples are hybrid seed production, tissue culture-propagated plants, organic farm products, biological software for sustainable agriculture such as biopesticides, biofertilizers, and pheromones as well as herbal products, fruits, flowers and vegetables, vaccines and sero-diagnostics, and veterinary pharmaceuticals based on medicinal plants. There is also scope for becoming a global outsourcing hub in the areas of plant and animal genomics and information and communication technology (ICT) for the rural poor. Farm, veterinary, fisheries, and home science graduates should be trained to become genome and digital entrepreneurs. To start with, a few of our agricultural, animal sciences, and fisheries universities could set up bureaus for outsourcing business in agriculture to facilitate contact between farmers' organizations as well as agri-business centers operated by farm and home science graduates and external agri-business enterprises. Outsourcing should not only be from other countries to urban India, but also from urban to rural India, so that educated youth can continue to live in villages.

We need a new vision for agriculture. That vision should aim to spread happiness among farm and rural families. Bio-happiness through the conversion of our bio-resources into wealth meaningful to our rural families should be the goal of our national policy for farmers. Hidden and unrecognized opportunities for creating more skilled jobs and income in the farm and nonfarm sectors need to be tapped through appropriate public policies and programs. Technology missions should be revamped and revitalized on the lines envisaged by Bharat Ratna Rajiv Gandhi when he first proposed them as organizational and management tools to help the nation leapfrog in the production of essential commodities such as oilseeds and pulses.

A structurally progressive economy should reduce the share of people dependent on one sector as the share of that sector falls in gross domestic product (GDP). As the share of agriculture in GDP falls, the share of people dependent on agriculture is also expected to fall in the same proportion. However, in the Indian economy, though the share of agriculture in GDP is falling steadily, there is no corresponding decline in the share of the population dependent on agriculture. Because of population growth, the absolute number of people depending on agriculture is increasing, even if there is a decline in percentage terms. This is why a major integrated rural nonfarm livelihood initiative is needed, so that both on-farm and nonfarm livelihoods become productive and profitable.

The technology strategy for an ever-green revolution should have the following three components:

1. **Defending the gains**

   Punjabi farmers provide 60% of the wheat and 40% of the rice to the Public Distribution System and national buffer stocks. Net productivity increased in the Punjab in rice and wheat from 1.2 t ha^{-1} and 1.1 t ha^{-1} to 4.3 t ha^{-1} and 3.9 t ha^{-1}, respectively, from 1960-61 to 2004-05. However, in recent years, there has been stagnation in productivity improvement due to a variety of causes, of which the following are important:

   - Declining farm size and income.
   - Depletion of the natural resource base, for example, a steep decline in groundwater table and impaired water quality.
   - Increasing input costs, particularly diesel, and adverse economics of farming. Deficiency of micronutrients in the soil and deteriorating soil health. Inadequate postharvest technology.
   - Uncertain market prospects, except for wheat and rice, though a minimum support price is announced for the following 25 agricultural commodities:
     - Cereals—paddy, rice, *wheat,jowar, bajra*, maize, *ragi*, barley
     - Pulses—gram, *fur, moong, urad, masur*
     - Oilseeds—groundnut, soybean (yellow/black), rapeseed and mustard, toria, sunflower seed, safflower, nigerseed
     - Sugarcane, cotton, jute, tobacco

- High indebtedness of farmers—the total debt of Punjabi farmers, for instance, is estimated to be about Rs. 240,000 million.

Similar conditions prevail in Haryana and Western Uttar Pradesh. Thus, the heartland of the Green Revolution is in serious trouble. These areas need conservation farming, which will help farm families to conserve and improve soil health, water quantity and quality, and biodiversity. Some of the eco-technologies developed by the Punjab Agricultural University are bed sowing of wheat, saving 20% to 25% of water; the leaf color chart, saving 15% of N application in rice; tensiometer-based irrigation scheduling; zero-tillage technology for wheat; and integrated pest management in cotton, saving 40% of pesticides. Thus, there is vast scope to both promote green agriculture and reduce the cost of production through enhanced factor productivity. A course on sustainability science should be introduced in all agricultural universities. India will not be able to maintain a stable food security system if its "fertile crescent" (i.e., Punjab, Haryana, and western Uttar Pradesh) is not saved through adequate support for conservation farming. Defending the gains already made in this region is an urgent task.

An example of the need for support for conservation farming is provided by the situation of rice cultivation in the Punjab. At present, nearly 2.6 million hectares are under rice in the Punjab. Much of the irrigation water used is groundwater. The water table in the central districts of the state producing rice and having 70% of the tubewells is receding at an alarming rate of 60 to 75 cm annually. At present, about 30% of the tubewells have become submersible and it is estimated that during the next 10 years practically all the centrifugal pumps will become nonfunctional and will have to be converted into submersible pumps. It would therefore be advisable to restrict rice cultivation to 2 million hectares in the Punjab, with a yield target of 5 t ha^{-1}. The remaining area can come under maize, pulses, and oilseeds, which are all at the moment in short supply. Conservation farming in the Punjab as well as in other intensive agricultural areas will involve a scientific program of restructuring farming systems. Such a restructuring is an urgent need in the interests of the long-term livelihood security of Punjabi farmers and food security of the nation. The same is true in parts of Haryana, western Uttar Pradesh, and many of the early Intensive Agricultural Program Districts in the country.

In every state, the agricultural "bright spots" and "hot spots" will have to be mapped. The state should develop a strategy for enlarging the extrapolation domain of bright spots. Similarly, every state should develop a good weather code to maximize the benefits of adequate moisture availability, a drought code to minimize the adverse impact of drought, and a flood code to both prevent excessive distress and damage and promote a postflood production plan. In the desert areas of Rajasthan, the good weather code should include provision for raising nurseries of appropriate plants, so that, in years of excessive rainfall, an extensive tree planting and sand dune stabilization drive can be launched. This will help to strengthen the ecological infrastructure of the desert, and gradually convert the desert into an oasis. The drought code should include the adoption of crop life-saving technologies and contingency plans to change the cropping pattern according to moisture availability. "Be prepared"—both to take advantage of a good monsoon and to reduce the impact of adverse seasons—should be our national motto in agriculture.

2. **Increasing rice production**

   There is vast scope for increasing rice production in West Bengal, Assam, Orissa, Andhra Pradesh, Tamil Nadu, Karnataka, and even Kerala during the rabi season. The yield of boro rice is high in Assam and West Bengal. More than 27 high-yielding rice hybrids are now available to suit different agro-climatic and growing conditions, as well as grain quality requirements. They are from both the public and private sectors. Pusa RH-10 is a superfine, aromatic grain hybrid suitable for cultivation in northwest India. KRH2 is a high-yielding and widely adapted hybrid, and DRRH 2 is an early hybrid with good yield potential. States with an unused yield reserve in their agricultural production bank should be encouraged immediately to initiate action with the guidance of experienced farmers and scientists to use the yield reserve wisely to improve production and productivity. A precise agronomic package will have to be developed on a location-specific basis with the help of agricultural universities.

Rabi and boro rice production can be enhanced considerably by giving attention to balanced fertilization, particularly to the supply of need micronutrients such as zinc, boron, and sulfur. Together with plant protection, the enhancement of soil health will help to improve productivity by at least an additional ton per hectare. There are nearly 5 million ha under rabi and boro rice in the country and improved varieties are available for all the states where rice is cultivated between November and May. Striking progress in improving the yield of rainfed maize, soybean, sorghum, green gram, blackgram, pigeon pea, chickpea, finger millet, pearl millet, castor, etc., can be achieved through balanced fertilization (NPK and needed micronutrients). Seeds of improved varieties should be maintained in village seed banks in rainfed areas, so that alternative cropping strategies can be introduced depending upon monsoon behavior. Improved cultivars alone can enhance productivity by 10% to 50%. Varietal choice should be based on the likely moisture availability. The short-duration chickpea variety Shwetha (ICCV2) has revolutionized chickpea production in Andhra Pradesh. Its productivity increased from 470 kg ha^{-1} in 1993 to 1,084 kg ha^{-1} in 2004. Area also increased sevenfold. There are nearly 12 million ha of rice fallows in Madhya Pradesh, Orissa, Jharkhand, Chattisgarh, and West Bengal. In such rice fallow areas, chickpea can be grown by using residual soil moisture. Simple seed priming technologies such as soaking seeds in water and micronutrient solution for 6 hours and drying in shade will help in establishing a good chickpea crop in rice fallows. In Madhya Pradesh, 2 million ha remain fallow during the kharif season. Using a broad bed and furrow, balanced nutrient management, and a short-duration soybean cultivar such as Samrat, farmers in Vidisha District were able to grow a crop of chickpea or wheat during rabi and thereby double their income. Many such simple steps in soil-water-crop management can lead to major advances in both crop output and farmers' income. This is the pathway to making farming economically viable.

A timely and adequate supply of credit, seeds, and electricity, together with addressing micronutrient deficiencies in the soil, will help to offset losses in production during kharif. Those states that had heeded the NCF appeal made in December 2005 that 2006-07 would be observed as the Year of the Farmer and Agricultural Renewal will be in a much better position to improve rabi production. A 5-pronged strategy recommended consisted of soil health enhancement, water harvesting and management, credit and insurance, technology and inputs, and remunerative marketing.

Adaptation to climate change is an urgent task. The Climate Management Unit of the National Rainfed Area Authority should develop computer simulation models of weather behavior coupled with public policy and agronomic responses needed to meet diverse possibilities.

3. **Extending the gains**

Eastern India (eastern Uttar Pradesh, Bihar, Chattisgarh, Orissa, West Bengal, Assam, and northeast states) has a large untapped production reservoir even with the technologies now available. In these areas, poor water management, rather than water availability, is the major constraint. The Indo-Gangetic Plains offer scope for becoming the major breadbasket of India through an appropriate mix of technology, services, and public policies. In many of these areas, the aquifer should be enriched during the southwest monsoon period, and extensive groundwater use should be promoted during the October-April period. With the right strategy, the Ganges Water Machine could become the main anchor for our food security system. Bihar in particular is a sleeping giant in the field of agriculture. The work of the Indian Agricultural Research Institute in Dharbhanga District and Sone Command area has shown that wheat yield can be increased substantially with good seeds and improved agronomic practices. The major bottleneck, however, is the absence of grain machinery, which will provide the minimum support price to farmers.

Action to extend the gains of higher productivity and profitability should cover all rainfed areas. This should be a priority task of the National Rainfed Area Authority. The recommendations of the Swaminathan Committee on “More income per drop of water (2006)” should be converted into action plans by location and farming systems.

MAKING NEW GAINS

The immediate prospect for making new gains lies in the areas of postharvest technology, agro-processing, and value addition to primary produce. NCF has made several recommendations in this area in its first four reports. In the longer term, there is a need for new yield and quality breakthroughs in major crops through genomics and gene pyramiding. For example, super wheat varieties capable of yielding about 8 t ha^{-1} are now in the breeders' assembly line. Such wheat varieties have a complex pedigree and illustrate the importance of genetic resource conservation and exchange.

Super wheat varieties are semidwarf with robust stems, broad leaves, and large spikes with more grains per panicle and more grain weight. The super wheat architecture in the breeders' assembly line, at both the International Maize and Wheat Improvement Center and All India Coordinated Wheat Improvement Program, is derived from a blend of Tetrastichon (Yugoslavia), Agrotriticum (Canada), Tetraploid Polonicum (Poland), Gigas (Israel), Morocco wheat (Morocco), and semidwarf wheat currently grown in India. We can produce 100 million t of wheat by 2015, by the following two steps:

- Average yield of 4 t ha^{-1} from 25 million ha.
- Harnessing the large untapped yield reservoir in eastern, central, and western India.

Every state should develop a detailed agricultural strategy for its major farming zones and systems based on the 3-pronged approach outlined above.

Irrigation water is going to be a serious constraint since, as pointed out earlier, groundwater is being overexploited. Therefore, NCF supports the recommendation of the Swaminathan Committee set up by the Ministry of Water Resources that the Agricultural Year 2007-08 (1 June 2007 to 31 May 2008) be observed as the "Year of More Crop and Income per Drop of Water."

MORE INCOME AND CROP PER DROP OF WATER

The System of Rice Intensification method of rice cultivation results in a savings of irrigation water. A committee I chaired has suggested an extensive farmer participatory demonstration program to show how more income and yield can be obtained for every drop of water.

Rice will in the years to come be the flagship of our food security system. Therefore, a dynamic research program will be necessary to launch and sustain an ever-green revolution in rice.

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Bringing Hope, Improving Lives

Robert S. Zeigler

The world has changed enormously since IRRI developed its last strategic plan a decade ago. Recent scientific discoveries—particularly in genetics and genomics—now open up new opportunities to achieve impact that would have been difficult if not impossible as recently as the turn of the century. A reduction in poverty and sustainability of the rice production environment, through the use of modern technology and the latest communication tools, are at the heart of IRRI's exciting and innovative plan.

Rice remains the most important staple food on the planet since it feeds roughly half the population on a daily basis. Approximately 750 million of the world's poorest people depend on it to survive. So, an agenda for continued research on this vital crop is still very relevant.

This paper spells out how IRRI's plan (1) brings the best rice technologies to all regions of the world that need them, including East and Southern Africa where demand is increasing; (2) focuses on health and nutrition; and (3) is committed to the long-term conservation and use of rice genetic resources.

Five strategic goals and seven programs embodied in the plan are described as are three Frontier Projects being designed to continue beyond the life of the plan in research areas that have the potential to make an enormous impact on the lives of poor rice farmers and consumers.

The new plan endeavors to take IRRI over a modest 9 years so that it can join colleagues and partners from around the world to reach the Millennium Development Goals by 2015. Nevertheless, much of the work outlined here will obviously extend well beyond that date.

Rice feeds roughly half the planet's population and approximately three-quarters of a billion of the world's poorest people depend on the staple to survive. A carefully focused agenda for continued research on this vital crop is more imperative than ever. And if all goes as planned, in 2010—while the International Rice Research Institute (IRRI) is celebrating its 50th anniversary—the initiatives spelled out in the Institute's new Strategic Plan (the Plan) will already be starting to have impact.

This Plan, *Bringing hope, improving lives*, which I am publicly unveiling to you today, is also designed to enable IRRI to do its part in helping partners and nations across the globe to reach the United Nations Millennium Development Goals (MDGs) by 2015.

Certainly, the world has changed enormously since we developed our last strategic plan a decade ago. Recent scientific discoveries—particularly in genetics and genomics—now open up new opportunities to achieve impact that would have been difficult if not impossible as recently as the turn of the century. The reduction of poverty and the sustainability of the rice production environment, through the use of modern technology and the latest communication tools, are at the heart of our exciting and innovative Plan.

Developing the Plan took nearly 12 months. IRRI consulted widely among its partners and stakeholders and sought expert guidance throughout. During these deliberations, we concluded that the MDGs related to hunger, poverty, environmental sustainability, and nutrition and health formed a sound basis and direction for IRRI's future activities. So, we developed five strategic goals and seven research programs to achieve them to reflect this thinking.

GOAL 1: REDUCE POVERTY THROUGH IMPROVED AND DIVERSIFIED RICE-BASED SYSTEMS

Achieving IRRI's first goal—*Reduce poverty through improved and diversified rice-based systems*—will take the Institute beyond its traditional focus on rice production (increasing productivity or "filling the rice bowl"), which required an emphasis on favorable irrigated areas, to "filling the purse," a major effort to improve farmers' incomes in unfavorable rainfed areas. Nevertheless, rice supplies will need to remain plentiful to provide reliable food that even the poorest can afford. In Southeast Asia, South Asia, and sub-Saharan Africa, rice consumption in 2015 is projected to be, respectively, 13.4 million tons (11%), 22.3 million tons (13%), and 9.5 million tons (51%) above 2005 levels.

This means relatively less research emphasis for IRRI on yield gains for irrigated rice—for which there is now strong capacity among the national agricultural research and extension systems (NARES), particularly in Asia. Instead, IRRI's focus on intensive production systems will shift more to sustainability. In addition, by targeting the MDG on eliminating extreme hunger and poverty as our first strategic goal, we are opening profound new opportunities for IRRI to improve the economic and social well-being of poor rice consumers and farmers.

Program on raising productivity in rainfed environments: attacking the roots of poverty. Rainfed areas coincide to a large extent with regions of severe and extensive poverty where rice is the principal source of staple food, employment, and income for the rural population. Up to now, success has been limited in increasing productivity in rainfed rice ecosystems—home to 80 million farmers on 60 million hectares. Rice yields in these ecosystems remain low at 1.0 to 2.5 tons per hectare and tend to be variable due to erratic monsoons. Poor people in these ecosystems often lack the capacity to acquire food, even at lower prices, because of poor harvests and limited employment opportunities elsewhere.

Our primary objective will be to enhance household food security and income in these rainfed areas of Asia. With rapid advances in genetics and genomics, the chances of developing high-yielding, drought- and flood-tolerant varieties for the rainfed system—and, consequently, helping farmers to diversify their farming systems and thus their income—are much greater now than ever before.

Program on East and Southern Africa: rice for rural incomes and an affordable urban staple. Sub-Saharan Africa is now one of the world's major poverty zones and Goal 1 targets this vast region as well. About 130 million people in East and Southern Africa (ESA) alone live in extreme poverty and more than 85% of these depend on agriculture. A large number of these people are rice consumers and many are small rice producers. A significant investment in agriculture is critical to eradicate hunger and poverty in ESA.

Rural poverty in the ESA region could be significantly reduced if the efficiency of local rice production were improved in the key rice-growing areas of Kenya, Mozambique, Tanzania, and Uganda. Our research agenda here will also focus on enhancing small farmers' access and linkage to markets. We will collaborate closely with the Africa Rice Center (WARDA), the national programs, and advanced research institutes to capitalize on both the existing knowledge within the countries and the available international expertise.

GOAL 2: ENSURE THAT RICE PRODUCTION IS SUSTAINABLE AND STABLE, HAS MINIMAL NEGATIVE ENVIRONMENTAL IMPACT, AND CAN COPE WITH CLIMATE CHANGE

It is critical that the stability and productivity of rice agroecosystems in Asia and Africa not be taken for granted and that their use by future generations not be jeopardized. Rice-growing areas are among the world's most enduring, environmentally sound, and productive agroecosystems, and increased rice production in recent decades has had a significant impact on poverty reduction.

Program on sustaining productivity in intensive rice-based systems: rice and the environment. Rice ecosystems provide basic commodities and regulatory services, including nutrient and water cycling, and biological control to reduce pest and disease outbreaks. Poor people often depend on these "ecosystem services" to provide their needs as they are often without infrastructure to obtain clean water, food, and fuel. Environmental sustainability and ecosystem services are threatened, however, by the loss of biodiversity, climate change, and inappropriate management systems often caused by land, water, or labor shortages.

Strategies are urgently needed to preserve the natural resource base while improving productivity in rice agroecosystems in the face of changing physical and socioeconomic environments. IRRI will focus on land management, biodiversity, water availability and productivity, and the impact of climate change to develop and promote technologies and options to sustain rice-producing environments.

GOAL 3: IMPROVE THE NUTRITION AND HEALTH OF POOR RICE CONSUMERS AND RICE FARMERS

Nutritional deficiencies, especially in women and children in both Asia and Africa, often go hand in hand with extreme poverty because poverty is a major factor limiting diversity in the diet. Reliance on a single staple, such as polished rice, does not provide the requisite suite of minerals and vitamins necessary for healthy growth and development and leads to widespread nutritional deficiency in many of the 1.2 billion people in Asia and sub-Saharan Africa living in extreme poverty.

Program on rice and human health: overcoming the consequences of poverty. This program will bring together the multiple rice biofortification projects (including the HarvestPlus Challenge Program) and other health-related efforts that already investigate germplasm, farm practices, and policy options.

Underpinning maximum success in meeting many of the MDGs is the need to solve the widespread problems of health and nutrition that debilitate people and hinder economic growth. Poor nutrition is manifested in invisible nutritional deficiencies (hidden hunger) and in malnutrition (visible hunger). In addition, poor health in the context of rice cultivation may be related to chronic and infectious diseases from water and from vectors such as rodents and mosquitoes, as well as illness attributed to the improper handling of farm chemicals.

For much of the work in this program, the delivery chain includes partners in NARES for the co-development and deployment of germplasm (seeds and the genetic material they contain) and agricultural practices. However, IRRI will greatly expand its interactions with the public health sector in developing countries, for both policy and delivery effectiveness.

This process has already begun in the Golden Rice Network for India and the Philippines and this will serve as a model for other products. The existing structures in the Golden Rice Network and in HarvestPlus have already brought together many of the relevant national and regional institutions needed for impact.

GOAL 4: PROVIDE EQUITABLE ACCESS TO INFORMATION AND KNOWLEDGE ON RICE AND HELP DEVELOP THE NEXT GENERATION OF RICE SCIENTISTS

Developments that will affect all of the efforts mentioned so far are the rapidly increasing availability and affordability of information and communication technology, such as the Internet, mobile phones, and powerful computers. These new technologies have created important opportunities to allow people with common interests to form communities, communicate, and collaborate.

They have also raised new obligations for IRRI to curate, exchange, and share not only its own body of information, data, and experience but also that of the world's knowledge about rice in all its forms. This will not only enhance global rice research efforts but also empower developing-country rice scientists with state-of-the-art information and knowledge and their associated tools.

Program on information and communication: convening a global rice research community. This effort will build on many global investments in information and technology within and outside IRRI's parent organization, the Consultative Group on International Agricultural Research (CGIAR).

Through this program, we are formally attempting to consolidate all IRRI research and development on information and communication technology for rice science and extension under a single coordinated activity. We plan to place bioinformatics and communication tools directly in the hands of crop scientists, extension agents, and farmers to deliver impact through two major pathways, which will enhance the capacity of IRRI's six other research programs to deliver impact more effectively.

The first pathway is Internet dissemination via a World Rice Community Portal of restructured and cross-linked information on crop science and extension. The second pathway is direct engagement of science and extension communities using current communication technologies, both new, such as Web portals, videoconferencing, and cell phones, and traditional, such as radio and television.

GOAL 5: PROVIDE RICE SCIENTISTS AND PRODUCERS WITH THE GENETIC INFORMATION AND MATERIAL THEY NEED TO DEVELOP IMPROVED TECHNOLOGIES AND ENHANCE RICE PRODUCTION

Another ingredient in the mix that will continue to contribute to the impact of IRRI's research agenda is the rice germplasm it has assembled over nearly half a century. IRRI now maintains, on behalf of humanity, the world's most complete and diverse collection of rice germplasm and this leads to our fifth and final goal.

Program on rice genetic diversity and discovery: meeting the needs of future generations for rice genetic resources. There are still significant gaps in IRRI's germplasm collection and, despite the advanced state of knowledge of the rice genome, information is scant on what diversity of genes exists within the rice gene pool, what these genes do, and how they can help meet the needs of rice producers and users. Meanwhile, genetic erosion in the field continues.

We expect a greater demand for specific genetic resources to address production and environmental problems in the future. This will translate into a greater demand for the genetic knowledge and tools that are needed to identify and use resources that meet specific needs.

Through genomics (the science of discovering genetic structure, variation, and function, and the interrelationships among these), genetic knowledge can now be integrated across species, leading to accelerated discovery of gene functions. Furthermore, genome-wide analysis has the potential to reveal new insights about genetic pathways, and create new opportunities to meet both anticipated and unforeseen challenges.

Bringing together germplasm conservation, diversity analysis, and gene discovery under this single program presents a unique opportunity to maximize the utility of conserved and customized germplasm. This program will offer a comprehensive, well-documented germplasm base, a public research platform to enable gene identification, and genetic knowledge for priority traits. Building on the investments and achievements made in germplasm characterization, functional genomics, and bioinformatics, IRRI is poised to play a major role in gene function discovery, applications of genetic knowledge, and conservation and sharing of genetic resources.

POLICY SUPPORT AND IMPACT ASSESSMENT

One last new program, which will be critical to achieving the five Plan goals, is *Rice policy support and impact assessment for rice research*. The impact of rice research on poverty reduction and environmental sustainability depends on policies and appropriate technologies that address farmers' livelihood needs.

To effectively set research priorities, we must understand the broad trends in socioeconomic and policy environments that affect the economics of rice production. This involves analyzing trends in rice production and consumption at national and subnational levels and shifts in comparative advantages in rice production relative to other crops across regions and ecosystems.

IRRI aims to provide sound advice to policymakers, research managers, and donors regarding research priorities and the design of agricultural interventions through policy analyses, livelihood studies, and impact assessments focused on rice-based systems of Asia.

By making regional comparisons of rice economies and associated livelihoods, the program will help produce a global view of the drivers of change and their impacts. In addition, we will develop research approaches and tools that will have wider application for policy research and impact analysis. We will also closely partner with NARES to help build their capacity for broader socioeconomic and policy analyses of the agricultural sector. NARES, sister CGIAR centers, and advanced research institutes will all have key collaborative roles in the program.

VISIONARY FRONTIER RESEARCH

IRRI has a 46-year history of investing in visionary "frontier" research–research that, when successful, has revolutionized agriculture. The original frontier project was none other than the incorporation of semidwarf genes to create the modern high-yielding varieties that began with the release of IR8 in November 1966 and spurred the Green Revolution in rice.

Three new Frontier Projects, involving work on drought tolerance, climate change, and producing a more productive and efficient rice plant, are intended to accentuate the Institute's commitment to achieving its new goals. They will constitute novel and focused research on problems of strategic importance to future rice production and the environment. The projects will be undertaken by multi-institutional, international research teams, and we expect that significant portions of the research will be conducted at collaborating institutions in both developed and developing countries.

Drought and productivity in unfavorable rice environments (tied to Goal 1). Recent IRRI research has shown that the drought tolerance trait is strongly influenced by genes and gene networks with large effects. This project will scale up their detection, analysis, and delivery for use in marker-aided breeding. By incorporating genes for this trait from rice and other species into widely grown rice varieties, technologies can be developed with national agricultural research systems and provided to farmers to enhance and stabilize their rice yields and income.

Climate change and sustainability (tied to Goal 2). Climate change brings new problems for the sustainability of rice production. Further, changes in air quality and composition, acid rain, and Asian "brown" clouds will produce a new bio-climate for food production systems. Rice cultivation is often viewed as a contributor to climate change through the production of greenhouse gases. Given the essential role of rice in the food system, solutions must be sought that not only minimize the impact of rice production on the environment but also sustain productivity and environmental quality. Strong science will decipher the causes and effects involved, improve germplasm adaptation to expected future climatic conditions, and mitigate the negative effect of agriculture on climate.

A much more productive and efficient rice plant (tied to Goal 5). Plants like maize and sorghum have a more efficient photosynthetic mechanism (called C_4) for converting energy to biomass than rice (a so-called C_3 plant). C_4 plants are also more efficient in nitrogen and water use, and are generally more tolerant of high temperatures. Genomic sciences and comparative biology may be able to break the yield ceiling of rice and enhance its water- and nitrogen-use efficiency by changing the photosynthetic mechanism in rice to that of the more efficient plants. IRRI has formed a C_4 rice consortium of senior scientists from both advanced research institutes and developing countries to chart and conduct research to develop a C_4 rice plant.

CONCLUSIONS

We have identified five strategic goals, have set targets by which our performance can be measured, and have established seven programs to achieve them. While the targets are realistic, they still remain challenging for all of us. The new Plan endeavors to take us over a modest 9 years so that we can contribute significantly to reach the MDGs by 2015. Nevertheless, much of the work outlined here today to bring hope to millions and improve their lives will obviously extend well beyond that date.

So, I believe IRRI's future is certainly something truly to get energized about and that, all-in-all, we are well positioned to move forward aggressively and take advantage of new opportunities and, most importantly, address some very difficult challenges that we only dreamed of meeting not too many years ago. IRRI is truly reinvigorated and is clearly relevant to the MDGs broadly accepted by the global community. I am excited about what IRRI will accomplish over the next years and am sure that you our partners and colleagues will join in and support us.

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Public Policy and International Collaboration for Sustaining and Expanding the Rice Revolution

Joachim von Braun

Rice continues to shape the lives of millions of people. Public policy is therefore attracted to all production, distribution, and consumption aspects of rice, as well as its environmental implications. Public policy is changing, however, in view of developmental and societal change, especially in Asia. The importance of rice in the diet of Asia is expected to decline over time with urbanization and the increase in incomes beyond the level at which people begin to diversify their diets. This pattern is not observed in other parts of the world; in Africa and Latin America, rice is becoming increasingly important. Rice is a strategic commodity because it is a most important element in the diet of the poor and a main source of income and employment for farmers in Asia. Traditionally, governments have sought to maintain stable prices for consumers in urban areas and to provide input subsidies to farmers. A shift of policies toward less intervention in the rice market is noted. Governments are increasingly pulling out of managing rice and private enterprises play the main roles. Appropriate policies need to facilitate the private actors' roles in the rice-related food chain. Rice is increasingly a "health food" with many characteristics and diverse tastes, and can be developed further in such directions. New science on rice focusing on the diet quality aspects of rice may actually transform rice into an even more important agent of change, especially for the poor. At the same time, high-income consumers are expected to increase their demand for specialty rice. The expanded supply of rice must be achieved by increasing yields. To achieve this, increasing investments in research and development are needed in international cooperation, especially to reduce water and energy use in rice production. These objectives will need to remain high on the agenda of rice research for decades to come. Public policy in support of making the best of rice needs adaptation to the new circumstances at national and global levels.

Rice, being the second largest consumed cereal (after wheat), shapes the lives of millions of people; over half of the world's population depends on rice for 80% of its food calorie requirements. The "revolutionary" feature of rice is its steady, long-term evolution with societal change. Certainly, rice has been a good partner to humankind, and adaptive ecological, economic, and technological changes around rice facilitated this “partnership between humans and rice.” For instance, in times of rapid population growth, soaring rice demands were met largely because of the Green Revolution. We must therefore continue to nurture this partnership.

The rice environment today is more complex than ever before. For one, the policy environment for rice is changing. Particularly in Asia, where rice is the main staple, public policy has always been attracted to all production, distribution, and consumption aspects of rice, as well as its environmental implications. Traditionally, governments have sought to maintain stable prices for consumers in urban areas and to provide input subsidies to farmers. However, now that many Asians are diversifying their diets, a shift in public policy is noted; governments have been increasingly pulling out of managing rice, thus enabling more engagement from private enterprises. Additionally, new science in rice focusing on its diet quality aspects gives rice a “health food” aspect, which is enabling rice to become an agent of change in tackling the complex malnutrition issues across the developing world. The actors in rice research have also become more diversified; for decades, almost all rice research was done by the public sector through national and international agricultural research centers, but now, with advances in crop technology, the private sector, which in the past played only a minor role, is expected to engage more actively in rice research. The appropriate mix of incentive-oriented policies for private-sector orientation and of public investment policies in support of agricultural research requires increased attention.

The purpose of this paper is to consider the emerging issues in the rice policy environment and recognize the risks and challenges ahead, with the objective of identifying opportunities for effective collaboration between the public and private actors at national and international levels. The paper outlines policy challenges and options to sustain and expand the rice (re-)evolution, given the new demands for rice quantities and qualities and the crop’s ecological properties. It starts by elaborating a conceptual framework outlining the three key policy domains along the four main segments of the rice value chain. Then, using this framework, these main policy domains are reviewed. Subsequently, risks and opportunities and the need for international cooperation in science and trade policy for rice are highlighted. Finally, the conclusions delineate priorities for coherent rice policies. It is important to note that policy priorities will differ across developing regions and countries, given the diversity in the importance of rice in people’s diets, and the diversity in the level of economic development achieved.

EMERGING ISSUES FOR RICE AND A FRAMEWORK FOR ANALYSIS

Key issues along the current *rice value chain*, starting from the consumers' end, include

1. A value chain increasingly driven from its consumption and retail ends, rather than the production front. In effect, consumers' demand for higher quality rice and improved standards and regulations in the processing and marketing of rice are becoming important determinants of the future of rice.
2. An increasing demand for processed rice products.
3. The continued relevance of productivity gains, not only in terms of "producing the pile of rice" efficiently per unit of land or water, but increasingly also in terms of labor productivity.
4. The predominant concern of natural resource use of rice ecosystems and the increasing stress on water resources.

In this context of the value chain, sustaining and expanding the rice (re-)evolution entails a more comprehensive set of policy objectives that go beyond just increasing rice yields. In view of the close linkages between production, markets, and consumption of rice, any outlook on rice must take a holistic perspective, and the future of rice cannot be assessed without due consideration of the broader economic context and developments related to other foods, especially other cereals, and the expansion of high-value agriculture competing for resources. Moreover, achieving these objectives requires action in a wider array of policy areas, and also requires more extensive collaboration between the public and private sector, as well as the international community.

The *policy domains* affecting the elements of the rice value chain can be broadly structured into three categories:

1. Market, trade, and price policies, including regulations and standards
2. Environmental and ecosystem policies
3. Research and development policies for innovations

As shown in Table 1, this gives us a *3-by-4 framework* to analyze policies in the context of the value chain. The paper is structured along the lines of the four policy domains, and also considers some cross-cutting structural issues. The table in the Annex summarizes the suggested policy actions within the value chain, as well as those looking at cross-cutting structural issues.

Valuation of rice along the value chain becomes more complex when sustainability and externality issues are considered. Indeed, the value of rice today cannot just be assessed at prevailing market prices; broader economic and noneconomic concepts such as the insurance value of rice for food security, the "existence" value (e.g., for traditional varieties, even for nonconsumers), and the inheritance value (passing rice varieties onto

Table 1: Framework for analyses of policies on rice along the value chain.

	The rice value chain			
Policy domains	Resource management	Farm production	Processing and marketing	Retailing and consumption
Market, price, trade policies, including regulation, and standards	X[a]	XX	XX	XX
Environmental policies and risk-coping policies	XX	X	XX	X
Innovation and R&D policies	XX	XX	XX	X

[a] XX and X indicate the degree of relevance of the policy domain for the respective elements of the value chain (XX = strong, X = less strong).

coming generations) should be considered. To the extent these "nonuse" values deviate from current market prices, public investment and other policy actions may be called for to assure the efficient production of these values. The goals of efficiency, sustainability, equity, and poverty reduction to be served by the rice-related policy domains in Table 1 may become more conflicting, as is generally the case with complex sets of policy objectives. Ignoring these conflicts, for instance, by simply postulating short-term productivity-oriented policies would be inappropriate and inefficient. Further, policymakers are called upon to handle policy processes around competition policy goals and instruments that translate into competing group interests in society. If anything, rice is bound to be at least as "political" as in the past.

PUBLIC POLICIES AND INTERNATIONAL COOPERATION FOR ENHANCING THE NET BENEFITS OF RICE

Market, Price, Trade Policies, and Standards

Market functioning, prices, and trade of rice are a result of demand and supply, and of policy interventions in either side of the market (or at borders). With approximately 650 million people living on less than one dollar a day in Asia,[1] any effort to reduce poverty will require attention to rice, as a large

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[1] This represents 64% of the total number of people living on less than a dollar a day.

Table 2: Contribution of rice consumption to total daily calorie intake.

Region	1974	2003
	(% of total calories per capita per day)	
Asia	38.0	29.4
Latin America	9.0	9.0
Africa	5.5	8.2
Near East	7.0	8.3
North America	1.0	2.5
Europe	1.0	1.5

Source: FAO (2006b).

share of the income of poor households goes to purchase rice, and many poor farmers depend on rice production for their income. However, with urbanization and the increase in income beyond the level at which people begin to diversify their diets, the importance of rice in diets in most Asian countries will continue to decline over time. This pattern is not observed in other parts of the world, where rice consumption is increasing rapidly; in the Middle East and North Africa and sub-Saharan Africa, the consumption of rice increased by about 50% since the early 1990s, while in Latin America it increased by approximately 20%. The industrialized world is also experiencing an increased demand for rice, particularly for high-quality special rice varieties (von Braun and Bos 2004).

Demand for rice. The key factors affecting demand for rice include population growth, income level, urbanization, and changes in taste. In terms of the relationship between income and demand, as income rises, rice becomes an inferior good because consumers tend to diversify their diet, shifting initially toward the consumption of wheat, and later to livestock and other products (IRRI 2002, Barker and Dawe 2002). Additionally, as income increases, consumers' preferences move toward higher quality rice varieties. These two trends are particularly evident in Asia; although rice still accounts for a large share of calorie intake per capita, its share in total calorie consumption is rapidly declining (Table 2).

Urbanization has had mixed effects on the demand for rice; on the one hand, in countries where rice is a staple, growing urbanization has translated into changing eating habits, which in turn has resulted in reduced rice consumption (IRRI 2002). On the other hand, in places where rice is not the main staple, urbanization has meant an increase in rice consumption; in Africa, for example, demand for rice grew on average by 3.2% a year from

Table 3: Total rice production by region, 2005.

Item	World	Asia	Latin America and the Caribbean	North America	Africa	Europe
Production (000 t, paddy)	618,441	559,350	26,431	10,126	18,850	3,340
Percentage of world production	100.0	90.5	4.3	2.0	1.6	0.5

Source: FAO (2006b).

1990 to 2003. This growth is partly due to growing urbanization (and the different lifestyle that it entails, such as the increased participation of women in the formal labor force), which has meant that consumer preferences are shifting from traditional staples that require more preparation time (such as cassava, sorghum, millet, and maize) to rice (Hossain 2006).

Other socioeconomic factors such as changing demographics of a country's population can also affect the demand for rice. For instance, growing demand in industrialized countries can be partly explained by increases in Asian and Hispanic populations, who generally prefer rice. Another factor that may be affecting rice demand in the West is increased consumer awareness and concern about health and diet quality (von Braun and Bos 2004).

Rice production and labor market. More than 90% of the world rice production takes place in Asia (Table 3). China and India are the two largest producers; in 2005, they jointly produced 51% of the world's rice and occupied 47% of the world rice area. In Africa, rice production has increased dramatically; from 1970 to 2005, rice production increased by over 130% (FAO 2006b).

Most rice in the world originates from *small farms*. Rice-related policies are therefore intimately related to the challenge of transforming small-farm agriculture, especially in Asia. In general, the next generations of rice farmers aim to get bigger, grow through high-value agricultural production, shift to part-time farming in combination with other rural employment, or move out of agriculture altogether.

The income and employment problem of today's small rice farmers cannot be effectively solved through just yield-increasing technologies or new forms of cooperation in production and marketing, for example, through cooperatives or contract farming. The gap between aspirations and on-farm realities is too wide in most of the fast-growing Asian economies and the potential contribution of rice-specific interventions is too minor to make a difference in the long run. Thus, the small rice farmers' income problem needs broader rural and economy-wide policy actions, including rural infrastructure and education policies, in order to facilitate a long-run transformation of the rural sector. Nevertheless, in the coming decade, productivity enhancements and more efficient market functioning remain of importance for the income of poor rice farmers (Swaminathan 2005).

As a result of the economic challenges faced by small farmers, the rice market increasingly interacts with the labor market. The growing economic prosperity in Asia is reducing the incentives for farmers to engage in rice cultivation. The expansion of the nonfarm rural sector and rising labor productivity have pushed up nonfarm wage rates, which has motivated labor migration—particularly of the youth—from rural areas to cities and from farm to rural nonfarm activities. Since traditional rice farming is a highly labor-intensive activity, increases in wages have pushed up the cost of rice production and reduced farmers' income and profit (Hossain and Narciso 2004).

Besides labor, the energy market and, in particular, rising energy costs are increasingly affecting rice production. Among other things (such as typhoons, drought, flooding, diseases, and insect attacks), the rising cost of energy has contributed to rising production costs, translating into increasing prices for rice (FAO 2006a). Additionally, to ensure their energy security, many developing countries are undertaking an aggressive growth in biofuel production, which has prompted concerns that biofuel production may be "crowding out" food production (Rosegrant et al 2006, von Braun and Pachauri 2006)

Rice trade and pricing policies. Developing countries dominate most of the rice trade, accounting for over 80% of both imports and exports. The five major exporters are Thailand, Vietnam, China, the United States, and India, while the main importers are Indonesia, Bangladesh, the Philippines, Brazil, Iran, and Nigeria. However, only about 7% of the total rice produced is traded internationally. There are numerous reasons for this, including the residual nature of trade in national policies pertaining to rice; much rice is consumed where it is produced, as many rice-producing countries concentrate on meeting local demand (UNCTAD 2006, Gulati and Narayanan 2002). Further, both developing and developed countries protect their rice markets. During 2002-03, OECD rice producers received US$22 billion of support per year, and developing countries' level of market price and producer support is increasing; for example, in India, Indonesia, and Vietnam, the level of support has increased by as much as 30–40% (Orden et al 2006). Additionally, exchange rate appreciation in Asia (e.g., China) may be the single biggest force in diminishing the competitiveness of rice, and may further increase the call for protection in the coming years.

Trade liberalization commitments for rice have been minor under the WTO. Still, the liberalization of rice trade has potential in terms of economic gains, and can play a role in stabilizing rice prices. For example, when major floods hit Bangladesh in 1998 and negatively affected rice production, the government's reaction was to relax restrictions on rice imports. This paved the way for increased imports from India, which was crucial for avoiding major disruptions and spikes in rice prices that would have hurt poor households most.

One consequence of the small share of trade is large fluctuations in rice prices, reinforced by the lack of collective action among the main rice-producing countries to expand international trade. This in turn may be a force behind national policy aimed at price stabilization and policy demand for high shares of domestic supply. Over the past four decades, due to increased yields and a decrease in cost per unit of production, rice prices have shown a declining trend, but continue to fluctuate substantially. Indeed, 85% of rice exports are concentrated among the five major exporters, and any change in the production or consumption of rice in these countries would have a strong effect on prices.

Given the sensitive nature of rice, most Asian rice-producing countries have traditionally taken an interventionist role in rice markets. Nevertheless, the importance of private exporters is growing. In Thailand, for example, private trading has risen over the past ten years from 20% to 80%. In Vietnam, private negotiators have also appeared progressively following the national economic reforms that took place in the 1990s (UNCTAD 2006).

Regulations and standard-setting policies. The growing consumer demand for higher quality produce and stricter food safety regulations have meant that national governments around the world (especially in industrialized countries) and private food companies are paying more attention to food quality and food safety measures. This poses several challenges. For one, many producers in developing countries may not have the required resources to meet stringent quality standards. Second, there is a wide diversity of safety standards across the globe, and this can be a serious impediment to trade. European countries, having experienced relatively more food scares in recent years, tend to have more stringent food safety requirements. In addition, many developing countries do not have the required regulatory institutions to test food products to see whether they meet quality standards (Umali-Deininger and Sur 2006, Henson and Jaffee 2006, Saxena and Singh 2002).

One of the more contentious issues in food standards is the use of genetically modified organisms (GMOs) in food production. While GMOs could potentially result in significant gains for both farmers and consumers, concerns remain about risks (or simply aversion for other reasons). As a result, some governments have imposed restrictions on imports and/or have strict labeling requirements on GM products (Anderson and Nielson 2000). Thus, the discovery of GMO "contamination" can be disruptive to rice production and trade. For instance, in 2006, when food safety authorities in the U.S. learned that an unapproved, experimental GMO rice had been found in U.S. rice exports, it led to a suspension of U.S. long-grain rice imports in Japan, whereas, in Europe, importers were required to produce a certificate demonstrating that rice imports did not contain unauthorized GM rice. Additionally, rice futures prices fell by more than 5% at the Chicago Board of Trade, and many supermarkets across Europe were forced to make product withdrawals (Mekay 2006). This GMO contamination case highlights the need for harmonizing quality and food safety standards at the global level. The WTO's Agreements on Sanitary and Phytosanitary Measures (SPS) and Technical Barriers to Trade (TBT) allow member states to set their own food safety measures and to impose trade barriers based on food safety measures, and so do not solve the problem. Of increasing importance are corporate rice standards and rule-of-origin criteria for the fast-growing specialty rice qualities. Transparent labeling policies and/or trademarks are needed to facilitate market functioning for these rice products.

Environmental Policies and Addressing Risks

Increased pressure on *water and land resources* is today the chief concern related to rice. By far, most of the rice produced in Asia depends on irrigation, and irrigation is the single largest user of water resources. However, inappropriate management of irrigation has contributed to environmental problems, including water depletion, water quality reduction, waterlogging, and salinization (Rosegrant et al 2002). Further, in many developing countries, average irrigation efficiency is low, thus contributing to a wasteful use of the water supply. In rainfed environments, to meet immediate food demand, farmers have expanded production into marginal lands; these lands are sometimes susceptible to environmental degradation (Rosegrant et al 2002). The biggest priority in the sustainable management of rice ecologies today is water-use efficiency.

Institutional reforms in *irrigation management* are therefore necessary, as Gulati et al (2005) highlight for India. Irrigation agencies were set up with little attention to long-term performance of the system, as, among other things, the agencies were not financially autonomous, lacked accountability, and irrigation rates did not cover operations and management expenses. From their studies of irrigation management in two Indian districts, Rajasthan and Karnataka, Gulati et al (2005) conclude that reforms must address the incentives of water suppliers and users and lead to new arrangements for joint management of irrigation.

The mismanagement of irrigation systems is only part of the water scarcity story. The precarious future water supply situation in Asia, with potential macro-watershed change around the Himalayas due to reduced ice cover, could have huge implications for rice ecologies, as some of the current production systems might become nonviable under such circumstances.

But what would be the impacts of a breakdown in rice yields—maybe as a consequence of unforeseen or new pests and crop diseases? The consequences of such a hypothetical event are explored next.

Simulating a rice disaster. A significant drop in rice production will both negatively affect farmers through the income effect and set off second-round effects through forward and backward linkages with other sectors through price effects. Given the global role of rice, the impacts of a rice disaster in Asia would also be global. To illustrate this, a simulation using IFPRI's IMPACT model is employed.[2]

The simulation assumes a rapid decline in rice yield that gets progressively worse over three years (due, for instance, to a spreading pest or disease attack), corresponding to a low of 25% of the normal yield in the third year and then returning to full "normal" yield over the following three years.[3] The results of such a (hopefully unrealistic) shock with regard to prices are dramatic: global rice prices would more than triple in year 2 after the shock and increase tenfold in year 3 before they would come down again.[4] The prices of other cereals would increase too, for example, looking at wheat and maize, making the crisis global, not just an Asian one. The simulation exercise also looks at the potential impacts of such a rice disaster on the production, demand, trade, and prices of other cereals, particularly wheat and maize.

Additionally, the potential impacts of a rice disaster on food calorie availability and child malnutrition are presented (Tables 4, 5). One striking result is that an additional 12 million children across the developing world would be malnourished at the peak of the disaster, and thereby would be adversely affected for life.

The modern and globally integrated food system may suggest that the negative impacts of a rice disaster could be somehow mitigated through trade

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[2] The objective of the International Model for Policy Analysis of Agricultural Commodities and Trade (IMPACT) model, developed by Mark Rosegrant and his team at IFPRI, is to provide insights into the management of the dynamic risks and forces that shape the factors affecting people's access to food and the links with malnutrition through appropriate policy actions. It allows the exploration of the potential impacts of different policy alternatives to manage hunger, malnutrition, commodity prices, demand, cereal yield, production, and net trade by projecting future global food scenarios in the medium and long term (see Rosegrant et al 2002, 2005, for detailed descriptions of the IMPACT model).

[3] The rice yield assumptions in the scenario are as follows: in the first three years after the shock, there is a progressive decline in rice yield. In year 1, yields are approximately 70%; in year 2, 40%; and in year 3, 25% of baseline scenario yields. Rice yields then start regressing in years 4 and 5, when rice yields, respectively, account for approximately 40% and 70% of baseline scenario yields. Finally, in year 6, rice yields get back to their baseline scenario level.

[4] The simulation results with respect to global rice prices are as follows: in the first three years, rice prices keep increasing; as compared to the baseline level, in year 1, prices are 66% higher; in year 2, they are 342% higher; and in year 3, they are 937% higher. Then, prices start declining in years 4 and 5; prices are, respectively, 354% and 69% higher than the baseline scenario prices. Finally, prices reach baseline levels in year 6.

Table 4: Difference in per capita calorie availability between the rice disaster scenario and the baseline scenario.

Region	2005	2010 (no. of calories)	2015
South Asia	0	–265	–5
Southeast Asia	0	–632	–10
East Asia	0	–320	–5
Sub-Saharan Africa	0	–111	–3
Latin America	0	–105	–2
West Asia and North Africa	0	–45	–1
Total for developing countries	**0**	**–266**	**–5**

Table 5: Difference in the number of malnourished children aged 0 to 5 (in thousands) between the rice disaster scenario and the baseline scenario.

Region	2005	2010	2015
South Asia	0	4,277	66
Southeast Asia	0	3,609	48
East Asia	0	2,298	35
Sub-Saharan Africa	0	1,496	36
Latin America	0	499	9
West Asia and North Africa	0	169	5
Total for developing countries	**0**	**12,349**	**199**

and substitutions, but, in the case of rice, due to the weight of the rice crop and its specialized production capital, this may not be the case. Thus, there is no better insurance against such risks than continuous investment in yield risk-reducing research and appropriate safeguarding of the diverse genetic resource base of rice. This remains an international task for generations to come. Moreover, emerging global climate change may pose increased risks for yields and thus require accelerated investment in adaptation of rice ecologies. We currently lack capacity for comprehensive risk assessment at the large scale.

Research and Development Policies for Innovations

Future rice research and development (R&D) has to focus mainly on a set of goals that are on the one hand driven by rice consumers and on the other hand by the ecological effects of rice. The former entails yield stability, quality traits of relevance for the poor (i.e., micronutrient content as a latent demand) as well as those required by high-income consumers, and processing qualities that can facilitate further use of rice in fast foods (maybe competing with noodles). The latter entails resource efficiency (especially water use) and adaptability to climate change.

Given the current context of rapid globalization and the speed at which new technological innovations are emerging, an adequate institutional framework needs to be urgently put in place to facilitate the development and distribution of pro-poor technological innovations. And, even as the private sector is increasingly getting involved in rice R&D, pro-poor public rice R&D remains relevant and important.

Providing adequate institutional frameworks. Institutions provide the environment of incentives for technologies to flourish, and, conversely, the absence of adequate institutions blocks innovations. In India, for instance, the Agricultural Prices Commission and the Food Corporation were established in 1965 to make possible the success of Green Revolution technologies and to lift the food equation to a higher balance.

Current and future rice technologies such as hybrid, GMO (including pest-resistant and drought-resistant varieties), and micronutrient-enhanced rice also need institutional arrangements to facilitate them in productive and safe ways. In particular, institutional frameworks for intellectual property rights (IPR) and biosafety are needed, and both require clarity in rules as well as transparency and reliability in implementation, and need to be worked out through international cooperation.

The global IPR regime remains inadequate. For one, instances of bio-piracy, the appropriation of indigenous knowledge, and innovation by foreign bodies through patent rights occur. A recent case involving Basmati rice, the high-quality long-grained aromatic rice known for its unique flavor and aroma, is a good illustration of this.[5] Second, as the research environment gets

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[5] Basmati rice has been cultivated for centuries in northern India and Pakistan, and has deep cultural value in both countries. It also has important economic value, as it represents India's primary rice export. The Basmati dispute started in 1997 when a U.S. company, RiceTec Inc., was issued a patent by the United States Patent and Trademark Office (US PTO) for the use of the word "Basmati" for an aromatic rice variety grown in the U.S. After three years of intense research and investment, the Government of India (GOI) reacted in 2000 by filing a "request for reexamination" with the US PTO, and also by filing a legal petition, along with Indian and U.S. nongovernmental organizations, with the U.S. Department of Agriculture and the Federal Trade Commission (FTC) to limit the use of the term "Basmati" to rice grown in India and Pakistan. The results of these filings were mixed. While the US PTO reexamination rejected most of RiceTec's claims, which led the company to change its patent name from "Basmati Rice Lines and Grains" to "Rice Lines Bas 867, RT 1117, and RT 1121," the FTC rejected that the term "basmati" was generic and could not be region specific (Subbiah 2004).

increasingly proprietary and exclusive, progress in public goods research may be hindered and the systems of global exchange of plant genetic resources may increasingly be constrained. To prevent this, public-private and international collaboration are needed.

Regarding *regulatory issues in biosafety and* GMOs, what is observed is that there is a general consensus on the usefulness of transgenic crops, but that the related biosafety policies are complex and slow to be implemented. From an economic perspective, biosafety and biotechnology should follow essential safety standards and cost efficiency. And, by adding many layers of complexity to regulatory work, there is a risk of not allowing crops to get to the market.

In many countries, biosafety policies are often developed by isolated government ministries or departments and in view of different priority standards, which can become a major reason for conflict and can in turn cause delays in the implementation process. Thus, to make the process more efficient, interministerial coordination is necessary.

Furthermore, in the international arena, the regulatory decisions made at the Cartagena Protocol on Biosafety should be the object of rigorous cost/benefit analysis. In particular, regulations on labeling, documentation, liability, transboundary movement, or adventitious presence will play a significant role in the development of GMO technology.

In terms of labeling policies, it is important to note that labeling will not address safety concerns; these issues should be handled at the food approval stage, which comes before labeling. For the same reasons, GM food labeling should not be introduced for safety reasons but for consumer choice or consumer right to know. Further, introducing labeling in developing countries, be it either voluntary or mandatory, is a major challenge, but the cost of labeling should be accounted for.

The role of public R&D for rice. Given the slow progress in tackling malnutrition across the developing world, rice research needs to be accelerated. While several of the innovation needs such as market-valued quality traits (which can be identified by corporate labeling or are visible in the products) can be left to the private sector, pro-poor research needs and ecological properties must be addressed by public research and at an international level. This requires increased funding for public research.

In Asia, the large national rice research systems, particularly in China and India, can address these issues in cooperation with the international agricultural research system (IRRI and more generally the Consultative Group on International Agricultural Research). However, transmission to small countries with weak research systems may become a growing problem as research needs become more and more sophisticated. The International Rice Research Institute (IRRI) can play a significant role in facilitating this transmission.

CONCLUSIONS AND POLICY IMPLICATIONS

There can be no doubt that rice is important enough to be addressed with special policies. But rice policies must not be formulated in isolation from other food and agricultural policies related to markets, technology, and the environment. As the demand for rice and the perceptions of rice-related external effects in consumption and environments are changing, optimal policies along the rice value chain must change accordingly.

Here, the needed policies within each of the three policy domains used to structure the paper are highlighted:

1. Where they are high relative to benefits, *transactions costs between and within all elements of the rice value chain must come down.* This can be done through reforms and improvements in market information flows, institutions, and organizations. Improved access to information and communication technologies and improved rural infrastructure provide significant benefits for productivity. In many locations, connecting rice farmers to the fast-changing retail industries and supermarkets through cooperatives and contracts will be beneficial. Providing favorable legal conditions for that is also important. Rice, despite being the most important food item in the fastest globalizing economies of Asia, has been largely kept out of trade dynamics. A gradual opening up of rice markets seems overdue.
2. One main task for policy related to rice is the *facilitation of increased water-use efficiency.* This would include a complex package of irrigation management, crop management, and rice breeding research and development. These measures are partly location specific and need local capacity strengthening.
3. The rice crop cannot be taken for granted. Environmental risks must be considered, especially as environments are changing with global climate change. *Continuous research efforts are needed to ensure the stability and security of the rice crop* as such research addresses the insurance value of rice in the global food system. International cooperation remains significant for that because no single country may sufficiently invest in this task. At least an additional 2 billion people need to be fed in the next generation, and they will be mainly living in Asia and Africa. Rice will be one of their main food items. Thus, an efficient supply from the sustainable production of rice will be a challenge for research and science policy.
4. Genomics allows increasingly well-understood biological properties of the rice crop. This knowledge can be brought to use for adaptation of rice to the emerging challenge. *Sound regulatory institutions and their transparent operations are needed.*

5. The policy objectives related to rice are highly varied, and include ecological goals, nutritional goals, the goal of risk reduction, and productivity increasing goals. It will be increasingly challenging to identify *coherent policies to aim for these different goals*. This requires economic and environmental assessments that take risks and opportunities explicitly into account and involve participatory policy processes. The rice (re-)evolution must continue for the benefit of poor people and sustainable development. At the front line remain the technology innovators, including researchers and farmers, and the institutional innovators, and they need bold support from policymakers.

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NOTES

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Annex

Policy domains	Resource management	Farm production	Processing and marketing	Retailing and consumption
Policies along the rice value chain				
		Support farmers to adapt to higher quality standards Investment in irrigation infrastructure in rainfed areas		Improve consumer understanding of food safety risks
Market, price, and trade policies, including regulation and standards	Introduce economic incentives in the allocation of water	Safety regulations and standards: — Harmonize quality and safety standards across the globe (across countries as well as between private and public standards), including through labeling — Improve quality and safety management and regulation capacity in developing countries (improving legislative frameworks, surveillance and inspection systems, and procedures, etc.) Markets and trade: — Progressive trade liberalization — Privatization of rice		

Annex continued

Annex continued.

Environmental policies and risk-coping policies	Improve water rights for farmers and other water users Reform irrigation systems Protect biodiversity in rice	Promote environmentally sustainable production methods (e.g., minimizing pesticide use)	Ecological standards in processing and retailing	
Innovations and R&D policies	Water- and land-saving technologies	Labor-saving technologies Drought- and insect-tolerant varieties for improved productivity Make new technologies available to small producers, i.e., link research results to farmers' realities—address the yield gap	Provide enabling environment for private-sector innovation in rice processing and in retail (e.g., addressing the needs of the increasingly time-constrained consumer with processed rice products)	Responding to taste changes Enhanced nutritional content of rice (e.g., biofortification)
		Intellectual property rights issues: — Preventing biopiracy — Public, private partnerships for rice research ● Addressing the challenge of access and exchange of rice plant genetic resources for public goods research		
Policies enabling structural change in rice-dominated systems				
Enabling a sustainable transition for poor farmers in an increasingly globalized and commercialized system ● Diversification of income of small rice farmers ● Enhancing market performance (market institutions and information) ● Investment in labor-saving technologies				

Competing Claims for Natural Resources and the Need for System Transitions in Rice Cultivation

M.J. Kropff, P.S. Bindraban, and M.A. Slingerland

The world entered the 21st century facing many challenges, often in an agricultural context. Prominent is the concern for feeding an ever-growing population with safe and healthy food. A sustainable living environment and socioeconomic development are major issues as well. All these concerns are strongly related to the management of natural resources such as land, water, energy, and minerals and the distribution of the products. Many resources are limited (e.g., land and fresh water) and several resources are not renewable, such as oil. The Millennium Development Goals attempt to resolve these concerns, aiming to increase benefits from Earth's resources for people living in developing countries. Now, the political arena shows the dependency of the world on an oil-based economy, in which demand for oil increases rapidly due to economic growth and political instability, driving market prices up. Not surprisingly, demand for bio-based products, and especially bio-based fuel as a renewable resource, is booming. The strongly increasing demand for food and nonfood agricultural produce challenges our agricultural production capacity worldwide.

As many natural resources have multiple uses and multiple users, increasing demand can create constraints and be a trigger for conflicts at different scales, from local to international. To minimize these constraints, it is essential that current uses, increased demand, and resulting constraints at different scales be analyzed simultaneously to identify socially and economically viable options for local innovation in which the different objectives of a variety of stakeholders are met. Such options can be identified only through the involvement of these stakeholders, including scientists. When they work closely together, this may result in increasing space for solutions and co-innovation. Scientists can contribute in several ways in the policy-making process from problem identification to implementation. They can raise awareness of competing claims at different scale levels and identify options based on which stakeholders can make decisions about the way they want to deal with multiple uses of natural resources. In other words, the stakeholders who are responsible have to set goals. Of course, scientists have to continue their contributions to new technology development at different scales based on clearly defined questions.

This technology should focus on a major increase in resource-use efficiency and expand the scope for solutions. In this way, we move from a technology push to a technology pull strategy and we need close interaction between social and natural scientists.

This paper discusses the challenge we face, which is to address the increase in different and often conflicting claims by transforming our systems, with specific attention to rice production systems. While transition in production systems calls for adjustments in socio-political conditions, the drastic transformations required cannot be achieved without technological breakthroughs using our best technical knowledge and means.

At the dawn of the 21st century, we realize that the increasing demand for virtually all commodities to meet human needs puts enormous pressure on the global resource base. With reducing availability of and access to resources, social tension and conflicts may arise, the divide between rich and poor might increase, and ecosystems may become overexploited.

The major concern still is the fact that more than 800 million people suffer from hunger and malnutrition and more than a billion people earn less than 1 dollar a day. For these people to escape these conditions, a sustainable living environment should be created that provides opportunities to also benefit from socioeconomic development. Inadequate access to food and production factors because of a lack of purchasing power and decreased productivity due to malnourishment causing health problems lead to a negative spiral into poverty that has to be broken. Some of the elements to help solve these problems are the production of more food and better food products, improved nutrition with the right balance of components, a better distribution of and access to food and natural resources, and sufficient education for people to make sensible choices.

These concerns are expressed in the Millennium Development Goals, which seek more equitable sharing of the limited resources to reduce hunger and poverty and to improve health, which compel us to make more efficient use of these resources for a sustainable environment, which call for better education to allow people to make informed choices, and which stress the need to stimulate partnerships in seeking development solutions (www.unmillenniumproject.org).

Many of these challenges in development have an agricultural background in a development context and relate to the management of natural resources, including land, water, minerals, energy, and products derived from them. Several resources have a limited capacity and are fragile, such as land and fresh water, and others are not renewable such as oil. The pressure on these resources is high indeed as described below, but humankind has faced such difficulties before and turned them into challenges. Dramatic food shortages as forecast by Ehrlich in the 1960s (Ehrlich 1971), for instance, have not become a reality, nor has the depletion of our energy sources as was predicted by The Club of Rome (Meadows et al 1972), but we cannot become complacent and should continue to tackle the challenges.

Land use is changing rapidly worldwide as a result of the growing population and urbanization, expansion for agricultural lands, as well as the need to conserve natural ecosystems. The fertility of agricultural land is continuously under pressure due to overexploitation resulting from the lack of inputs to sustain nutrient balances, in particular in sub-Saharan Africa (e.g., Sheldrick and Lingard 2004). Also, the claim on land for urbanization or wildlife conservation pushes poor people into marginal and vulnerable areas. Land degradation is often the result of timber harvesting in former forest zones, on slopes, or on fragile soils (Oldeman 1999).

The struggle for sufficient water for drinking and food production sets social groups and nations against each other, even leading to conflict. Major problems arise for farmers facing drought they cannot escape, such as in the south of India and in Africa. On the other hand, excessive water consumption by agriculture, for instance, in flooded rice production systems, contributes to decreased water availability for other sectors in society.

Some nutrients needed for plant growth, such as phosphorus, are available in limited quantities only. This essential nutrient is needed to realize the urgently required increase in crop productivity in Africa. Currently, a local lack of availability hampers production, while absolute shortages might become a threat in the long term.

Within a shorter period of a couple of decades, our major sources of energy, economically exploitable oil and gas, will be depleted. Although oil companies indicate having reserves to suffice for several decades, the costs of exploitation will increase. Our oil-based economy already reveals its severe energy dependency by suffering from large fluctuations in prices due to limited production capacity and geo-political issues. The current energy crisis has triggered politicians to seek alternatives. The demand for bio-fuels, for instance, is soaring because of requirements set by governments such as the European Union and the United States. By 2010, 5.75% of the diesel for transport should have a biological origin, creating an enormous, though artificial subsidy-driven, market. As the maximum energy efficiency of crops is 3% only (for C_3 crops), vast cropping land area will be required to provide the energy for our cars, especially if the fuel is to be derived from oilseeds (and sugar), that is, first-generation bio-fuel. Interestingly, developments are under way to produce second-generation bio-fuels, that is, ethanol produced from materials such as straw. We should realize, however, that materials such as straw are very important for soil improvement in many soil types. The massive use of straw for bio-fuel would create a problem there. So, bio-based fuel is an opportunity for agriculture (as its demand may push prices up) but also a threat to food production.

Economic development increases claims on natural resources and associated increases in income directly affect demand for agricultural produce because of rising meat consumption. As the production of 1 kg of meat requires many more kilograms of plant material, a meat consumer requires more agricultural produce than a vegetarian.

Large and sudden changes in the global system, either political or natural, are likely to occur more frequently, as we are stretching our global ecosystems toward their limits to provide us with the necessary goods. The increasing frequency of extreme events, such as floods, drought, heat, and typhoons, is perceived as adverse effects of climate change and these alarm nations to take adaptive measures and reduce emissions. Several local disputes are about the control and benefit of valuable resources such as the conflict in Nigeria about oil and, for instance, in 2005, the conflict between crop growers and livestock keepers in Kenya about water when the country was hit by a drought.

In this paper, we discuss the implications of these global changes for local systems. We will discuss them from an agricultural perspective as the production of sufficient, safe, and healthy food is a basic requirement for all development scenarios and, in addition, agriculture needs to provide biomass for fuel and feed. We first stress the need to examine these issues at different levels of scale and share our views on the changing role for scientists to provide new options to overcome any problems. The increasingly complex dynamics of global developments requires policy-driven transformation processes, leading to local solutions with relevance at all scale levels. The required development of technological options to increase resource-use efficiency is placed in this context. We illustrate the relevance of the various components of transformation processes as much as possible from a perspective of rice. We will mention some options as to how rice-based systems could be (re-)designed to meet future challenges.

THE ROLE OF SCIENCE AND DEVELOPMENT IN AN AGRICULTURAL CONTEXT

Concerted actions of decisive policies, potent institutions, and technological breakthroughs led to the Green Revolution during the 1960s and 1970s. From a technological perspective, the real breakthrough was achieved by raising the harvestable proportion of major cereal crops in combination with agronomic practices (irrigation, pesticides, and fertilizer) that allowed the new varieties to express their yield potential. Along with the accompanying policies that created the appropriate institutional and market conditions, a process of change was realized. Hence, a combination of actions and a multitude of actors were involved in carrying out the transformation of the agricultural sector. However, in Africa, to date, technological breakthroughs have not been implemented due to a lack of coordination of these multiple conditions (InterAcademy Council 2004).

Following this period of technological breakthroughs, the productivity of the major cereals and other crops per unit of land and unit of nutrient input has constantly been improved to comply with changing demands that moved from increased needs for food toward the prevention of adverse environmental impact. Resistances to pests and diseases and location-specific adjustments maintained the performance of varieties, while fine-tuning in time and space of input applications minimized their requirements and reduced adverse side effects.

Systems approaches have been developed to support these interdisciplinary studies (e.g., Kropff et al 2001). They can be applied at different scale levels: plot, farm, watershed, region, country, continent, world. In general, the approaches can be described as the systematic and quantitative analysis of agricultural systems, and the synthesis of comprehensive, functional concepts underpinning them. The systems approach uses many specific techniques, such as simulation modeling, expert systems, databases, linear programming, and geographic information systems (GIS). However, these tools have a biological/technological basis. For system improvement, socioeconomic aspects have to be included in the overall process.

TOWARD A NEW FRAMEWORK FOR THE ROLE OF SCIENCE IN AN AGRICULTURAL CONTEXT

For the coming decades, incremental improvements alone are no longer likely to suffice to meet drastically changing global demands. The magnitude of these demands urge for complete transformations of production systems in their local context while accounting for global issues as well. We should thereby address the competing claims by transforming our production systems to minimize trade-offs and to exploit any thinkable synergy. Figure 1 shows the sustainability triangle with its major components related to the environment, development, and equity. We could to a certain extent aim for a more efficient distribution of resources over the ever-increasing claims or sustainability domains. This leads to shifts in the interior of the small triangle in Figure 1. Yet, at a certain moment, technological innovations will be needed to increase resource-use efficiency for all resource uses, thereby enlarging the space for sustainable development. This is represented by the larger triangle.

One might also say that technological innovations widen the window of opportunities. For example, better nutrient-use efficiency, better land-use efficiency through higher production per hectare, and improved labor productivity through mechanization, etc., are essential technological developments for further agricultural development.

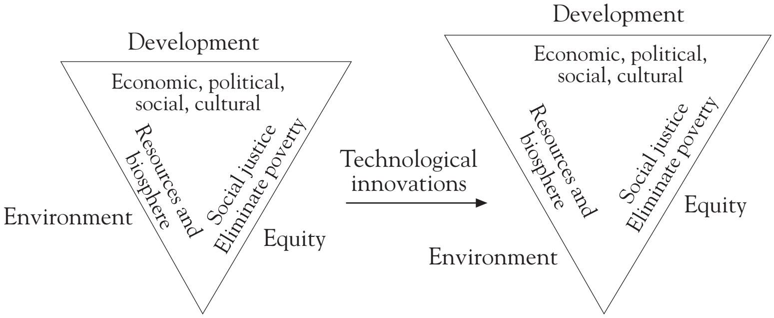

Fig. 1: Increasing the surface of the triangle of sustainability through technological innovations.

At the field level, the optimization of resource use is a key component to achieve the different goals with respect to food supply, income, and protection of the environment. That requires the understanding of genotype × environment × management interactions to better adjust genotype selection and management options to specific local conditions and objectives. Systems approaches are now being used to increase the efficiency of breeding efforts, to determine yield potential in different environments, to optimize water and N use at the field level, and to improve crop protection (through prevention and the use of natural enemies to minimize pesticide requirements (Kropff et al 1997).

C.T. De Wit introduced a forceful theory on resource-use efficiency in agriculture (De Wit 1992). The basis of the theory is the law of diminishing returns when availability of a single resource is increased. De Wit postulates that "most production resources are used more efficiently with increasing yield levels." De Wit also pointed out that higher input-use efficiency reduces the risk of environmental pollution and improves economic performance by lowering the cost:benefit ratio. This law of increasing returns indicates that all resources are most optimally used when the others are close to their maximum as well. Interestingly, it seems that this theory also holds for negative side effects of our systems. Denier van der Gon et al (2002), for instance, show a linear reduction in methane (greenhouse gas) emissions with increasing yield of rice in a specific environment when resources are optimized, confirming the concept of De Wit. The theory and the example point clearly to the possibility of synergy creating a larger triangle at both the development (yield) and the environment (less methane) axis by using resources at the optimum level.

In (re-)designing our systems, many dimensions have to be considered (Fig. 2). Food production systems can be designed at the field scale, while maintenance of nature and wildlife necessitates land-use system designs at the regional scale. Whereas changes at the field scale can be introduced in days

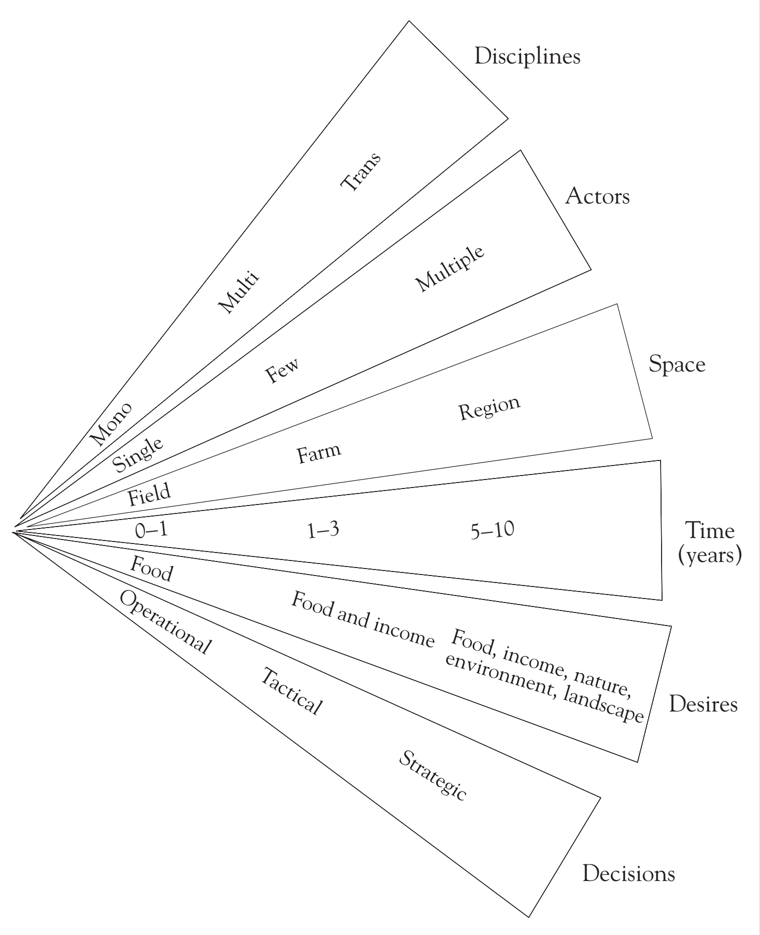

Fig. 2: Multiple dimensions that should be considered in systems design and in transformation processes.

as they concern operational decisions, changes at the farm level are generally of a tactical nature and may take one or more years. To alter the design of a region in order to combine various functions, strategic choices have to be made that may take up to 5 years or more. And finally, operational decisions at the field scale can be made by the farmer alone, and single disciplinary solutions can suffice in addressing occurring field problems. At the regional scale, however, many actors have a stake in the developments and several disciplines should address the complexity of problems.

Methodologies and technologies are generally developed at a specific scale or to link two specific scales. Bouma et al (2006) describe the different phases in the policy cycle that basically apply at all scales: signaling, design,

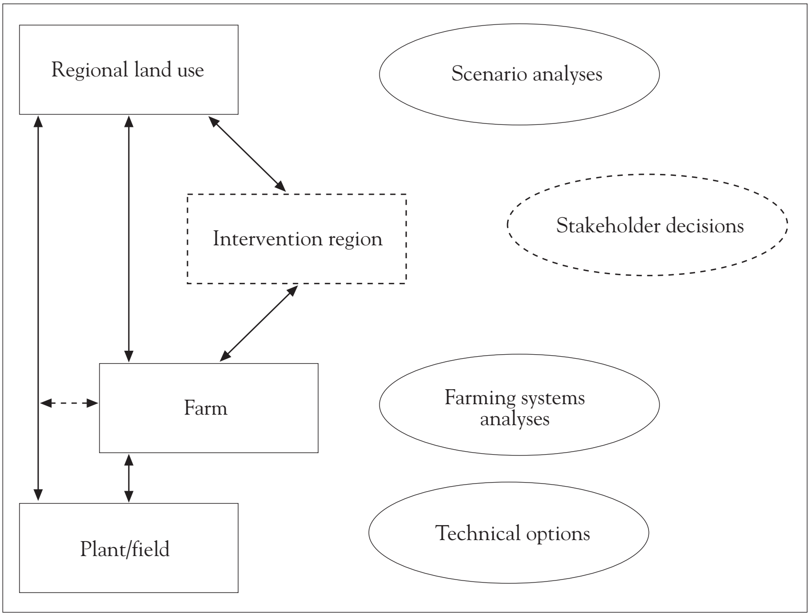

Fig. 3: The missing link in our approaches to enhance the impact of science.

decision, implementation, and evaluation. In all these phases, long-term joint-learning processes are required in which stakeholders and scientists cooperate. Each stakeholder, including the scientists, has a different role in the different phases. Technological solutions are developed based on clear questions to ensure that they will fit in the socioeconomic context in which they will be used. At higher levels of scale, new tools become available that help to explore spatial and temporal opportunities for development assuming specific goals (Bouma et al 2006). Especially when large land reform programs are carried out, a multitude of objectives at various scale levels have to be addressed simultaneously. Also, solutions at one level of scale may not work out when they are applied at a larger scale. A process of transition should be stimulated through the participation of relevant stakeholders from several sectors and administrative scales and, in addition, a systematic search for technological breakthroughs is needed.

Schematically, the scientific analyses at the various scales can be presented as in Figure 3. We develop technological options at the plant and field scale and assess farm livelihood strategies at the farm level considering biophysical and socioeconomic aspects. Scenario analyses for regional land use in fact aggregate field-scale parameters, ignoring the socioeconomic complexity of farming systems and configurations. In some methods, information at the farm level is incorporated through constraints or objectives, but the interaction between farm and region remains minimal.

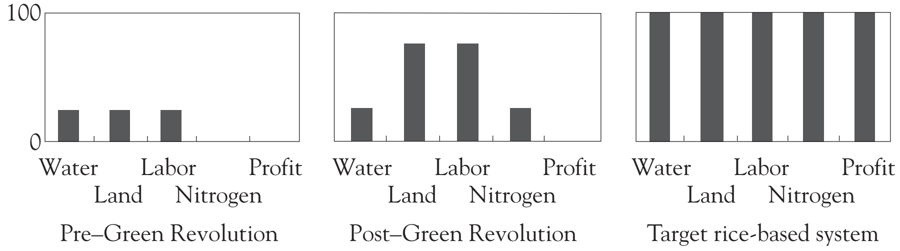

Fig. 4: Schematic evolution in relative resource productivity and profitability of rice-based systems. The latter is derived from the ability to diversify rice-based systems (derived from Bindraban et al 2006).

The missing link in our current approaches is the dashed levels and relations that indicate the actual level of intervention beyond the farm scale, where the farmer has the final decision to act, and below the options given in scenario analyses at the regional scale. Embedding production systems in its landscape calls for interventions that affect multiple actors, the need to integrate multiple objectives, etc. This coincided with the outer spheres of the fan of Figure 2.

Actual implementation of options at the regional scale calls for "postmodern science approaches," with a direct involvement of scientists in the process of transition. Here, technical scientists are supposed to design options that comply with various goals, and social scientists are assumed to take an active part in shaping the process, rather than only studying the process. Likewise, politicians should not only set theoretical conditions that provide the scope and limits to operate but should also actively participate in the process. At the farm level, approaches as used in farmer field schools or practical networks are means to involve farmers in co-innovation at the field level and decision processes at larger-scale levels.

In the following section, we will elaborate on some of these approaches at various scales for the specific case of rice and discuss our achievements so far and challenges ahead.

NATURAL RESOURCE MANAGEMENT AND RICE-BASED SYSTEMS: SCIENTIFIC CHALLENGES AT DIFFERENT SCALES

Resource-Use Efficiency in Rice Systems

In the case of rice, enlarging the surface of the sustainability triangle calls for increasing the use efficiencies of resources that are low compared with those of other crops (Fig. 4). Between 2,000 and 10,000 liters of water are needed to produce 1 kilogram of rice (Bouman and Tuong 2001) compared with 700–1,000 liters for wheat (Rockström 2001). Nitrogen losses in rice fields are high, with efficiencies as low as 30%, whereas efficiencies for wheat can be as high as 70%. The global average yield of rice and wheat per hectare is within the same range, but the inundated cultivation practices of rice hamper the growth of subsequent nonrice crops as a result of poor soil structure after puddling. This strongly limits the ability of farmers to diversify their activities and secure income. Labor demand for rice is as much as 50 to 100 times higher in most systems than for mechanized wheat or rice cultivation.

Maintaining the balance between the sustainable development parameters of rice-based systems seems particularly fragile. They are challenged by the simultaneous demand for increased land and labor productivity, the contribution to poverty alleviation, reduced environmental impact, and increasingly for lower water use. For the coming two decades, rice production volume should increase by 25% to keep up with growing rice consumption, which should be realized on the same and preferably less land area. More stringent is the need to enhance labor productivity. Labor-intensive operations in rice cultivation are under pressure due to the rapid expansion of the nonagricultural sector, stimulating migration of the rural population to urban areas, reducing labor availability, and increasing rural wage rates. Some farmers are seeking to diversify their activities by introducing nonrice crops to stabilize and increase income. Others may continue rice cultivation by minimizing labor input to peak activities only and generating off-farm income during the crop growth period. For the past two decades, high inputs of nutrients and biocides have raised concerns about the environmental impact of intensively managed systems. More recently, the worldwide decline in availability of water resources urges a drastic reduction in the amount of water used for rice production.

For the coming decades, designing rice-based systems requires reconciliation of different and possibly conflicting objectives, within and outside the systems. In the search for rice cultivation practices with higher productivity of water, nutrients, land, labor, and capital, and with safe and nutritious produce, while well embedded within the landscape, dramatic changes in the system should not be disregarded. The largest gains can be expected in current high production areas as the use efficiency of inputs will increase. An array of rice cultivation systems will probably be required, ranging from inundation under monsoon conditions to rice grown as any other irrigated cereal crop elsewhere. In current low-input systems, such as rainfed rice, use efficiencies can be increased strongly only when all other resources are optimized as well. Policy measures that assure proper conditions to enhance the use of inputs in the systems should be developed. The more remote the transformed system will be from current practices, the larger the ecological, economic, and socio-institutional implications and the more pressing the research agenda to support the transformations.

Options to Increase Resource-Use Efficiency in Rice

For various reasons, rice has been predominantly cultivated under inundated conditions for more than 5,000 years. Inundation strongly reduces weed pressure, while the rice plant thrives well. Standing water serves as a buffer for periods of low and unreliable water supply, in particular for rainfed rice systems and for rice grown in poorly managed irrigation systems. Water entering the field carries nutrients, while inundated conditions further increase the availability of other nutrients, especially phosphorus, because of the dissolving effect and the lack of oxygen in the soil (De Datta and Patrick 1986). Under inundated and shaded conditions in rice fields with elevated CO_2 concentration in the water and high availability of phosphate, biological nitrogen fixation may provide up to 100 kg N ha^{-1} per year. In the prefertilizer era, this was the main nitrogen source explaining the sustainability of this ancient cultivation practice; however, yield often did not exceed 2 tons ha^{-1} per year. Land preparation, that is, puddling of heavy soils, was made feasible by animal traction. Finally, soil-borne pathogens such as nematodes were suppressed (George et al 2002).

In the pre–Green Revolution, the production in kg rice per unit of resource was very low, but satisfied the needs and technical possibilities then. Some of the reasons became obsolete after the introduction of high-yielding varieties, chemical fertilizer, biocides, and improved irrigation as part of the Green Revolution. As a consequence, land productivity at the global scale has tripled, with rice yields averaging almost 4 t ha^{-1} today, while in some countries such as China national average yields exceed 6 t ha^{-1}. This increase in land productivity and the associated improvement in labor productivity were realized through an increased use of external inputs, yet water and nitrogen are still not efficiently used.

The interventions in rice systems so far have not changed the basic principle of inundated cultivation of rice, that is, water use as a dominant factor remained untouched. Similarly, other pressing concerns such as labor requirement and cost reduction have not been strongly considered apart from high-tech systems in the United States and Australia. Clearly, rice cultivation systems are resistant to many external influences or absorb them by adaptations within the existing system. However, when pressure increases further as currently is the case, the resilience of the system may be affected and even a small intervention may lead to a drastic change. Scheffer et al (2001) show different stages of systems that may start with gradual changes over time, evolving toward a status of turmoil pushing the system toward a new equilibrium. In terms of Scheffer and colleagues, we may be looking at a rice system that has reached a stage where it is likely to make sudden changes to another state.

In the following sections, we will describe some biological/technological options to modify rice-based systems, illustrated by examples from rice as well as other crops and systems. We thereby incorporate the role of various technical tools, such as crop modeling, information and communication technology, and biotechnology, to support research and we will look at several scale levels from a systems perspective.

Redesigning the Rice Plant

The largest scientific gains in rice have been achieved through the increase in the harvestable portion of the plant and the increased resistance to pests, diseases, and weeds. Further adjustments in plant design may be necessary to better use resources. The penetration ability of rice roots may have to be increased, while the transpiration rate needs to decrease when the crop is grown under drier conditions. Other options are the elongation of the grain-filling period, morphological adjustments, targeting genotypes for specific environments, etc. (e.g., Boote et al 2000, Kropff et al 1997). New tools will be needed in research linking different scales such as systems biology (Yin et al 2004).

The photosynthetic capacity of plants has not been modified so far. Photosynthesis in rice, a C_3 plant, is less efficient than that of C_4 plants such as maize that use an extra chemical process for capturing carbon dioxide. C_4 plants are 50% more efficient at turning solar radiation into biomass. Biotechnology provides the means to increase the photosynthetic rate of the C_3 species by incorporating mechanisms from C_4 crops, for instance (Surrigde 2002). Transforming rice into a C_4 plant would require major morphological and physiological changes in the rice plant, but this is attractive as it might lead to 50% higher yields. Nitrogen-fixing characteristics could be introduced to reduce fertilizer requirements of nonfixing species, and symbiotic relations with bacteria could facilitate the uptake of nutrients such as phosphorus. Also, bacteria can form plant-bacteria associations that protect crops against losses from diseases. Modification of the biochemical processes of the rice plant should be looked into for achieving new system breakthroughs.

Drought and salinity are major abiotic stresses to crop production, also in rice. About 7% of the world's total land area is affected by salt, as is a similar percentage of its arable land (Ghassemi et al 1995). The area is still increasing as a result of irrigation or land clearing. Molecular markers are particularly useful for identifying different traits for salt tolerance (Flowers et al 2000), and other accompanying stresses, such as drought or waterlogging. QTLs (quantitative trait loci) for salt tolerance have been described in several cereal species, including rice (Flowers et al 2000). When salt tolerance and drought resistance could be bred into highly productive rice varieties, the area for rice cultivation could be expanded to marginal areas that currently suffer from salt stress or drought.

Worldwide, more than 2 billion people suffer from anemia and stunted growth due to Fe and Zn deficiency and another 500 million from blindness due to vitamin-A deficiency. Nearly all of the widely grown Green Revolution varieties have similar densities, with iron at about 12 mg kg^{-1} and zinc at about 22 mg kg^{-1}. The potential exists for developing improved rice varieties with enhanced beta-carotene, iron, and zinc in the grain. Because a large part of the diet of the poor in South and Southeast Asia consists of rice, these added micronutrients would have a meaningful impact on human nutrition and health, especially for anemic women and children. Breeding for micronutrients would thus increase solutions for the health-care sector. Certainly, diversifying the diet may have a similar impact, but this requires alternative, more socioeconomic measures such as an increase in income, availability of markets, etc.

The implications of these changes for both plant design and biochemical plant processes would be impressive in terms of natural-resource use, the design of rice-based systems, and land use. Enhanced radiation absorption through optimized morphology and increased photosynthetic rate would potentially reduce the need for land expansion because of higher yields. Nitrogen fixation would lower the need for fossil fuels because of less need for fertilizers, while drought and salt tolerance would allow the cultivation of currently marginal lands. Improved nutritive value of rice through increased micronutrients could solve health problems. Here, the role of technology is prominent.

Redesigning the Rice-Based System

At present, farmers are already modifying their rice cultivation practices to meet their immediate needs. Also, several changes are introduced to farmers from external sources. Although some ways have been found by researchers and other groups to enhance the productivity of land, labor, and water, farmers are not inclined to adopt such practices if these do not fit their economic and social considerations. To prevent the proliferation of unrealistic claims and derailing of the system with strong social implications, more systematic research support is required to truly initiate a process of transition based on co-innovations through the involvement of multiple stakeholders. Sound science should be underlying new technologies and claims should be carefully tested in interaction with farmers.

As the extremely low water-use efficiency of paddy rice systems is a major problem, scientists have been looking for systems to reduce water use, for example, by alternate wetting and drying and systems without standing water. However, a major reduction in water use can be expected only when rice is grown in a dryland system. Such dryland systems exist as upland rice systems in subsistence farming systems with extremely low yield levels. However, it must be possible to reach the same productivity in rice in a dryland situation as in a paddy system. Recent studies on so-called aerobic rice show that this is not yet possible with the current varieties. So far, results are promising in that water use can be reduced by approximately half without a loss in rice yield (Bindraban et al 2006, Bouman et al 2002). In order to lower water use toward that of dry systems such as wheat, modifications in plant design will be necessary, in particular tolerance of drought.

A telling example of a redesigned rice system is the mixed cultivation of various lines. Rice suffers from severe yield losses due to many diseases. Improved varieties respond well to inputs and are generally resistant to major diseases such as blast. However, consumers pay high prices for glutinous rice produced by traditional varieties that lodge and are sensitive to blast. Farmers in Yunnan, China, were exploring the interplanting of traditional glutinous rice together with modern hybrid rice. It was found that yields in carefully co-designed mixtures were higher and blast was not able to infect the glutinous rice plants. Successful proof of principle turned the target location into a demonstration location to disseminate the "new" technology and knowledge. Practical success led to rapid adoption by many farmers.

Planning at the Farm and Regional Level: Options for Decision Making by Stakeholders

At the farm level, many decisions need to consider the trade-offs between different biophysical and socioeconomic objectives. Integrated approaches for farm-level decision support have been developed that consider both biophysical and socioeconomic approaches (e.g., Kropff et al 1997).

At the regional level, methodologies have been developed for ecoregional studies in which the use of systems models converts huge databases into valuable information that can be geographically visualized using GIS for easy interpretation. Scaling issues play a role here and novel approaches have been developed in an ecoregional research program (Bouma et al 2006). Different stakeholders have contrasting ideas and there is not a single truth. The way in which science should deal with this has been studied intensively (e.g., van Ittersum et al 2004). The identification of windows of opportunity can improve the decision-making process of policymakers. Scientists should be involved at all phases in the policy cycle as defined before, by contributions as mediators, facilitators, and suppliers of scientific information in the debate. So, not only in the design phase are scientists needed but also in the evaluation phase to generate new scientific insight based on observations of the processes. One of the cases of the ecoregional program deals with rice-based systems in Southeast Asia. The SYSNET project examined post–Green Revolution issues such as stagnating crop yields in India, Vietnam, and the Philippines (Roetter et al 2005). This prospect developed a Land-Use Planning and Analysis System (LUPAS), which is a modeling framework using multiple-goal linear programming as an integrative component for identifying land-use options that fit best to specific scenarios and policy choices. It presents land-use maps based on these scenarios. For example, in the Philippines in Ilocos Norte Province, the effect of better sharing of irrigation water making water use more efficient would lead to major land-use changes and a farmers' income increase of 16%. All examples from the ecoregional studies reviewed by Bouma et al (2006) show that new methodologies are becoming available but that the main issue is the involvement of the different stakeholders and scientists simultaneously to ensure that scientific information is used effectively in the different phases in the policy-making process.

CONCLUDING REMARKS

The major challenges we face today are related to natural resources in an agricultural context. Especially, the increasing energy demand and strong reduction in fossil fuel resources increase the interest in biological production of fuel. That will cause major changes in agricultural systems, with strong effects on food and feed production and prices as a result of competing claims for natural resources (land, water, minerals), labor, and energy. A major key to addressing these concerns is enhanced resource-use efficiency at different levels of scale. Several examples from rice production systems show that the range of options to enhance resource-use efficiency can be enlarged by biological/technological breakthroughs ranging from new stress-resistance genes to completely new production technologies such as highly productive dryland rice ecosystems. Scientists have to keep on developing new technologies to enhance resource-use efficiency to cope with the reduced availability of many resources in the future.

However, the development of new technology may not automatically lead to adoption or implementation (e.g., absence of a Green Revolution in Africa). And, even successful adoption and implementation such as the Green Revolution in rice systems in Asia may have negative consequences for several groups in society. These problems have to be tackled by new approaches in which problem definition, analysis, design, and implementation of new technologies are conducted in a participatory manner. In this way, technological solutions fit the socioeconomic context in which they can be used. In social sciences, this process is defined as mode-2 science or postmodern science. We call it co-innovation. At the farm level, approaches such as those used in farmer field schools or practical networks can be applied for this purpose of co-innovation. However, the number of issues that should be considered in the process is scale dependent and may even be interrelated. Especially when large land reform programs are carried out, a multitude of objectives at various scale levels have to be examined simultaneously. Also, solutions at one level of scale may not work out when these are applied at a larger scale. To take into account the multitude of issues, objectives, and interests, a process of transition should be stimulated through the participation of relevant stakeholders from several sectors and administrative scales, including a systematic search for technological breakthroughs.

The mode of operation of researchers and research institutions will have to change drastically. Today, most scientific projects are carried out separately from the large-scale development programs in which systematic use of new insights from science could be beneficial. Researchers should participate in platforms of multiple stakeholders for a more effective articulation of their research questions. These regular contacts will also facilitate a more effective implementation of research findings. However, not all responsibility for effective demand articulation or implementation lies with researchers. Embedding the research effort in mega implementation projects such as those being undertaken by development banks and governments should be facilitated by policymakers. A current water reformation program being implemented in Indonesia, for instance, could benefit from ongoing research on growing rice with less water. Vice versa, the research community could formulate its research questions much more effectively. We have illustrated, though for rather small projects, that participatory processes for systems innovations are feasible and are currently being implemented. However, better interaction between scientists and other stakeholders is an essential component to make science for impact possible.

We realize the need for researchers and other stakeholders to actively engage in development processes. The reality is, however, that such processes are not easy to implement. We are still far away from proven examples of the missing link as indicated in Figure 3 where actual implantation of change takes place at scale levels going beyond the farm. Examples show that participatory research linked to explanatory biological/technological research may help to understand and optimize the system. Similarly, integrated pest management programs operated at the level of farm decision making, though implemented at a regional scale, enhanced the impact of reduced pest and disease incidence.

The number of examples to illustrate successful interventions at higher scale levels is scarce. At these higher scale levels, a multitude of system components such as farms, infrastructure, nature areas, urban centers, markets, factories, etc., are present, holding complex relations with each other. These components and relations tend to resist change as the change of one requires the change of all. It is therefore a challenge to achieve an impact of scientific findings through deliberate and coherent policy to change agricultural systems at the regional scale.

The rice system faces a multitude of challenges that should be addressed simultaneously and at various scale levels. We have to realize that the drastic socioeconomic and ecological disturbance of the conventional system of inundated and transplanting cultivation of rice may have positioned it in a stage that could lead to sudden large-scale changes as described in the theories of Scheffer et al (2001). Scientists should be alert to this situation and look for innovative and realistic options and rewarding synergies with developments at other scale levels. The proliferation of unfounded recommendations to change the system may find its roots in the susceptibility of farmers to jump into solutions because of pressing conditions, but may lead to unforeseen side effects, only temporary incremental change, and disappointments. We should not just look at mitigating adverse side effects or at better distribution of resources within the existing triangle, but we should provide technological innovation to increase the solution space by increasing resource-use efficiency for all resource uses. To facilitate a process of fundamental change, we need to develop options that comply with production ecology principles (De Wit 1992), we need systems approaches, and we need co-innovation at all scale levels. We will not be able to realize these drastic transformations that are required without technological breakthroughs using our best technical knowledge and means. We should at the same time realize that any transition of production systems calls for adjustments in socio-political conditions and may come with severe socioeconomic and political implications, yet these adjustments will be utterly necessary. A closer relation between science and policy will therefore be needed to marry technological innovation and socioeconomic well-being.

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Rice Breeding for the 21st Century

Gurdev S. Khush

The adoption of Green Revolution varieties led to major increases in rice production. Between 1966 and 2005, the population of densely populated low-income countries grew by 95% but rice production increased by 140% from 257 million tons in 1966 to 618 million tons in 2005. In spite of these advances in rice production, 800 million people still go to bed hungry every day and most of them are poor rice consumers. Micronutrient deficiencies affect millions of rice consumers. Per capita rice consumption is increasing due to rising living standards, particularly in Africa. The population of rice consumers continues to grow. It is estimated that we will have to produce 38% more rice in 2030. This increased demand will have to be met from less land, with less water, less labor, and fewer chemicals. This additional rice must be produced from good land without opening up more fragile lands for rice cultivation.

To meet this challenge, we need rice varieties with higher yield potential, greater yield stability, and dense micronutrients. Although the yield potential of rice is 10 tons per hectare, farmers on average still harvest 5 tons. To close this yield gap, we must develop varieties with more durable resistance to diseases and insects and tolerance of abiotic stresses. Various strategies for increasing rice yield potential include (1) conventional hybridization and selection procedures, (2) ideotype breeding, (3) hybrid breeding, (4) wide hybridization, and (5) genetic engineering. Various conventional and biotechnological approaches are being employed to develop durable resistance to diseases and insects and tolerance of abiotic stresses. Rice varieties with higher levels of iron and zinc have been identified and are being used as donors to develop improved varieties with dense micronutrients. Natural variation for beta carotene (a precursor of vitamin A) does not exist in rice. Therefore, a team of Swiss and German scientists has introduced the biosynthetic pathway through genetic engineering, leading to the production of beta carotene in rice endosperm. The capability of beta carotene production is now being transferred into widely grown national varieties.

Keywords: Yield potential, yield stability, ideotype breeding, hybrid breeding, wide hybridization, genetic engineering, micronutrient deficiency

Rice is the world's most important food crop and a primary source of food for more than half of the world's population. More than 90% of the world's rice is grown and consumed in Asia, where 60% of Earth's people live. Rice accounts for 35% to 75% of the calories consumed by more than 3 billion Asians. It is planted on about 154 million hectares annually or on about 11% of the world's cultivated land.

Rice is probably the most diverse food crop. It is grown as far north as Manchuria in China and as far south as Uruguay and New South Wales in Australia. Rice grows at more than 3,000 meters elevation in Nepal and Bhutan and 3 meters below sea level in Kerala in India. Rice-growing environments are classified into four major categories: irrigated, rainfed, upland, and flood-prone (Khush 1984). This categorization is based on several criteria such as water regime, drainage, soil, and topography.

Major advances have occurred in food production during the last four decades because of the adoption of Green Revolution technology. Since 1966, when the first high-yielding rice variety was released, the rice area harvested has increased only marginally from 126 million hectares in 1966 to 154 million hectares in 2005 (18%), and average rice yield has doubled from 2.1 tons per hectare to 4.02 tons per hectare during the same period. Total rice production increased from 257 million tons in 1966 to 618 million tons in 2005 (140%). Between 1966 and 2005, the population of densely populated low-income countries increased 95%. In 2000, average per capita food availability was 18% higher than in 1966. The technological advance that led to dramatic achievements in world food production during the last 40 years was the development of high-yielding and disease- and insect-resistant varieties of rice. The adoption of Green Revolution technology was facilitated by (1) the development of irrigation facilities, (2) availability of inorganic fertilizers, and (3) benign government policies.

The increase in per capita availability of rice and decline in the cost of production per ton of output contributed to a decline in the real price of rice in international and domestic markets. The unit cost of production is about 20–30% lower for high-yielding varieties than for traditional varieties of rice. The cost of rice is 40% lower now than in the 1960s. The decline in food prices has benefited the urban poor and rural landless, who spend more than half of their income on food grains.

THE RICE SCENARIO IN THE NEW MILLENNIUM

The world's capacity to sustain a favorable food-production–population balance has again come under the spotlight in view of continued population growth and a drastic slowdown in the growth of cereal production (Brown 1996). Rice production increased 2.5–3.0% per year during the 1970s and 1980s. However, during the 1990s, the growth rate was only 1.5%. According to UN estimates, the world population will grow from 6.3 billion in 2003 to 8 billion in 2025. Most of this increase (93%) will occur in developing countries, whose share of population is projected to increase from 78% in the 1990s to 83% in 2020.

In spite of all the achievements of Green Revolution, serious food problems exist in the world. Every 3.6 seconds, somebody dies of hunger. Chronic hunger takes the lives of 2,400 people every day. Currently, the developing world has more than 800 million undernourished people, 300 million children under the age of five die because of hunger and malnutrition, and one out of five babies is born underweight.

FEEDING 5 BILLION RICE CONSUMERS IN 2025

According to various estimates, we will have to produce 38% more rice by 2030 to satisfy the growing demand without affecting the resource base adversely (Khush 2005). This increased demand will have to be met from less land, with less water, less labor, and fewer chemicals. If we are not able to produce more rice from the existing land resources, land-hungry farmers will destroy forests and move into more fragile lands such as hillsides and wetlands, with disastrous consequences for biodiversity and watersheds. To meet the challenge of producing more rice from suitable lands, we need rice varieties with higher yield potential and greater yield stability. Rice varieties with dense micronutrients are needed to alleviate micronutrient deficiencies.

INCREASING THE YIELD POTENTIAL OF RICE

Various strategies for increasing the yield potential of rice include (1) conventional hybridization and selection procedures, (2) ideotype breeding, (3) heterosis breeding, (4) wide hybridization, and (5) genetic engineering.

Conventional Hybridization and Selection Procedures

This is the time-tested strategy for selecting crop cultivars with higher yield potential. It has two phases. The first phase involves the creation of variability through hybridization between diverse parents. In the second phase, desirable individuals are selected on the basis of field observations and yield trials. It has been estimated that on average about a 1.0% increase has occurred per year in the yield potential of rice over a 35-year period since the development of the first improved variety of rice, IR8 (Peng et al 2000). The yields of crops where there is enough investment in research have been continuously increased and there is no reason why further increases cannot be attained.

Ideotype Breeding

Ideotype breeding aimed at modifying plant architecture is a time-tested strategy to achieve increases in yield potential. Thus, selection for short-statured cereals such as wheat, rice, and sorghum resulted in a doubling of yield potential. Yield potential is determined by the total dry matter or biomass and the harvest index (HI). Tall and traditional rice had an HI of around 0.3 and total biomass of about 12 tons per hectare. Thus, its maximum yield was 4 tons per hectare. Biomass could not be increased by applying nitrogenous fertilizers as the plants grew excessively tall, lodged badly, and their yield decreased instead of increasing. To increase the yield potential of tropical rice, it was necessary to improve the harvest index and nitrogen responsiveness by increasing lodging resistance. This was accomplished by reducing plant height through incorporation of a recessive gene, *sd1*, for short stature.

The first short-statured variety, IR8, developed at the International Rice Research Institute (IRRI), also had a combination of other desirable traits such as profuse tillering, dark green and erect leaves for good canopy architecture, and sturdy stems. It responded to nitrogenous fertilizer much better and had a higher biomass (about 18 tons) and HI of 0.45. Its yield potential was 8–9 tons per hectare (Chandler 1969).

To increase the yield potential of rice further, a new plant type was conceptualized in 1988. Modern semidwarf rice produces many unproductive tillers and excessive leaf area, which cause mutual shading and reduce canopy photosynthesis and sink size, especially when the plants are grown under direct-seeding conditions. To increase the yield potential of this semidwarf rice, IRRI scientists proposed further modifications of plant architecture, with the following characteristics:

- Low tillering (9–10 tillers for transplanted conditions)
- No unproductive tillers
- 200–250 grains per panicle
- Dark green, thick, and erect leaves
- Vigorous and deep root system

This proposed ideotype became the “new plant type” (NPT), highlighted in IRRI’s strategic plan (IRRI 1989), and breeding efforts to develop the NPT began in 1990. The objective was to develop improved germplasm with 15–20% higher yield than that of the existing high-yielding varieties. Numerous breeding lines with desired ideotype were developed (Khush 1995) and shared with national rice improvement programs. Three NPT lines have been released in China and two in Indonesia. Other national agricultural research and extension systems (NARES) are evaluating and further improving NPT lines.

Heterosis Breeding

Yield improvement in maize has been associated with hybrid development. Yields of maize in the United States were basically unchanged from the mid-19th century until 1930 and accelerated after the introduction of commercial double-cross hybrids. The subsequent replacement of double-cross hybrids by single-cross hybrids in 1960 is associated with the second acceleration in maize yields. The average yield advantage of hybrids versus cultivars is approximately 15% (Tollenaar 1994).

Rice hybrids with a yield advantage of about 10–15% over the best inbred varieties were introduced in China in the mid-1970s and are now planted on about 45% of the rice land in that country. Rice hybrids adapted to the tropics have now been bred at IRRI and by NARES and show a similar yield advantage. The increased yield advantage of tropical rice hybrids is due to increased biomass, higher spikelet number, and to some extent higher grain weight. Increased adoption of hybrids in the tropics should contribute to increased productivity.

Wide Hybridization

Crop gene pools are widened through hybridization of crop cultivars with wild species, weedy races as well as intrasubspecific crosses. Such gene pools are exploited for improving many traits, including yield. For example, Lawrence and Frey (1976) reported that a quarter of the lines from BC_2-BC_4 segregants from *Avena sativa* × *A. sterilis* crosses were significantly higher in grain yield than the cultivated recurrent parent. Nine lines from this study, when tested over years and sites, had agronomic traits similar to those of the recurrent parent and 10–29% had higher grain yield. The higher yield potential of these interspecific derivatives was attributed to higher vegetative growth rates or early seedling vigor.

Xiao et al (1996) reported that some backcross derivatives from a cross between an *Oryza rufipogon* accession from Malaysia and cultivated rice outyielded the recurrent parent by as much as 18%. They identified two QTLs from wild species with a major contribution to the yield increase. These QTLs are now being transferred to several modern semidwarf varieties. Upland rice varieties with improved yield potential were developed at the African Rice Center (WARDA) through interspecific hybridization between Asian rice *Oryza sativa* and African rice *O. glaberrima*.

Genetic Engineering

Since protocols for rice transformation are well established (Christou et al 1991), it is now possible to introduce single alien genes that can selectively modify yield-determining processes. In several crop species, incorporation of the "stay green" trait or slower leaf senescence has been a major achievement of breeders in the past decade (Evans 1993). In some genotypes with slower senescence (stay green), Rubisco degradation is slower, which results in a longer duration of canopy photosynthesis and higher yields. The onset of senescence is controlled by a complement of external and internal factors. Plant hormones such as ethylene and abscisic acid promote senescence, whereas cytokinins are senescence antagonists. Therefore, overproduction of cytokinins can delay senescence. The *ipt* gene from *Agrobacterium tumefacions* encoding an isopentenyl transferase (Akiyoshi et al 1984) was fused with a senescence-specific promoter, SAG 12 (Gan and Amasino 1995), and introduced into tobacco plants. The leaf and floral senescence in the transgenic plant was markedly delayed, biomass and seed yield increased, but other aspects of plant growth and development were normal. This approach appears to have great potential in improving crop yields by slowing the senescence and Rubisco degradation and thus improving canopy photosynthesis.

C_4 plants such as maize and sorghum are more productive than C_3 rice and wheat because C_4 plants are 30–35% more efficient in photosynthesis. Ku et al (1999) and Matsuoka et al (2001) are trying to alter the photosynthesis of rice from the C_3 to C_4 pathway by introducing cloned genes from maize that regulate the production of enzymes responsible for C_4 synthesis. If successful, the yield potential of rice could increase by 30–35%.

BREEDING FOR DURABLE RESISTANCE

Full yield potential of modern rice varieties is not realized because of the toll taken by attacks by diseases and insects. It is estimated that diseases and insects cause yield losses of up to 25% annually. Genetic improvement to incorporate durable resistance to pests is the preferred strategy to minimize these losses. There is no cost to farmers and resistant cultivars are easily adopted and disseminated, unlike "knowledge-based" technologies. Also, concern for the environment has become an important public policy issue and pest management methods that minimize the use of crop protection chemicals are increasingly finding favor.

Diverse sources of resistance to major diseases and insects have been identified and rice varieties with multiple resistances to diseases and insects have been developed. However, no sources of resistance to sheath blight are available and there is a paucity of donors for resistance to virus diseases and stem borer. Recent breakthroughs in cellular and molecular biology have provided tools to develop more durably resistant cultivars and to overcome the problem of lack of a donor for resistance.

Wide Hybridization for Disease and Insect Resistance

Wild species of rice are a rich source of genes for resistance breeding. For example, none of the cultivated rice was found to be resistant to grassy stunt. *Oryza nivara*, a wild species closely related to cultivated rice, was found to be resistant and the dominant gene for resistance was transferred to improved germplasm through backcrossing. This gene for resistance has been incorporated into many widely grown varieties. When genes are to be transferred from more distantly related species, special techniques such as embryo rescue are employed to produce interspecific hybrids. Jena and Khush (1990) transferred genes for resistance to three biotypes of brown planthopper from O. *officinalis* to an elite breeding line. Multani et al (1994) transferred genes for resistance to brown planthopper from O. *australiensis* to cultivated rice. Similarly, genes for resistance to blast and bacterial blight have been transferred form O. *minuta* to improved rice germplasm (Brar and Khush 1997).

Molecular Marker-Assisted Breeding

Numerous genes for disease and insect resistance are repeatedly transferred from one varietal background to another. Most genes behave in a dominant or recessive manner and require time-consuming efforts to transfer. Sometimes, the screening procedures are cumbersome and expensive and require a large field space. If such genes can be tagged by tight linkage with molecular markers, time and money can be saved in transferring these genes from one varietal background to another. The presence or absence of the associated molecular marker indicates at an early stage the presence or absence of the desired target gene. A molecular marker very closely linked to the target gene can act as a "tag" that can be used for indirect selection of the target gene (Jena et al 2003).

Two of the most serious and widespread diseases in rice production are rice blast caused by the fungus *Pyricularia oryzae* and bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae*.

The development of durable resistance to these diseases is the focus of a coordinated effort at IRRI using molecular marker technology. Efforts to detect markers closely linked to bacterial blight resistance genes have taken advantage of the availability of near-isogenic lines having single genes for resistance. Segregating populations were used to confirm co-segregation between RFLP markers and genes for resistance. Protocols for converting RFLP markers into PCR-based markers and using the PCR markers in marker-aided selection (MAS) have been established (Zheng et al 1995). The PCR markers were also used for pyramiding genes for resistance to bacterial blight. Thus, *xa4*, *x5*, *xa13*, and *Xa21* were combined into the same breeding line (Huang et al 1997). The pyramided lines showed a wider spectrum and higher level of resistance than lines with only a single gene for resistance. MAS has also been employed for moving genes from pyramided lines into the new plant type (Sanchez et al 2000) as well as into improved varieties grown in India (Singh et al 2001).

Genetic Engineering

Protocols for rice transformation have been developed that allow the transfer of foreign genes from diverse biological systems into rice. Direct DNA transfer methods such as protoplast-based (Datta et al 1990) and biolistic (Christou et al 1991) as well as *Agrobacterium*-mediated (Hei et al 1994) are being used for rice transformation. Major targets for rice improvement through transformation are disease and insect resistance.

As early as 1987, genes encoding for toxins from *Bacillus thuringiensis* (*Bt*) were transferred to tomato, tobacco, and potato, in which they provided protection against Lepidopteran insects. A major target for *Bt* deployment in transgenic rice is the yellow stem borer. This pest is widespread in Asia and causes substantial crop losses. Improved rice cultivars are either susceptible to the insect or have only partial resistance. Thus, transgenic *Bt* rice has much appeal for controlling the stem borer. Codon-optimized *Bt* genes have been introduced into rice and show excellent levels of resistance in the laboratory and greenhouse (Datta et al 1997). *Bt* rice has also been tested under field conditions in China (Tu et al 2000) and has excellent resistance to diverse populations of yellow stem borer. Besides *Bt* genes, other genes for insect resistance such as those for proteinase inhibitors, α-amylase inhibitors, and lectins are also beginning to receive attention. Insects use diverse proteolytic or hydrolytic enzymes in their digestive gut for the digestion of food proteins and other food components. Plant-derived proteinase inhibitors or α-amylase inhibitors are of particular interest because these inhibitors are a part of the natural plant defense system against insect predation. Xu et al (1996) reported transgenic rice carrying the cowpea trypsin inhibitor (*Cpti*) gene with enhanced resistance against striped stem borer and pink stem borer.

Several viral diseases cause serious yield losses in rice. A highly successful strategy termed coat protein (CP)–mediated protection has been employed against certain viral diseases such as tobacco mosaic virus in tobacco and tomato. A CP gene from rice stripe virus was introduced into two japonica varieties by electroporation of protoplasts (Hayakawa et al 1992). The resultant transgenic plants expressed CP at a high level and exhibited a significant level of resistance to virus infection and the resistance was inherited by the progenies.

BREEDING FOR ABIOTIC STRESS TOLERANCE

A series of stresses such as drought, excess water, mineral deficiencies, toxicities in soil, and unfavorable temperatures affect rice productivity. Progress in developing crop cultivars for tolerance of abiotic stresses has been slow because of a lack of knowledge of mechanisms of tolerance, poor understanding of inheritance of resistance or tolerance, low heritability, and lack of efficient techniques for screening germplasm and breeding materials. Nevertheless, rice cultivars with varying degrees of tolerance of abiotic stresses have been developed.

Rainfed rice is planted on about 40 million hectares worldwide. Vast areas suffer from drought at some stage of the growth cycle. QTLs for various component traits of drought tolerance have been mapped (Champoux et al 1995) and the information is being used to develop improved cultivars with drought tolerance.

Genetic engineering techniques hold great promise for developing rice with drought tolerance. Garg et al (2002) introduced *ots A* and *ots B* genes for trehalose biosynthesis from *Escherichia coli* into rice and transgenic rice accumulated trehalose at 3–10 times the rate of nontransgenic controls. Trehalose is a nonreducing disaccharide of glucose that functions as a compatible solute in the stabilization of biological structures under abiotic stress. Transgenic rice lines had increased tolerance for abiotic stresses such as drought and salinity.

Accumulation of sugar alcohols is a widespread response that may protect plants against environmental stress through osmoregulation. Mannitol is one of the sugar alcohols commonly found in plants. Tobacco plants lacking mannitol were transformed with a bacterial gene, *mtlD*, encoding mannitol (Tarczynski et al 1992). Mannitol concentrations exceeded 6 μmol g^{-1} (fresh weight) in the leaves and roots of some transformants, whereas this sugar alcohol was not detected in these organs of control tobacco plants. Growth of plants from control and mannitol-containing lines in the absence and presence of sodium chloride (NaCl) in culture solution was analyzed. Plants containing mannitol had an increased ability to tolerate salinity (Tarczynski et al 1993). After 30 days of exposure under concentrations of 20 mg NaCl in culture solution, transformed plants increased in height by a mean of 80%, whereas control plants increased by only a mean of 22% over the same interval. This approach is worth trying in rice.

In some areas, the rice crop suffers from floods when it is submerged underwater for up to 10 days. Rice cultivars cannot survive such prolonged submergence. A few rice cultivars have been identified that survive submergence for 8–10 days. Using FR13A, one of the submergence-tolerant donors, improved rice cultivars with submergence tolerance have been developed (Mackill et al 1993).

TACKLING HIDDEN HUNGER

The International Food Policy Research Institute's global model for Policy Analysis of Commodities and Trade projects the future world food situation according to several scenarios (Rosegrant et al 1995). Under the most-likely or baseline scenario, 150 million children under the age of 6 years will be malnourished in 2020, just 20% fewer than in 1993. Child malnutrition is expected to decline in the major developing regions, except in sub-Saharan Africa, where the number of malnourished children is likely to reach 40 million in 2020. In South Asia, home to half of the world's malnourished children, the number is expected to decline by more than 30 million by 2020. With more than 70% of the world's malnourished children, sub-Saharan Africa and South Asia are expected to remain "black spots" of child malnutrition in 2020. According to Smith and Hadad (2000), per capita availability of food is not the only determinant of child malnutrition. Other factors such as women's education and status in society, the health environment, and political stability play an important role.

At least 100 million young children suffer from vitamin-A deficiency and as many as 3 million children die annually as a result of this. Fourteen million children suffer from clinical eye problems, and increased risk of respiratory diseases and diarrhea (Sommer 1990).

Rice grains do not contain beta carotene, the precursor of vitamin A. Therefore, children who derive most of their calories from rice suffer from vitamin-A deficiency. In many Asian countries (Bangladesh, Cambodia, India, Laos, Myanmar, and Vietnam), poor people get more than 60% of their calories from rice. A genetic engineering project to introduce the biosynthetic pathway leading to the production of beta carotene into rice endosperm was implemented by a team led by Ingo Potrykus in Switzerland (Ye et al 2000). Two genes from a plant (daffodil) and one from a bacterium (*Erwinia uredovora*) were introduced into rice variety Taipei 309. Ten plants had a yellow endosperm (due to the presence of beta carotene) and a normal vegetative phenotype and were fully fertile. Taipei 309 was used to introduce the beta carotene biosynthetic pathway as it is easy to transform. However, it is not cultivated due to its low yield potential compared with modern high-yielding varieties. Efforts are now under way to introduce the genes for beta carotene production into widely grown improved varieties through transformation, as well as through conventional backcrossing techniques using transformed Taipei 309 as a donor. It is anticipated that elite varieties with beta carotene will become available during the next 2–3 years. This so-called "golden rice" is being evaluated for phenotypic stability, biosafety, food safety, and bioavailability. It will be field-tested for yield performance.

Because rice consumers are used to eating white rice, consumer acceptance of golden rice will also be studied and education programs might be necessary. When widely grown, golden rice will help reduce child mortality.

According to various estimates, 2 billion of the world's population suffer from iron (Fe) deficiency. Fe deficiency results in diminished work performance, impaired body temperature regulation, impaired psychomotor development and intellectual performance, detrimental behavioral changes, and decreased resistance to infection (Dallman 1990). Women are particularly at risk of Fe deficiency because of their elevated requirements for childbearing and growth. An estimated 58% of pregnant women in developing countries are anemic, and their infants are more likely to be born with a low body weight. According to WHO estimates, 31% of these children under 5 years old are also anemic.

A logical strategy for supplying micronutrient Fe to poor women in developing countries involves making staple foods such as rice more nutritious by using conventional plant breeding and biotechnology. This strategy is low-cost and sustainable and it does not require a change in eating habits and does not impose recurring costs. The greatest potential for improving nutritional status on a large scale involves rice, which is the staple of billions of poor people in Asia.

A research project to develop improved rice varieties with enhanced Fe content started at the International Rice Research Institute (IRRI) in 1992. More than 7,000 entries from the rice germplasm bank were evaluated in cooperation with the Department of Plant Science, University of Adelaide, Australia. Considerable variation was observed in the germplasm for Fe content in the grain. Among a subset of 1,138 samples analyzed, Fe concentration ranged from 6.3 to 24.4 mg kg^{-1}. In comparison, widely grown rice varieties IR36 and IR64 have Fe content of about 12 mg kg^{-1}. Traditional varieties Jalmagna and Zuchen contained almost twice as much Fe. Crosses between high-yielding varieties and traditional varieties with high Fe content have produced progenies with high yield potential and elevated levels of Fe content. One of these progenies has been released as a variety for on-farm production in the Philippines.

The Fe content of rice was also raised through genetic engineering. Goto et al (1999) introduced the soybean ferritin gene into japonica rice variety Kita-ake through *Agrobacterium*-mediated transformation. The Fe content of transgenic seeds was twice as high as that of untransformed controls.

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Rice Production and Hybrid Rice Research in China

Cheng Shihua, Cao Liyong, and Zhai Huqu

Rice is the main staple food in China. More than 60% of the population in the country lives on it. The performance of the rice sector in production and yield has been very impressive in most of the last five decades. The wide adoption of semidwarf varieties facilitated an increase in rice yield from 2 t ha^{-1} in the 1960s to 3.5 t ha^{-1} in the 1970s. In 1973, the development of the first cytoplasmic male sterile (CMS) line in China made it possible to exploit the heterosis of hybrid rice in commercial use. Hybrid rice outyields the leading conventional varieties by 10–20%, enabling China to increase its rice yield to more than 6.0 t ha^{-1} and increase production by nearly 450 million tons on 370 million ha from 1976 to 2005.

China's experience with hybrid rice research could be attributed to the use of various CMS resources, the high outcrossing rate of CMS lines and stable environmentally induced genetic male sterile (EGMS) lines, improvement of resistance to diseases and in grain quality, and a combination of ideo-plant type with heterosis in the hybrid rice breeding program. Innovative breeding techniques, for example, for the root system, molecular marker-aided selection, and wide hybridization should be considered in the further development of hybrid rice in China.

Keywords: Rice production, hybrid rice, molecular marker-aided selection (MAS)

Rice is the main staple food in China. More than 60% of the population in the country lives on it. Rice is planted over a wide range, extending from 18°N to 53°N latitude. Over the recent decade, rice has contributed about 40% of grain production with less than 30% of the grain crop area. Rice also has the highest yield of all grain crops in China. In 2005, the average yield in rice, wheat, and maize was 6.26 t ha^{-1}, 4.27 t ha^{-1}, and 5.29 t ha^{-1}, respectively. Rice yield was 46.6% and 18.3% higher than that of wheat and maize, respectively. China's rice also has an important place in the world. Recently, China produced more than 31% of the total world rice production

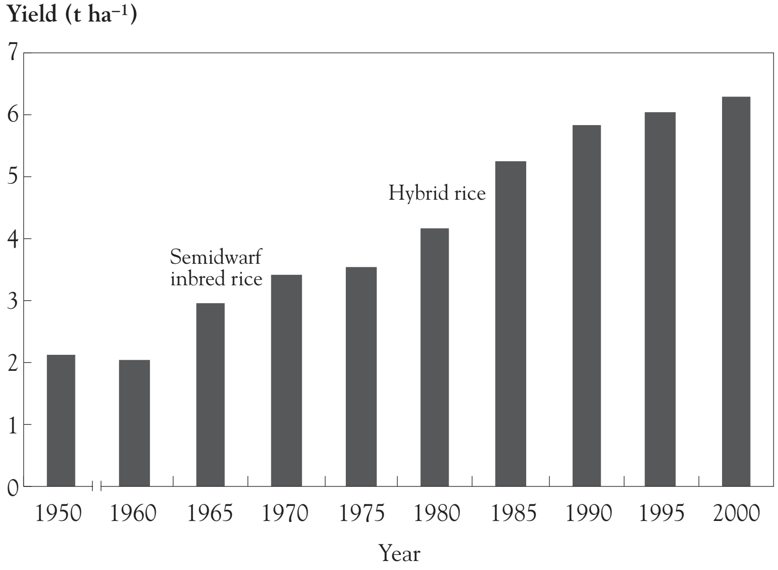

Fig. 1: Increase in yield of rice through genetic improvement in China.

using less than 19% of the total rice-planting area. China has about 70% of the average rice yield vis-à-vis the world average level.

China has made great efforts to increase its rice yield by exploiting the genetic resources of rice. The performance of the rice sector in production and yield had been very impressive in most of the last five decades. With the wide adoption of semidwarf varieties with the *sd1* gene, rice yield in China increased from 2.0 t ha^{-1} in the 1960s to 3.5 t ha^{-1} in the 1970s. Subsequently, hybrid rice with a yield advantage of 10–20% over that of conventional varieties was developed and commercially grown in 1976, which resulted in an increase in yield to over 6.0 t ha^{-1} (Fig. 1). This has contributed to self-sufficiency of the food supply in China.

However, rice production and yield have stagnated since 1990. This implies that in order to match the future population's food demand further increases in rice yield will be more difficult. In addition, arable land available for rice cultivation has decreased during the last three decades because of other uses of the land such as for basic construction, adjustments in agricultural production structure, and limited land for expanded cultivation. This resulted in reduced rice-planting area from 31.8 million hectares in 1997 to 26.5 million hectares in 2003 (Fig. 2). As a consequence, the total output of rice grain fell from a record high of 200.7 million tons in 1997 to 160.7 million tons in 2003. To ensure food security for the increasing population, raising the yield ceiling of rice remains a priority in China. The exploitation

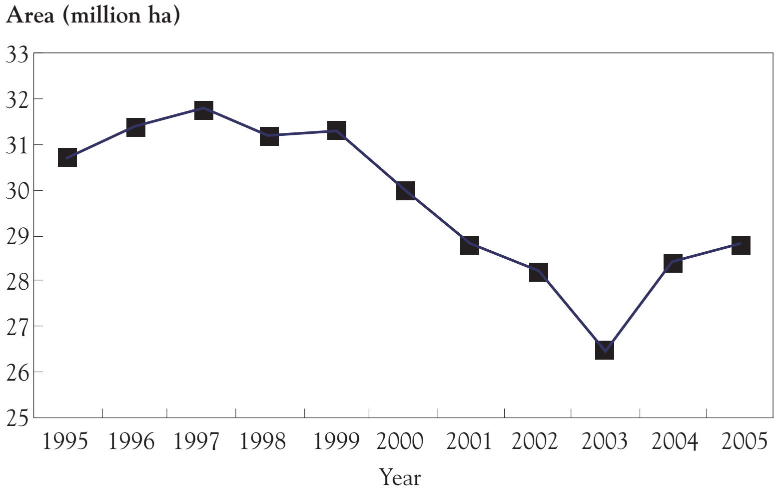

Fig. 2: Changing trend of rice planting area in China.

of intersubspecies heterosis in rice became the important choice for producing more rice (Yuan 1997, Cheng et al 1998).

HYBRID RICE RESEARCH IN CHINA

Role of Hybrid Rice in Increasing Rice Production in And Outside China

Prof. Yuan initiated heterosis research in rice in 1964. He found a natural male sterile mutant plant in indica rice, but couldn't find a restorer line. Fortunately, pollen abortive materials were found in the natural population of wild rice (*Oryza rufipogon*), which had been the donor of cytoplasmic male sterility (CMS) to develop CMS lines. The development of the first CMS line in China in 1973 made it possible to exploit the heterosis of hybrid rice in commercial use. Hybrid rice outyields leading conventional varieties by 10–20%. This enabled China to increase its rice production by nearly 450 million tons, including 370 million ha of hybrid rice, from 1976 to 2005. Hybrid rice has been developed for 40 years. Its area increased from 0.14 million ha in 1976 to about 15 million ha in recent years, more than 50% of the total rice-planting area in China (Table 1). In regions such as Guangdong and Sichuan provinces, more than 90% of the rice varieties grown are hybrid rice. It is anticipated that the area under hybrid rice will reach 70% of the total rice area in 2010.

China plays a very important role in the worldwide development of hybrid rice. China's successful commercial exploitation of hybrid rice encourages

Table 1: Yearly area of hybrid rice and percentage of the total rice area in China (1976-2002).

Year	Hybrid planting area (million ha)	% of total rice area
1976	0.14	0.4
1978	4.34	12.6
1982	5.62	17.0
1986	9.00	27.9
1990	13.62	41.2
1997	17.73	55.8
1999	16.55	52.9
2002	15.48	54.9

many other countries to promote research on and extension of hybrid rice. It was estimated that the planting area in 2005 reached 1.5 million ha in the Asian region outside China, with a 15–60% yield advantage over local inbred rice. It is also anticipated that the total planting area under hybrid rice outside China will reach 3–4 million ha in 2010 and 30–35 million ha in 2020.

Diversification of Male Sterile Sources Used in Hybrid Rice Breeding

To date, CMS has been found to be the most effective system for developing rice hybrids in China and elsewhere. Wild abortive (WA)-type CMS was the first type to be used in hybrid rice breeding. So far, the combination of CMS-WA is still the dominant one in terms of three-line hybrid rice production. To minimize potential damage from rice diseases caused by the unique CMS genetic background, Chinese rice scientists have exploited other CMS sources and developed different CMS lines for breeding new combinations of hybrids. Seven kinds of CMS are being used in China's hybrid rice breeding program. For planting area in recent years (2000-02), the combinations of CMS-ID and those of CMS-G&D accounted for 18.3–21.9% and 12.8–14.6% of the total hybrid rice area in China, occupying second and third place for CMS hybrids, respectively (Table 2).

At first, hybrid rice was developed mainly for high yield. With economic development and people's increased need for food quality and low cost, great efforts have been made to improve hybrid rice quality and the outcrossing rate in CMS lines. CMS-ID types developed by a CNRRI scientist, such as II-32A and Zhong9A, have been used rapidly and have occupied second place in planting area following CMS-WA for a long time. The reason is that CMS-ID type has high grain quality and outcrossing rate and can bring

Table 2: Planting areas of different CMS hybrid types in 2000-02.

Hybrid type	2000		2001		2002	
	Area (million ha)	%	Area (million ha)	%	Area (million ha)	%
WA	6.528	48.3	7.008	50.8	6.025	39.7
ID	2.849	21.1	2.527	18.3	3.329	21.9
G&D	1.775	13.1	1.763	12.8	2.214	14.6
DA	1.330	9.8	0.793	5.7	0.703	4.6
K	0.133	0.9	0.222	1.6	0.113	0.7
BT	0.063	0.5	0.074	0.5	0.106	0.7
HL	0.019	0.1	0.022	0.2	0.047	0.3

Table 3: Grain quality and outcrossing traits in Zhong 9A (ID-CMS) and Zhenshan 97A (WA-CMS).

Grain quality items	Zhong 9A	Zhenshan 97A
Brown rice recovery (%)	80.4	81.0
Milled rice recovery (%)	71.1	73.3
Milled head rice recovery (%)	31.3	34.2
Grain length (mm)	6.7	5.8
Grain length/width ratio	3.1	2.3
Chalky grain percentage	8	84
Chalkiness	0.6	16.6
Translucency	3	4
Alkali digestion value	6	6
Gel consistency	32	30
Amylose content (%)	23.7	22.7
Outcrossing traits		
Exserted stigma %	82.3	39.6
Outcrossing seed setting %	75.6	35.7
Seed yield (t ha^{-1})	3–4.5	2.2–3

about high-yielding hybrids and produce more hybrid seeds than other CMS types. We can compare the grain quality and outcrossing traits between Zhong 9A(ID-CMS) and Zhenshan 97A (WA-CMS) (Table 3).

Although the CMS system has been successful in the exploitation of heterosis in rice, it is cumbersome as it involves three lines (CMS, maintainer, and restorer). Its use is also restricted to that germplasm whose maintainers and restorers are not abundant. Shi (1981) first reported that Nongken 58', a male sterile mutant from the japonica variety Nongken 5, was a

Table 4: Yield targets of different types of super rice varieties (Ministry of Agriculture, China, 1996).

Year	Conventional rice (t ha^{-1})^a				Hybrid rice (t ha^{-1})^a			Increase (%)^b
	EI(Y)	E&LI(S)	SJ(Y)	SJ(N)	EI(Y)	SI&J	LI	
2000	9.00	9.75	9.75	10.50	9.75	10.50	9.75	15
2005	10.50	11.25	11.25	12.00	11.25	12.00	11.25	30

[a]Performance at two sites, 6.67 haor more at each site, successive two years. EI(Y) = early-season indica rice in middle and lower reaches of Yangtze River. E&LI(S) = early- or late-season indica rice in southern China. SJ(Y) = single-season japonica rice in middle and lower reaches of Yangtze River. SJ(N) = single-season japonica rice in northern China. SI&J = single-season indica or japonica rice. LI = late-season indica rice. [b]Yield advantage over the control variety in multilocation trials.

photoperiod-sensitive genetic male sterile (PGMS) line. The development of environmentally induced genetic male sterile (EGMS) rice, including PGMS, thermosensitive genetic male sterile (TGMS), and photo-thermosensitive genetic male sterile (P-TGMS) rice, has laid the foundation for using a two-line system to produce hybrid rice seeds (Cheng et al 1996). In 2002, the planting area of two-line hybrids amounted to 2.745 million hectares and 9.7% of the total national rice area. Two-line hybrid Liangyou Pei9, occupying first place in planting area instead of Shanyou 63, a WA-CMS type hybrid (Yang et al 2006), showed promising prospects for producing two-line hybrids in China if the unstable fertility problem in EGMS could be solved.

Use of Intersubspecies Heterosis Between Indica and Japonica Rice

To solve future food insufficiency in China, exploitation of intersubspecies heterosis for high yield is increasingly needed. Based on the experience of breeding for high yield of rice in China and the experience of new plant type (super rice) breeding at IRRI, a special collaborative research program on breeding of super rice has been established by China's Ministry of Agriculture. The program mainly focuses on breeding of super hybrid rice, which was defined as the varietal type combining a harmonious plant type with heterosis through hybridization between indica and japonica to achieve super high yield (Cheng et al 1998). Besides high quality and resistance to pests, the yield targets of super rice under favorable conditions are expected to meet the future requirement (Table 4).

According to the pedigree analysis, the majority of inbred cultivars and hybrids of rice grown in China have few ancestors. The genetic backgrounds were confirmed to be unique based on the results of RFLP variations in indica cultivars and their parents (Zhuang et al 1997). In the indica rice-growing

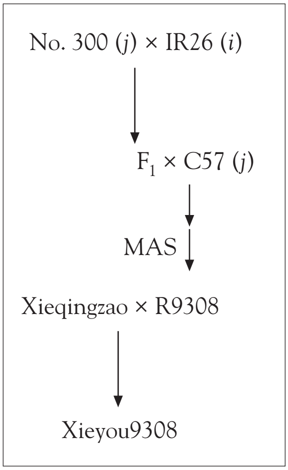

Fig. 3: Development of medium-type restorer line R9308 and its super hybrid Xieyou9308.

regions of China, breeders adopted the methodology of introgressing japonica traits into an indica rice background to develop indicalinous germplasm, and in the japonica rice-growing regions introgressing indica traits into a japonica rice background to develop japonicalinous germplasm. So far, a set of indicalinous or japonicalinous germplasm for super rice breeding has been intentionally developed. Some germplasm has been successfully used in breeding super hybrid rice. For instance, R9308, an indica restorer line from a cross of intersubspecies, was successfully used in the breeding program on super hybrid rice by CNRRI. Xieyou9308, a hybrid with super high yield, multiple resistance to diseases, and good grain quality, was registered in Zhejiang Province in 1999 (Fig. 3) (Cheng et al 2005) and its total planting area has surpassed 1 million ha. We estimated that there are about 25% japonica genetic components in R9308. Its hybrid Xieyou9308 was estimated to have about 12.5% japonica genetic components and it has a good combination of super high-yielding capacity with harmonious plant type. Another example is two-line super indica hybrid Liangyou Pei9 developed by the Jiangsu Academy of Agricultural Sciences in collaboration with the Hunan Hybrid Rice Research Institute. Its female is Peiai64S, a TGMS line with the pedigree of tropical japonica (Yuan 1997). Under good management, these two super hybrids showed super high yield with ideo-plant type in demonstration trials (Table 5).

Table 5: Yield performance of super hybrids Xieyou9308 and Liangyou Pei 9.

Hybrid	Trial site	Year	Average yield (t ha^{-1})	Area (ha)	Highest yield (t ha^{-1})	Area (ha)
Xieyou9308	Xinchang, Zhejiang	2000	11.84	6.8	12.22	0.07
	Zhuji, Zhejiang	2000	11.42	10.0	11.69	0.13
	Xinchang, Zhejiang	2001	11.95	6.9	12.40	0.07
	Xinchang, Zhejiang	2002	10.52	70.0	11.46	16.70
	Xinchang, Zhejiang	2003	11.54	82.5	12.03	28.87
Liangyou Pei 9	Longshan, Hunan	2000	10.65	66.7	11.13	0.07
	Chunzhou, Hunan	2000	11.67	7.7	12.12	0.69

Marker-Aided Selection (MAS) on Restorer Lines of Hybrid Rice

Bacterial leaf blight (BB) is one of the major diseases in rice, especially in hybrid rice. All commercial rice hybrids currently used in China have high heterosis, but most of them lack resistance to BB or have poor agronomic traits although showing BB resistance. It has been estimated that the disease causes nearly 10% rice yield loss annually. To date, more than 20 major genes have been identified and nominated. Among them, the *Xa21* gene originated from *O. longistaminata* is a dominant one, with broad-spectrum resistance, and sequence tagged site (STS) markers closely linked to *Xa21* have become available.

Backcrossing was made using L1 as the recurrent parent and IRBB60 as the donor parent. L1 is a restorer line selected from Duoxi 1/R2070, and it has good combining ability but is susceptible to BB. IRBB60 introduced from the International Rice Research Institute (IRRI) is a restorer line resistant to BB carrying genes *Xa4* and *Xa21* with dominant resistance and genes *xa5* and *xa13* with recessive resistance. The offsprings of F_1 hybrids and backcrossing of IRBB60 and L1 were detected with a DNA marker tightly linked to *Xa21* to select resistant lines, while their restoring abilities were tested by conventional testcrossing. Four bacterial blight strains with a density of 1×10^9 mL^{-1} were inoculated artificially to verify the resistance of candidate lines.

On the basis of phenotypic selection in each generation, the individuals carrying heterozygous *Xa21* were selected. By means of four successive backcrossings and selection, 43 individuals from BC_4F_1 carrying *Xa21* were selected. After selfing, the individuals carrying homozygous *Xa21* were screened by a DNA marker. Two elite restorer lines (R8006 and R1176) with resistance to BB and excellent agronomic traits were selected (Cao et al 2003).

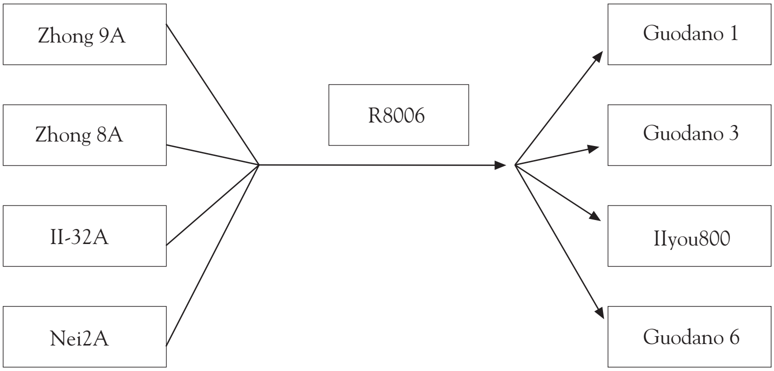

Fig. 4: Four hybrids with high resistance to BB and excellent agronomic traits derived from R8006, a new restorer line developed through MAS.

R8006 and R1176 show great potential as elite restorers in a hybrid rice breeding program. A total of four hybrids have been developed through crossing R8006 with various CMS lines (Fig. 4) and two hybrids developed through R1176. All hybrids have been released nationally or provincially for commercial use and showed high resistance to diseases, good quality, and high yield potential in national and provincial adaptability and yield trials.

FUTURE OUTLOOK ON HYBRID RICE RESEARCH

Great achievements in hybrid rice breeding have been made in China. However, it seems that a further increase in yield will be more difficult. Some issues for future research should be considered.

The root system is the foundation of plants. However, the proportion of research effort devoted to the root system has been much smaller than that devoted to the rest of the plant. Root system vigor at various growth stages, particularly during the grain-filling period, should be comprehensively considered. Our primary study indicates that the ideal root system for rice will be adequate in morphology, effective in physiology, and friendly for environmental protection. To improve rice roots, control root number, and improve root depth, more efficient root activity per unit of root biomass will be needed for high-yielding rice in a future breeding program (Wu and Cheng 2005).

Exploitation of indica/japonica heterosis could heighten the level of yield. With the development of molecular marker technology in rice, subspecies differentiation of parents can be detected and a suitable contribution of indica and japonica traits in hybrids can be determined for high yield in combination with harmonious plant type. On the other hand, the availability of high-density genetic linkage maps now makes it possible to identify and study the effects of the individual loci underlying quantitatively inherited traits (QTLs). Classically, it was assumed that complex traits were determined by a large number of genes of relatively small and equal effect. QTL analysis has revealed that the effects of different loci may vary greatly. The MAS technique has provided an approach to pyramiding beneficial alleles of QTLs for improving yield and other important traits. Recently, some restorer lines pyramiding yield QTLs and major genes with resistance to disease are under evaluation in super hybrid rice breeding programs (Cheng et al 2004).

Incorporation of the characteristics of high photosynthetic rate in other species into the rice plant is of importance for future super hybrid rice breeding. Using a transgenic technique, the PEPC gene and ADP gene have now been transformed into rice (Zhu et al 2004). Photosynthetic capacity and yield potential in transgenic hybrid rice plants are being evaluated.

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Rice Culture in Agriculture: An Indian Perspective

Mangala Rai

Rice is cultivated year-round in many parts of India, and in diverse ecologies it covers more than 40 million hectares, with a production of around 90 million tons. Rice improvement efforts in India began as early as 1911 and received a major impetus with the setting up of the All India Coordinated Rice Improvement Project in 1965 to facilitate a free and rapid exchange of germplasm and breeding lines. This effort resulted in the release of more than 700 varieties/hybrids. As a consequence, over the last four decades, the number of districts having rice productivity of more than 2 tons per hectare increased from 2 to 103. Almost 50% of these districts have current yields of more than 3 t ha^{-1}. Hybrid rice is cultivated in India on almost 1 million ha, with an average yield advantage of 1–1.5 t ha^{-1}over pure-line varieties. Hybrids have also been developed for the fragile and unfavorable rice ecosystems. Aromatic rice hybrid Pusa RH 10 has been developed that has very fine grain and excellent cooking quality. India has released many high-yielding Basmati rice varieties. These varieties have short duration (120 days versus 160 days in traditional Basmati) and higher productivity (5–6 t ha^{-1} versus 2–2.5 t ha^{-1} for traditional Basmati). The area under Basmati rice has now increased to close to 1 million ha. These developments in production have led to a considerable increase in rice (including Basmati) exports to other countries. Over the years, India has developed a strong base in rice biotechnology. Our scientists have sequenced the long arm of chromosome 11 in partnership with the International Rice Genome Sequencing Project. Considerable progress has also been made in mapping, tagging, and map-based cloning of rice genes of agronomic importance. Based on DNA marker-assisted pyramiding of bacterial blight resistance genes, an improved version of Pusa Basmati 1 has recently been released for commercial cultivation. Several technologies such as precision land leveling, zero-tillage, bed planting, direct seeding, and the leaf color chart have become available and can help in resource conservation. Detailed experiments done at several places in the country have enabled us to develop inventories of methane and other greenhouse gases from rice paddies. These analyses have shown that total methane emissions from Indian paddies are 2.9 Tg per annum, which is far lower than the earlier estimates of international

organizations. In the future, we need to increase our production considerably to meet the demand of the rising population. Increasing climatic variability and climate change, however, could further affect rice supplies. Problems and challenges facing rice production require new technologies and simultaneous action for enabling policy, infrastructure, and market support.

Rice is a major staple crop of India and accounts for 40% of the total food grain production of the country. It is now cultivated on 43 million hectares, with a production of 92 million tons of milled rice (Fig. 1). Rice in India is a major contributor to national food and nutritional security. It provides one-third of the total calorie needs of the people. Though traditionally a rainy-season crop, it grows throughout the year in many parts of the country. With its long history of cultivation and selection under diverse environments, rice has acquired wide adaptability, enabling it to grow in a range of environments, including irrigated, rainfed uplands and lowlands, and deepwater and flood-prone areas.

Almost 56% of the rice crop grown in India is irrigated, and this provides 64% of the national rice production, with an average productivity of 3 t ha^{-1}. The productivity in various rainfed rice environments is stagnating between 1 and 1.5 t ha^{-1} (Fig. 2).

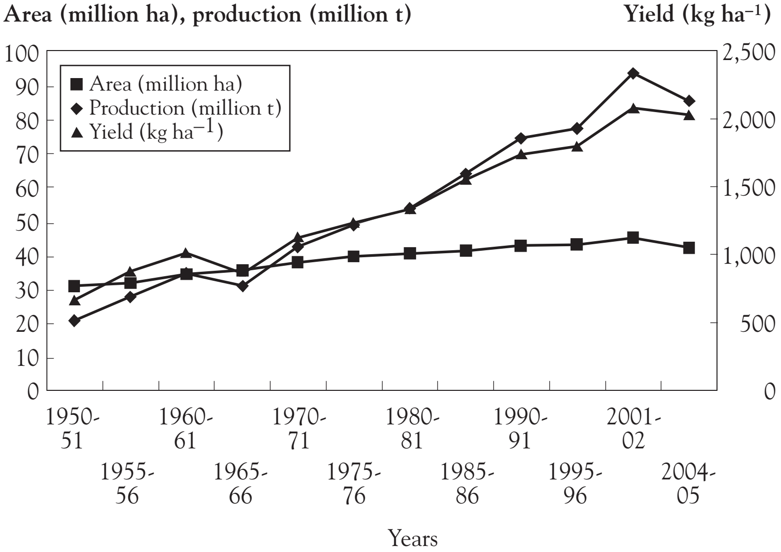

Fig. 1: Area, production, and yield of rice in India.

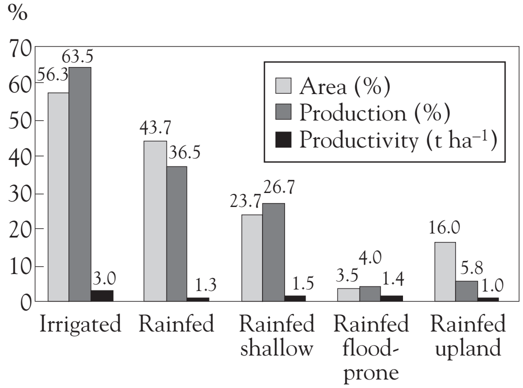

Fig. 2: Area (%), production (%), and yield (t ha^{-1}) of rice in different rice ecosystems in India.

Over time, because of research efforts, international cooperation, policy support, and farmers' entrepreneurship, India has made a lot of progress in agriculture. This paper provides a brief review of the progress made in rice.

RICE IMPROVEMENT RESEARCH IN INDIA

Until the 1960s, rice research efforts in India largely focused on pure-line selection. Several popular varieties were released during this period, including N22 of Nagina (UP), PTB 10 of Pattambi (Kerala), T141 and T1242 of Orissa, Basmati 370 of Punjab, GEB 24 of Tamil Nadu, and MTU 15 of Andhra Pradesh. SR 26B and FR13A were particularly bred for saline and flood tolerance situations, respectively, while Co25 and Co26 were developed for blast resistance. The indica/japonica hybridization program also led to the development of important hybrids. Nevertheless, during this period, there was only marginal improvement in the productivity of rice, from 771 kg ha^{-1} in the 1950s to 1,033 kg ha^{-1} in the early sixties.

In the second phase, the first semidwarf variety, Taichung Native 1, was introduced in India. Thereafter, IR8, developed in 1966 at the International Rice Research Institute (IRRI), Philippines, was brought for cultivation in India. Along with T(N)1, it revolutionized rice cultivation in India. Jaya and Padma were the first varieties released by the All India Coordinated Rice Improvement Project (AICRIP), established in 1965 to facilitate rice research and a free and rapid exchange of genetic material and to assist in developing and identifying rice varieties suitable for different rice ecologies. Its efforts led to the release of more than 700 varieties/hybrids by 2005 for irrigated and rainfed areas, respectively (Fig. 3). As a result, the spread of

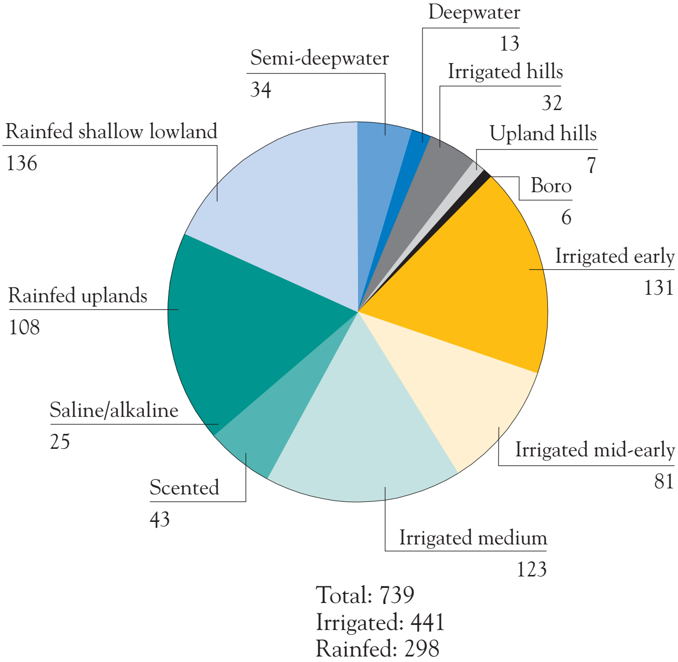

Fig. 3: Rice varieties released for various ecosystems by the Indian rice research program between 1976 and 2005.

high-yielding varieties doubled from a meager 38% in 1966-67 to nearly 80% by early 2000.

Hybrid Rice Technology

Hybrid rice technology and its large-scale adoption are a pragmatic way for raising rice production. In India, 29 rice hybrids have already been released for commercial cultivation in various rice-growing regions. Hybrid rice is now cultivated in India on 1 million ha, with a yield advantage of 1–1.5 t ha^{-1} over pure-line varieties. This has increased the total rice production by at least 1–1.5 million tons. Hybrids have also been developed for even the fragile and unfavorable rice ecosystems. Narendra Usar Sankar Dhan 3 is the first hybrid released for the saline-alkaline soils of Uttar Pradesh. We have also been able to develop aromatic rice hybrid Pusa RH 10, which has very fine grain and excellent cooking quality.

The production of genetically pure, good-quality hybrid seed of the required quantity continues to be the major challenge and requires a strong partnership among rice breeders, the private seed sector, and farmers. DNA marker-based technologies have been developed to make hybrid seed testing

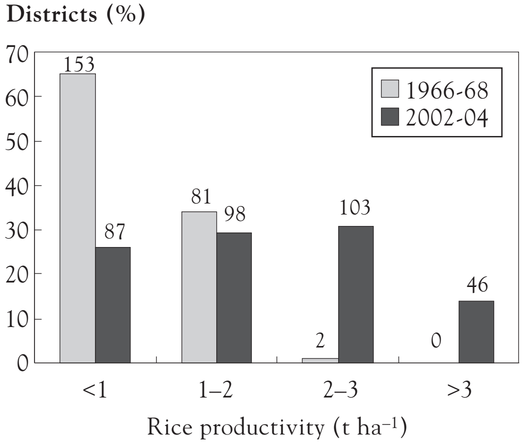

Fig. 4: Impact of technology adoption on rice productivity increases in various districts of India.

more effective and to ensure the timely availability of good-quality hybrid seeds.

These improved varieties and hybrids have greatly accelerated the production and productivity of rice in the country. In the pre–Green Revolution era, only two districts in the country had rice productivity of more than 2 t ha^{-1}. With the development and spread of new technologies, particularly the high-yielding varieties/hybrids, by 2004, 103 districts had productivity of more than 2 t ha^{-1} and 46 districts produced more than 3 t ha^{-1} (Fig. 4).

Basmati Rice Improvement in India

The traditional Basmati rice varieties are photoperiod-sensitive, tall, and prone to lodging, and have low productivity (2–2.5 t ha^{-1}). Combining Basmati grain and cooking quality traits with the high-yielding ability of semidwarf varieties had been a challenge to breeders in the past. The Indian Agricultural Research Institute developed in 1989 the first semidwarf high-yielding Basmati rice variety, Pusa Basmati 1. Since then, many high-yielding Basmati rice varieties with reduced duration have been developed, including Pusa Sugandh 2, Pusa Sugandh 4, and Pusa Sugandh 5. Thus, over time, we have been able to reduce the duration of Basmati varieties from 160 days in traditional Basmati to 120 days, while productivity has been enhanced from 2–2.5 t ha^{-1} to 5–6 t ha^{-1}. This is a very significant achievement as it breaks the well-established negative relationship between yield and duration (Fig. 5). Because of these developments, the area under Basmati rice has increased to 1 million ha. Basmati rice production also increased from 0.3

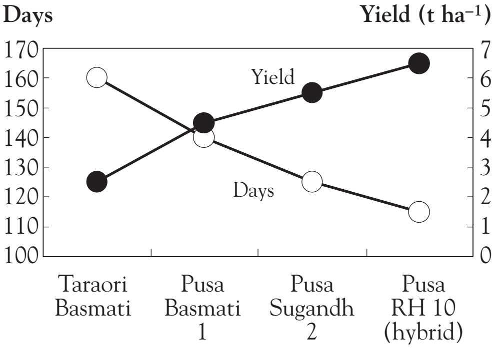

Fig. 5: Change in crop duration and grain yield with the development of new Basmati varieties.

million tons to 2 million tons, with productivity rising from an average of 0.78 t $ha^{-1}$to 2.42 t ha^{-1}.

In recent times, India has witnessed a large increase in rice exports. Starting in the 1990s, rice exports increased markedly from 0.55 million tons to 5.0 million tons in 2005-06. As a result, our foreign exchange earnings from rice exports increased from Rs 456.7 crores to Rs 7,174.35 crores in 2005. The foreign exchange earnings through Basmati rice exports alone increased from 865 crores in 1996 to 3,030 crores in 2006.

Rice Biotechnology

Complex traits such as drought, heat and salinity tolerance, grain quality, micronutrient-use efficiency, and durable resistance against the changing spectrum of diseases and pests require in-depth knowledge of the underlying genes and their interaction among themselves and with the environment. The permutations and combinations of genes controlling these complex traits are innumerable and hence a trial-and-error method of selection must give way to precision molecular breeding strategies with the help of DNA markers tightly linked to the agronomic traits. Moreover, for certain traits, such as yellow stem borer and sheath blight, there are no effective sources of resistance in the primary gene pool of rice. Therefore, bringing in genes from across the species barrier through the application of transgenic technology is the only viable option, a strategy very well demonstrated and validated in the case of *Bt*-cotton. Similar revolutions can be foreseen in rice also by the application of molecular markers and transgenic technologies.

Over the years, India has developed a strong base in rice biotechnology. One of the most visible contributions of India in rice biotechnology is the sequencing of the long arm of chromosome 11 in partnership with the

International Rice Genome Sequencing Project. The National Research Centre on Plant Biotechnology at the Indian Agricultural Research Institute and University of Delhi South Campus, New Delhi, achieved this important milestone. Indian scientists decoded more than 15 million base pairs of high-quality sequence of rice chromosome 11, with an average error rate of less than one per 10,000 nucleotides, and predicted 2,500 genes in this sequence. Rice chromosome 11 has 218 disease-resistance-like and defense-response genes accounting for more than 20% of the whole rice genome. The decoding of the rice genome has led to large-scale functional genomics and gene discovery projects worldwide and several genes of agronomic importance have been cloned using the genome sequence map information. In India, several functional genomics projects are under way for gene discovery for abiotic stress tolerance and grain quality traits.

Indian rice scientists have made notable progress in mapping, tagging, and map-based cloning of rice genes of agronomic importance. This includes cloning of blast resistance gene *Pi-kh*; mapping of QTLs for grain dimensions, amylose content, and aroma in variety Pusa 1121; functional annotation of more than 500 ESTs from drought-tolerant variety N22; DNA fingerprinting of Indian rice cultivars using RAPD and SSR markers; the development of a panel of SSR markers for authentication of Basmati varieties; development of DNA markers for distinguishing WA cytoplasm-based A and B lines of rice; molecular mapping of fertility restorer genes; molecular fingerprinting of rice hybrids; and marker-based assessment of the genetic purity of hybrid seed. On the molecular breeding front, DNA marker-assisted pyramiding of bacterial blight (BB) resistance genes *xa5*, *xa13*, and *Xa21* in widely grown rice variety BPT 5204 and that of *xa13* and *Xa21* in the genetic background of the most widely grown Basmati rice variety, Pusa Basmati 1, has been achieved. A BB-resistant version of Pusa Basmati 1 has already been released and made available for commercial cultivation as Pusa 1460 (Improved Pusa Basmati 1).

Rice Germplasm Collections

India is one of the centers of diversity for rice and is generally considered as the place of origin of Asian rice. A systematic attempt to collect, document, and conserve the genetic wealth of rice in India started as early as 1911 with the establishment of the Coimbatore rice germplasm collection. Now, the number of such collections has gone up to a whopping 89,947 entries as of August 2006 and these are being maintained by diverse agencies such as the National Bureau of Plant Genetic Resources and state agricultural universities and departments. Northeastern India, the tribal belt of central India, and the Andaman and Nicobar islands still remain hot spots for rice genetic diversity in India. The wild types and landraces of rice of these regions possess a fascinating diversity in grain shape, color, aroma, and other cooking quality traits. Recently released Pusa Sugandh 4 (Pusa 1121) has entered the Limca book of world records for its extraordinary kernel elongation after cooking and is among the most sought-after Basmati rice varieties in the international market.

Indian rice germplasm is also the treasure trove of much-needed biotic and abiotic stress tolerance genes that are widely exploited by rice researchers worldwide. Accessions of wild species of rice such as *Oryza longistaminata* and *O. nivara* identified in India are the sources of the extensively used bacterial leaf blight resistance gene *Xa21* and the gene for grassy stunt virus resistance, respectively. The other important bacterial leaf blight resistance gene (*xa13*) is from the Indian landrace Bhog Jeera 1 (BJ1). For abiotic stress tolerance, the *Sub1* gene from FR13A (submergence tolerance), *Saltol*, and *SKC1* from Pokkali rice and Nona Bokra (salt tolerance) and the drought tolerance genes from Nagina 22 and Kala Keri are being deployed by rice breeders in many elite breeding lines. These genes present some outstanding examples indicating how useful and vital well-conserved crop germplasm could be for ensuring food and nutritional security of people around the world.

Rice Agronomy

Intensification of agriculture during the last few decades has had some adverse environmental consequences such as the deterioration of natural resources. Yield trends from long-term continuous rice-rice experiments indicate that, even with the best available cultivars and scientific management, rice yields (holding input levels constant) have either stagnated or declined over time since the early 1980s. The challenge for us is to integrate productivity and profitability improvement while conserving and enhancing the quality of the natural resource base on which production depends.

The sustainability of rice farming can be maintained through the infusion of technologies that can increase efficiency in the use of inputs and thereby reduce production costs. In recent years, conservation agriculture involving zero- or minimum-tillage with direct seeding, bed planting with residue mulch, innovations in residue management to avoid straw burning, and crop diversification have been developed as alternatives to the conventional rice production system for improving sustainability and income. Some of the key developments in the field of rice crop management are

- Zero-tillage, which is now well established for wheat farming, is gaining favor for rice as well because of higher input-use efficiency and lower cost of cultivation.
- Considerable progress has been made in developing technology for direct drilling into stubbles on flat land, including double and triple disc assemblies and the star-wheel punch planter.
- Direct dry-seeded (DSR) rice, which avoids puddling and does not need continuous submergence and thus reduces the overall water demand for

rice culture, is developing as an alternative to conventional puddled transplanting. DSR has components of conservation agriculture (no-till/reduced-till, residue retention, and controlled traffic to minimize soil compaction), which lead us to find alternative options for replacing puddled transplanted rice. Studies have shown that DSR technology is cost-effective and environment- and farmer-friendly.

- Machinery has a key role to play if conservation agriculture is to succeed on a wide scale. For a start, recently developed machines allow more precise seeding. Seeders are now available that can meter the seed rate and simultaneously apply fertilizer. Such precision allows farmers to reduce the amount of seed and fertilizer they use and so save money. The new seeders can also plow through the residue of the previous crop.
- Recent research indicated that use of the leaf color chart would promote timely and efficient use of N fertilizer in rice, save costly fertilizer, and minimize the fertilizer-related pollution of surface water and groundwater.

Several challenges face us before these technologies can be adopted on a very large scale. For example, increased weed infestation in zero-tilled fields is a problem. The bed planting system is not yet perfect and often produces lower yield than conventional practices. Nevertheless, a paradigm shift in our management approach is required for enhancing the productivity and sustainability of rice-based systems. Resource-conserving technologies involving zero- or minimum tillage with direct seeding, improved water-use efficiency, innovations in residue management to avoid straw burning, and crop diversification should assist in achieving sustainable productivity and allow farmers to minimize inputs, maximize yields, conserve the natural resource base, reduce risk due to both environmental and economic factors, and increase profitability. In addition, long-term changes in (1) the performance of crop and soil and the efficiency of various inputs and (2) weed flora should be monitored to achieve this paradigm shift in farmers' practices. Appropriate integration of a crop residue component in zero-tillage plots is another crucial issue that needs to be examined. It is also important that small-scale farmers have access to, and are trained in, the use of these technologies.

Methane Emissions from Rice Paddies

The large paddy area of India has been considered as one of the major sources of methane emissions. According to a United States Environmental Protection Agency estimate in the early nineties based on extrapolation of measurements in the U.S. and Europe, annual methane emissions from Indian rice paddies were 37.8 Tg (1 Tg = 10^{12} g or 1 million tons). This estimate was lowered to a great extent after actual measurements were carried out in India. In

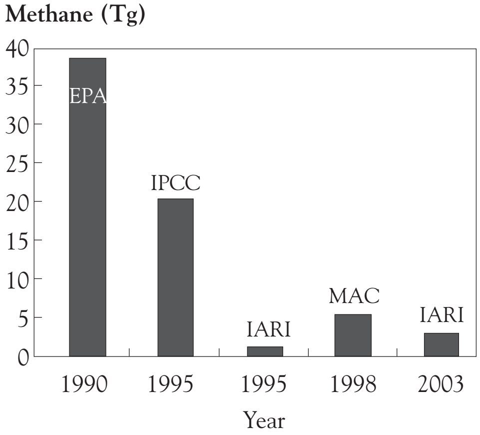

Fig. 6: Methane emission estimates from Indian rice fields in different years. Please note that the international estimates by the EPA (Environmental Protection Agency of the U.S.) and IPCC of the United Nations were far higher than those of IARI and MAC (Methane Asia Campaign).

1991, a campaign was carried out for methane measurements across the rice-growing states in India and this showed total methane emissions from Indian paddies to be 4.0 Tg per annum. Subsequently detailed experiments have being conducted at the Indian Agricultural Research Institute, New Delhi; Central Rice Research Institute, Cuttack, Orissa; and at other institutes. These studies indicate that the total methane emissions from Indian paddies are 2.9 Tg per annum (Fig. 6). These Indian estimates of methane emissions are much lower than those proposed earlier by international and western organizations.

Managing Pests

The increased incidence of new and more virulent races/biotypes of pests is gradually becoming a threat to the stability of rice production. Brown spot was the only major pest for rice in the 1940s but now we have 13 critical pests and 9 diseases. Among the pests, stem borer and brown planthopper occur in epidemic proportion, whereas gall midge and leaf folders are important only in some areas. Among diseases, bacterial leaf blight, tungro, leaf blast, and sheath blight are important. Therefore, breeding for multiple pathogen and pest resistance has become more important.

CONCLUSIONS

India has made considerable progress during the last four decades in agriculture and, as a consequence, rice production has reached 90 million tons. However, the country needs more than 120 million tons of rice to meet its growing needs. Increasing climatic variability and climate change could reduce our rice supplies. Problems and challenges facing rice production require action on several fronts—technology, policy, infrastructure, and markets. All these factors result in interacting influences on farm output, farm income, and sustainability. Several promising rice technologies have been developed in laboratories. But a large gap continues to persist between what is attainable through these technologies and what is actually attained in farmers' fields in most crops and states. That there are considerable yield gaps in all regions is evident from simulation studies that indicate that potential rice yield varies between 7 and 11 t ha^{-1} in different parts of the country. In most states, technologies are available to double the actual yield. Thus, it is more important to ensure that available improved technologies are used in farmers' fields. While doing this, it must be ensured that the state of natural resources is maintained or enhanced.

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The Complete Rice Genome Sequence: A Gold Mine for Innovation in Rice Research

Takuji Sasaki

The map-based complete rice genome sequence is now freely available to researchers worldwide, providing a fundamental tool that should further accelerate efforts to improve the staple crop that feeds more than half of the world's population. The finished quality sequence covers almost 95% of the 389 Mb genome, including virtually all of the euchromatin and two complete centromeres. A total of 37,544 nontransposable-element-related protein-coding genes were identified. The complete genetic information of rice will serve as a gold mine for genomic research in rice and other cereal species. It will facilitate the identification of many important genes by both forward and reverse genetics strategies, and clarify the relationships between sequence variation and phenotypes. The genome sequence derived from *Oryza sativa* subsp. japonica can be used as a reference sequence for comparative analysis among *Oryza* species that will help in understanding the major factors involved in speciation and searching for useful genetic resources. During the last couple of years, high-quality rice genome sequence data have led to several milestones in rice genomics such as the discovery of genes that contributed to domestication or modern rice breeding. Furthermore, the completed sequence also begins to prove its value as a standard for cereal genome comparison and identification of rice orthologous genes in other grass species, thereby providing a platform for establishing the genomics of the major cereal crops.

In the last ten years of the 20th century, significant progress was achieved in genome analysis because of a lot of technological innovations in the field of genetics and molecular biology. Extensive analysis of the genomes of many species, including microorganisms, plants, and animals, can provide a platform on how to understand the diversity of life. It also paves the way for a paradigm shift that may revolutionize various approaches in genetics and breeding similar to the formulation of Mendel's laws of genetics in 1865 and the discovery of the double-helical structure of DNA in 1953. As we focus on imminent food and energy problems, it is becoming clear that plant genome analysis could play a vital role in addressing this global crisis. Rice is not only the most important staple in the world but is also one of the most widely studied plant species. A paradigm shift in rice research must be widely accepted by various groups, from ordinary consumers and farmers to basic plant scientists, including geneticists, molecular biologists, and breeders. An urgent need to supply sufficient food to the increasing world population, particularly in Asian and African countries, is now widely recognized by the scientific community, including basic plant scientists, geneticists, molecular biologists, and breeders. At the same time, there is also a need to establish a model cereal crop that could be used in understanding other cereal crops that make up overall food sources for all humanity. Extensive analysis of the rice genome is probably one of the most important contributions of the rice research community to address these needs. Therefore, the genomic information and tools developed in the long course of rice genome research can now be used to address these major issues so that the large investment in various projects on rice genome analysis can be converted to public scientific and economic benefits.

The history of rice breeding must have started in accordance with the beginning of agriculture. Early farmers must have compared characteristics of rice plants and their seeds, selected more favorable seeds, and continuously sowed them for further harvest. At that time, farmers must have relied mainly on natural variation as a source of plants with good agronomic potential. Through the natural system of ecological diversification, which involved continuous cycles of hybridization, differentiation, and selection, the favorable agronomic characters of rice must have been maintained for thousands of years. Since there is no clear evidence of a definitive strategy that led to cross pollination between different rice plants, early cultivars must have been accidentally generated by chance through cross pollination that might have occurred when two different rice groups were grown at a proximate distance and flowered at almost the same time. In Japan, and also presumably in many other countries, such accidental crosses between different plant types might have led to the production of rice plants with better qualities, which were then selected by local farmers and replanted in succeeding planting seasons. Many so-called local varieties must have been generated in such a manner and later used as resources for more organized breeding strategies based on established theories of inheritance formulated about 100 years ago. As a result, we now have more than 120,000 rice varieties around the world well adapted to various cultural conditions. However, the increase in population, especially in Asia, where rice is the main staple, requires the further development of new breeding strategies to further increase rice production under a much restricted environment, such as decreasing lands for cultivation, a much-reduced water supply, and various stresses that continuously reduce production. A large-scale program in rice genome research, which was launched in the early 1990s in several countries and which led to the sequencing of the entire genome, is expected to provide the stimulus for a more innovative rice breeding strategy. This review will focus on what has been elucidated so far by extensive rice genome analysis in the last 15 years and how the results will be used for rice improvement.

STRUCTURAL ANALYSIS OF THE RICE GENOME

The fundamental characteristics of the rice genome such as gene models, gene duplication, segmental duplication, transposable element content, and crosstalk between nuclear and organelle genomes have been analyzed in detail based on the high-quality rice genome sequence. In addition, the structure of the centromeres of chromosomes 4 and 8 has been completely elucidated (Wu et al 2004, Nagaki et al 2004, Zhang et al 2004), representing the first two centromeres so far clarified in higher plants. The genome information that has been accumulated so far provides an overview of the diversity in the genus *Oryza* and the need to explore the genome structure of various rice species (AA to JJ genomes) as well as to discover new alleles, to identify genes involved in agriculturally important traits, and to understand the evolutionary history of the rice genome.

The availability of a standard genome sequence facilitates comparison among rice plants with high accuracy and within a short period. This is because of the combination of the gold standard Nipponbare genome sequence and the development of a more sophisticated sequencer generating 100 megabase nucleotides of short sequences (100–200nt) within a short period of time and at a much reduced cost (Margulis et al 2005). If these short sequences are overlaid on the standard sequence, it is expected that regions without repetitive sequences or insertions and/or deletions could be promptly aligned to generate a correct assembly of corresponding sequences. This was clearly shown by sequencing 10 contiguous BAC clones of *O. rufipogon* assigned to the sequential Hd3a and FT1 regions (Kojima et al 2002). This assignment was aided by using extensive fingerprint data generated by OMAP (www.omap.org/nsf.html). The genomic region of *O. rufipogon* corresponding to Hd3a and FT1 was completely sequenced without any gaps. However, overlaying of short sequences was not successfully attained outside the FT region. These two opposing cases might indicate the existence of conserved genic and diverged intergenic sequences between *O. sativa* and *O. rufipogon*. In the case of *O. sativa* subsp. indica, both the genic and intergenic BAC end sequences could be successfully overlayed on the japonica genome sequence, thereby facilitating the construction of contigs (IRGSP 2005). These two cases suggest how the *O. sativa* standard genome sequence can be efficiently used to detect single nucleotide polymorphisms (SNPs) and to reconstruct the genome sequence of other types of rice plants.

PUBLIC ACCESS TO RICE GENOME INFORMATION

Molecular analysis of the rice genome has made significant progress since the first rice molecular genetic map was published in 1989 (McCouch et al 1988). The ultimate goal of deciphering the compete genome sequence was eventually attained in 2004 (IRGSP 2005). In the process, many molecular tools have been generated, including RFLP markers and PCR-applicable SSR (simple sequence repeat) and SNP markers; BAC/PAC libraries and BAC clones with end-sequence information; cDNAs with full-length or partial sequences; a map-based genome sequence of a japonica cultivar; and a whole-genome shotgun sequence of an indica cultivar. These tools serve as the foundation for structural and functional analysis of the rice genome. All information is publicly available in well-established databases such as INE (http://rgp.dna.affrc.go.jp/E/giot/INE.html) and Oryzabase (http://shigen.lab.nig.ac.jp/rice/oryzabase/top/top.jsp). Upon completion of the genome sequence, the Rice Annotation Project Database (RAP-DB, http://rapdb.lab.nig.ac.jp/) was released to provide a comprehensive and highly reliable analysis of predicted genes. It primarily maps rice full-length cDNA sequences to the Nipponbare genome sequence and contains the manually curated annotation of gene models. So far, about 30,000 rice genes are unambiguously attributed to the genome sequence. Similar analysis of the complete genome sequence in the TIGR Rice Genome Database (www.tigr.org/tdb/e2k1/osa1/) provides automated annotation that uses several prediction programs to obtain all plausible genes in the genome. The rice genome information is integrated with information on other cereal crops in the Gramene database (www.gramene.org/). Gramene also aims to support the analysis of wild rice genomes to understand the domestication of rice and to facilitate the discovery of useful alleles for the improvement of modern varieties to overcome biotic and/or abiotic stresses, increase yield, and improve eating quality.

Genomics databases must be supported by controlled vocabularies for the description of the genes, molecular function, biological process, cellular component of gene products, and phenotypes to facilitate uniform queries across various systems. In the case of rice, the Gene Symbolization, Nomenclature, and Linkage Subcommittee of the Rice Genetics Cooperative (www.shigen.nig.ac.jp/rice/rgn/vol22/vol22_1.html) established general rules and standardized symbols for known genes. On account of the completion of the genome sequence, it has also recently provided the guidelines for a universal system for naming rice genes. The adoption of a common gene nomenclature for rice will facilitate structural, functional, and evolutionary comparisons of genes and genetic variation among cereal crops, plants, and other organisms.

FUNCTIONAL ANALYSIS OF THE RICE GENOME

The term "functional analysis" covers a wide range of meaning and, in accordance with the progress of technology in genome science, a much deeper understanding of the mechanism of phenotype expression has become available. Identification and functional analysis of genes by map-based cloning are now efficiently and successfully carried out in rice using various tools obtained so far such as SSRs or SNPs, which could be used to detect polymorphisms and to narrow down the target genomic region (McCouch et al 2002). Once a fine genetic map of the target region is established, screening of corresponding DNA fragments in BAC or fosmid clones can be accurately performed. However, it is still necessary to continue the fine genetic mapping by adding new markers designed using genome sequences of selected DNA fragments to narrow down the candidate region to less than 50 kb because of the relatively small size of the rice gene. Occasionally, the difference in gene expression profile corresponding to the phenotype can be used to identify the target gene. However, this approach is not always effective because the difference in gene expression does not necessarily correspond to the difference in phenotype. It is generally recognized that genes accompanying the phenotype are also variably expressed from time to time.

The forward genetics method relies on artificial disruption of the genome sequence and information on the flanking sequence of the disruption point. Combining this sequence information with the corresponding phenotype can lead to the identification of a genic or intergenic sequence responsible to the phenotype. Disruption tools that are now widely used in rice include T-DNA, *Ac/Ds*, and *Tos17*. Several researchers in several countries have generated many disrupted rice lines. An international collaboration has been established to facilitate the sharing of resources and to efficiently perform functional analysis of the rice genome. This strategy could be very effective if various regions of the whole genome could be disrupted evenly. However, most of the available disruption tools such as T-DNA, *Ac/Ds*, or *Tos17* show preference of insertion into the genic region. This should not be a problem if the phenotype is regulated only by the expression of the genic region of the sequence. It is now widely known that intergenic regions such as the promoter, *cis*-element, or distantly separated sequence can invariably affect phenotype expression (Konishi et al 2006).

One of the main focuses for current studies on rice functional analysis concerns the elucidation of molecular mechanisms involved in the expression of quantitative trait loci (QTLs). So far, QTLs have been considered a statistical trait with no clear definition of what type of gene or sequence contributed to the trait. However, by a combination of statistical genetics and molecular genetics, the molecular nature of QTLs has been identified and represents the actual interaction of genic or intergenic effects involved in QTLs. This is clearly shown in the case of heading date of rice controlled by photoperiod response (Yano et al 2000). However, a QTL is a complex trait and it is well known that detection of a specific trait is not guaranteed with any parental combination due to variation in the nucleotide sequence of each corresponding locus of the QTL. A study to prove this hypothesis is now under way to correlate nucleotide sequence variation and degree of expression (Kliebenstein et al 2006). The existence of a QTL is detectable only by forward genetics and also the isolation of each gene involved in the QTL is available by map-based cloning using chromosomal segment substitution lines (CSSL). Many reverse genetics resources are useful for assisting the acceleration of elucidation of the gene involved in a QTL. However, these resources must be systematically made available in comprehensive databases so that the relationship between a disrupted sequence and phenotype can be clearly elucidated.

TRANSFER OF NOVEL MOLECULAR INFORMATION TO BREEDING

Breeding aims to create new varieties with more preferable or novel characters. For this purpose, both cross-aided and vector-aided methods have been used. The cross-aided method involves hybridization between different rice types and has been used for a long time. The vector-aided method involves the introduction of nonrice genes or DNA by using *Agrobacterium tumefasciens*. This nonconventional method can overcome the breeding barriers most commonly encountered due to a lack of crossability resulting from chromosomal and genic differences. As a result, several agronomically important genes, including herbicide tolerance and insecticide tolerance, have been incorporated in rice. For example, the genetically engineered *Bt*-rice, which is resistant to naturally occurring soil bacterium, has been released and successfully commercialized in Iran since 2005 (www.isaaa.org/kc/CBTNews/press_release/briefs34/ESummary/iran.htm). The so-called "golden rice" containing pro-vitamin A synthesis genes is expected to reduce malnutrition in poor Asian and African countries, which results in blindness among children suffering from vitamin A deficiency (Hoa et al 2003). Transformation of rice itself does not require information on genome structure, but if targeted genome sequence is preferred for effective expression of an introduced alien gene, this study can be greatly facilitated by genome sequence information. In fact, homologous recombination of rice has been successful due to efficient use of the genome sequence (Terada et al 2002).

The utility of genome information for cross-aided breeding is realized in the marker-assisted selection system. This system could be very effective if markers closely linked to the target trait could be developed and the gene corresponding to the trait could be identified based on the position of the markers. Even if this is not possible, trials to find out polymorphisms in the sequence as close as possible to the target trait can be performed to get a reliable marker. In addition to establishing markers, a cross-aided method requires a vast supply of variable gene resources correlated to their degree of expression. Comparative genomics could provide the answer for analyzing the corresponding alleles in wild rice species.

Gene expression is highly influenced by the environment. Drastic changes in the environment such as global warming and water scarcity undoubtedly influence the growth of rice plants and finally rice yield. Recent advances in rice genomics offer new opportunities to enhance the efficiency of rice breeding strategies. The benefits of extensive genome research could be of great use to humanity if they could be used for sustainable production, thereby ensuring a stable world food supply. The challenge now is to develop viable strategies so that recent advances in genome research could be applied in actual breeding programs in order to generate rice varieties with higher yield potential, more nutritive value, and more resistance to biological and abiological stresses.

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Identifying Favorable Alleles in Host Defense Genes for Broad-Spectrum Resistance in Rice

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Broad-spectrum resistance (BSR) is generally considered more stable than disease resistance governed by major resistance genes. We have identified rice germplasm and mutants exhibiting resistance to multiple diseases or different races of a pathogen, providing the essential materials for understanding the genetic basis of BSR. There is also an extensive list of defense genes that are considered contributors to BSR. However, because of the relatively small effects of individual defense genes, validating their function and identifying useful alleles for breeding have proved difficult. We apply forward and reverse genetics as complementary approaches to identify candidate genes and validate their functions. Expression and gene-silencing experiments suggested that genes encoding oxalate oxidase–like proteins are important factors conferring BSR. We attempted to associate sequence variation of a collection of defense genes and blast resistance in Korean germplasm, though no clear pattern of association has emerged. To reveal new candidate genes, transcriptome analysis was conducted using well-characterized resistant genotypes. We detected discrete chromosomal regions where the expression of neighboring genes is significantly correlated. Such observations lead to the hypothesis that regions of correlated expression are related to the expression of quantitative resistance. If this is true, allelic composition of multiple genes in adjacent regions could be an important selection criterion for BSR.

Keywords: durable disease resistance, mutation, transcriptome, gene silencing, candidate defense genes, natural genetic variation, haplotypes

Defense genes that contribute to disease resistance are appealing for practical breeding because their effects are in general non-race- or non-pathogen-specific. These genes, if combined and expressed appropriately, can provide broad-spectrum resistance (BSR) against multiple pathogens, and would potentially be durable. Although accumulating defense genes for BSR is a sound strategy, it is difficult to identify and validate the functions of these genes because they are often encoded by multiple members of a gene family, and the phenotypic effects of individual genes are often small. We approach this problem by gathering convergent evidence based on QTL mapping, allelic variation of individual genes, and expression analysis. In this paper, we briefly present the approach of using a set of rice germplasm and mutants that exhibit BSR to blast or bacterial blight as a means to identify genes conferring BSR. Progress is made toward validating the function of selected candidate defense genes by gene silencing and mutational analysis. Whole-genome expression analysis also provides a new pool of candidate genes for further functional validation.

SPECIALIZED GENETIC STOCKS AND CANDIDATE GENES

A prerequisite to understanding the genetic basis of BSR is to identify genetic materials that exhibit the desired phenotype. Here we define broad-spectrum resistance as either resistance to multiple races of a pathogen or resistance to multiple pathogens. Through retrospective analysis of the agronomic performance of rice varieties in areas of high disease intensity, it is possible to identify varieties with a good "reputation" for having strong resistance in the field. One such variety is Shan-Huang-Zhan-2 (SHZ-2), an indica variety that was widely grown in the 1980s in southern China. SHZ-2 was cultivated over a large area for more than 10 years by farmers because the variety showed stable blast resistance as well as high yield. SHZ-2 was gradually replaced by new varieties with better grain quality but it remains prominent in the pedigrees of new varieties. Controlled inoculation experiments in China and in the Philippines with blast pathogen isolates also showed that SHZ-2 was resistant to >90% of the diverse isolates. Liu et al (2004) showed that disease resistance QTLs could be extracted from SHZ-2 and incorporated into new varieties.

The second source of BSR comes from systematic screening of mutants. In general, multiple-disease-resistant mutants can be grouped into two categories: those showing obvious lesion mimic phenotypes (e.g., the series of *sp*otted *l*eaf (*spl*) mutants) and those that do not have lesion mimics at least under normal growing conditions. A well-characterized lesion mimic mutant is *spl11*, which expresses enhanced resistance to multiple races of bacterial blight and blast pathogens. The wild-type gene *SPL11* encodes an E3 ubiquitine ligase, which acts as a negative regulator of host defense (Zeng et al 2004). From screening the collection of IR64 mutants (Wu et al 2005), we have identified another mutant (designated GR978) that exhibits resistance to blast and bacterial blight. But, unlike the *spl11* mutant, GR978 does not show lesion mimic under normal growing conditions, which makes this mutant particularly useful for identifying downstream genes conferring BSR.

Because of the large body of literature on disease resistance, information is abundant on the putative roles of candidate defense genes. Reverse genetics can be used for testing candidate genes in defense pathways. The completion of the rice genome (IRGSP 2005) provides the needed sequence information to extract allelic variants in natural germplasm as well as in mutants. Thus, reverse genetics is an excellent tool for validating gene function. The challenge is having the appropriate assay to detect subtle differences in resistance as well as their interactions with other genes.

VALIDATING THE FUNCTION OF CANDIDATE GENES AND ALLELES

Liu et al (2004) found a strong association of disease resistance QTLs with a cluster of genes encoding oxalate oxidase–like proteins on the short arm of chromosome 8. Of the 12 members of *OsOXL* (*Oryza sativa* oxalate oxidase–like) genes located in a 2.8-Mb region, 11 members are tightly linked within 80 kb and the twelfth member more distant from the centromere. These *OsOXL* genes are labeled from 1 to 12 based on their order on the chromosome.

A key question is whether the expression patterns of the *OsOXL* genes are causally related to the level of disease resistance observed in resistant and susceptible genotypes. We examined the differential expression of these *OsOXL* genes after pathogen inoculation or wounding in four genotypes—IR64, SHZ-2, LTH, and Azucena—that exhibit a range of resistance. SHZ-2 is the most resistant, whereas LTH is the most susceptible to blast. The time-course expression analysis suggested that six members are potential contributors to resistance, although the specific member varies with cultivar (Davidson et al, manuscript submitted). RNAi-mediated silencing of different *OsOXL* gene combinations revealed that the more genes that were suppressed, the more susceptible the plants were to blast, corroborating the results of expression analysis (Manoslava et al, manuscript in preparation). On the basis of the patterns of expression and effects of gene silencing, we concluded that *OsOXL3*, *6*, *7*, *8*, and 9 are potential contributors of resistance.

TILLING (Targeted Induced Local Lesion IN the Genome) is applied as a reverse genetics tool to identify target mutations (Bhat et al 2007, Raghavan et al 2006). From an EMS-induced population of IR64, we recovered five missense mutations in four oxalate oxidase genes. Based on a preliminary inoculation test, only one mutant (mutation in *OsOXL7*) appeared to show reduced resistance (Fig. 1). Because individual *OsOXL* genes are hypothesized to contribute only a portion of the overall resistance, any change in resistance must be measured quantitatively. More importantly, a cumulative measurement of disease severity over growth stages and time would be relevant. Backcross lines have been produced to enable replicated tests under field conditions.

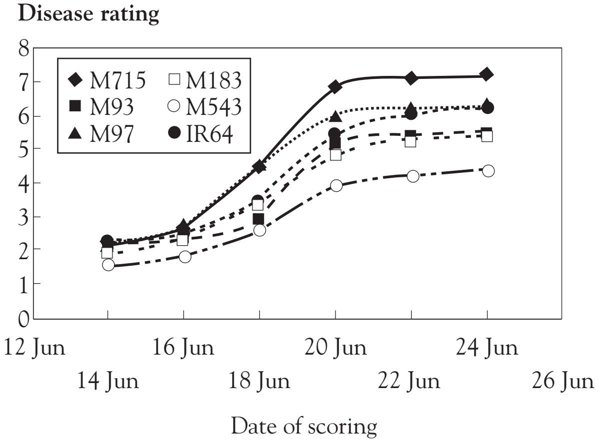

Fig. 1: Preliminary evaluation of five mutants with missense mutations in oxalate oxidase (*OsOXO*) and oxalate oxidase–like protein (*OxOXL*). Mutants were inoculated with isolate PO-6-6 in the greenhouse, and disease scored over a 14-day period. Only M715, which was identified as having a mutation in *OsOXL7*, appeared to become more susceptible relative to the parent IR64. These mutants were backcrossed to IR64 to remove background mutations and to confirm the inheritance of the SNP and phenotype. Confirmation of the phenotypic effect of the mutations will be obtained using BC_1F_3 lines.

ASSOCIATION ANALYSIS

If candidate defense genes play a role in resistance, one expectation would be an association between sequence variation (or unique sequence signatures) in candidate genes and quantitative disease resistance observed in germplasm. To test this hypothesis, we chose a collection of Korean rice germplasm with data on quantitative blast resistance. The Korean rice germplasm is particularly suitable for this experiment because it represents a relatively small but well-characterized set of germplasm used in blast resistance breeding. The lines have also been tested with multiple blast pathogen isolates in Korea and the Philippines.

We sequenced 11 candidate defense genes from 22 Korean and donor germplasm accessions for blast resistance (Table 1). These genes showed a modest level of single nucleotide polymorphism (SNP) in the 1-kb upstream and coding regions that defines the haplotype variation of each candidate gene locus. We observed some degree of association between the type/number of *cis*-elements and resistance in germplasm. For example, the *PR10* gene

Table 1: Variation in SNP haplotype at candidate gene loci for quantitative resistance to rice blast in Korean germplasm, donor parents, and breeding lines.

Germplasm	Degree of resistance to blast isolates[a]	Candidate gene (chromosome) haplotype[b, c]										
		OXO (3)	OXL (8)	ASP (7)	14-3-3 (2)	PR-1 (10)	PR10 (12)	HSP90 (6)	DHAP (6)	Thau (6)	Glyox1 (8)	ADH (11)
Palgong	R	B*	A	B	A	A	K*	A	A	A	A	A
Seomjin	R	A	A	C	A	A	A	A	A	A	B*	B*
Hwayoung	R	A	A	D*	A	A	B*	A	A	A	C*	C*
Donghae	R	A	A	B	A	A	A	A	A	A	C*	A
Milyang30	R	A	B	A	A	B*	G*	A	B	E	A	A
Suweon345	R	D*	C*	A	A	A	A	A	A	D	A	A
Zenith	R	A	A	A	A	A	C*	A	A	A	C*	A
GL33	R	E*	A	A	B	B*	A	A	A	B	D	A
Taebaek	R	A	D*	A	A	B*	A	A	A	A	A	D
Samgang	R	A	E*	A	A	A	A	A	B	G*	A	A
Sindongjin	R	A	A	A	A	A	A	B	A	A	A	A
Junam	R	F*	A	A	E	A	H*	A	A	A	A	A
Nampyoung	R	A	A	A	C	A	A	A	A	A	E*	A
Milyang23	R	A	A	A	A	C	E*	A	A	A	F	A
Milyang20	R	A	A	A	A	A	A	A	A	C*	A	C*
Suwon365	S	A	F*	E*	A	A	F*	A	A	F*	A	B*
Hwacheong	S	G*	A	A	A	D	A	C	A	A	G	A

Continuation on next page

Table 1 continued.

Germplasm	Degree of resistance to blast isolates[a]	Candidate gene (chromosome) haplotype[b, c]										
		OXO (3)	OXL (8)	ASP (7)	14-3-3 (2)	PR-1 (10)	PR10 (12)	HSP90 (6)	DHAP (6)	Thau (6)	Glyox1 (8)	ADH (11)
Giho	S	H*	A	A	A	E	A	A	C*	A	A	A
Nagdong	S	A	A	A	A	A	A	A	C*	A	G	A
Ilmibyeo	S	A	A	A	D	A	I*	A	A	A	C*	A
Ilpumbyeo	S	A	F*	A	A	A	J*	D	A	A	A	A
Dongjin	S	A	A	A	A	A	D*	A	A	A	A	A

[a] R = resistant to >50% of Korean blast isolates tested, S = susceptible to >50% of Korean blast isolates tested. [b] OXO (oxalate oxidase), OXL (oxalate oxidase–like protein), ASP (aspartyl protease), PR10 (probenazole-induced protein), HSP90 (heat shock protein), DHAP (putative 2-dehydro-3-deoxyphosphoheptonate aldolase), Thau (thaumatin), Glyox1 (glyoxylase 1), ADH (adenosyl homocysteinase). [c] A-K are SNP haplotype variants. A haplotype with * denotes SNP at the 1-kb upstream region; absence of * denotes SNP at the gene-coding region.

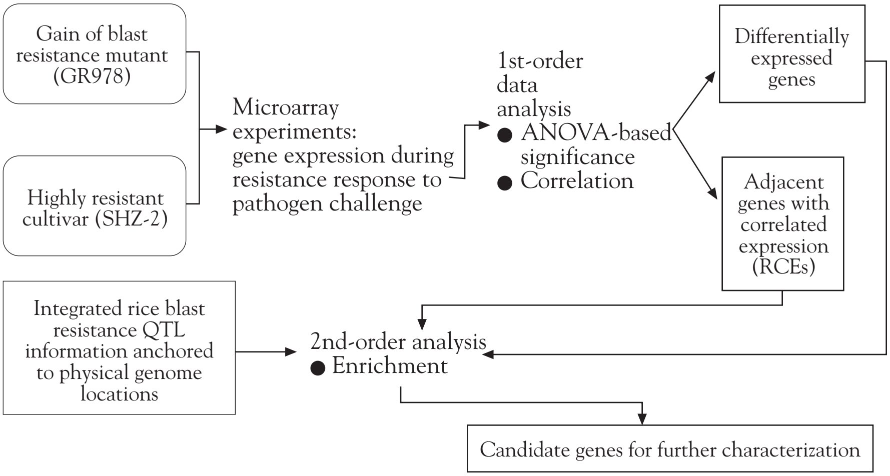

Fig. 2: Gene expression analysis of gain-of-resistance mutant GR978 and a resistant variety (SHZ-2) provides a data set for mining candidate genes important for broad-spectrum resistance. Genes that show differential expression patterns and correlated expression patterns are identified during the early stages of infection (24 and 48 hours after infection).

of Palgong, a resistant variety, has multiple copies of Wbox, WRKY, and ELRE in the promoter region. However, no conclusion can be drawn as any association needs to be validated using an unstructured germplasm collection or segregation analysis.

GENE EXPRESSION PATTERNS OF RESISTANT GERMPLASM AND MUTANTS

A limitation to using predicted defense genes is that we may miss unknown genes that are relevant to BSR. To identify additional candidate genes contributing to BSR, we analyzed the resistance transcriptomes of two genotypes that show resistance to blast. Figure 2 shows the workflow for generating expression data from GR978 and SHZ-2. Messenger RNA was isolated from leaves at 24 and 48 hours after pathogen infection and hybridized to the 22K oligoarray (Kikuchi et al 2007). In this analysis, we were particularly interested in expression patterns in the context of chromosomal position. We applied the genome scanning technique of Spellman and Rubin (2002) to identify regions of correlated expression (RCEs) using a moving window of 2 to 20 genes.

From the resistance transcriptomes of mutant GR978 and resistant variety SHZ-2, we identified nine groups of adjacent genes that showed correlated expression, with 18 to 20 genes in each group. The average size of the RCEs

Table 2: Ten genes within the overlapping region of correlated expression (RCE) in two resistant genotypes, SHZ2 and GR978, on chromosome 2.

Gene number	TGR4 LOC	Annotation
1	LOC_Os02g57180	NAD-dependent epimerase/dehydratase family protein, expressed
2	LOC_Os02g57200	Expressed protein
3	LOC_Os02g57220	Actin-related protein 2/3 complex subunit 1B, putative, expressed
4	LOC_Os02g57240	Voltage-gated potassium channel beta-1 subunit, putative, expressed
5	LOC_Os02g57250	Auxin-responsive protein IAA13, putative, expressed
6	LOC_Os02g57260	3-ketoacyl-CoA thiolase 2, peroxisomal precursor, putative, expressed
7	LOC_Os02g57290	Cytochrome P450 family protein, expressed
8	LOC_Os02g57310	Resistance protein, putative, expressed
9	LOC_Os02g57370	Zinc-finger DHHC domain containing protein 15 homolog, putative, expressed
10	LOC_Os02g57380	Thioredoxin-like 8, chloroplast precursor, putative, expressed

is approximately 620 kb, which is about six times larger than the correlated regions (100 kb) reported by Ma et al (2005) based on their transcriptome analysis using an oligoarray containing approximately 41,000 predicted rice genes. The use of a higher density array will probably provide a more accurate estimate of sizes of the RCEs.

An interesting observation from the comparative transcriptome analysis is the detection of the same RCE independently in two resistant genotypes. Table 2 shows the genes in two overlapping RCEs on chromosome 2. The genes in this "window" showed significant correlated expression in response to pathogen infection across experiments. Some genes in the RCE are known to be involved in stress response whereas others are not obviously considered stress response genes. Such an analysis provides a new pool of candidate genes for allele mining. We are evaluating the possibility that coordinated expression of multiple genes could be contributing a single QTL, a hypothesis with practical implications for selecting genotypes for effective resistance.

WHOLE-GENOME SNP DATA AS A FOUNDATION FOR IDENTIFYING FAVORABLE ALLELES

Through the International Rice Functional Genomics Consortium, we are generating genome-wide SNP data for diverse varieties to provide a foundation for genotype-phenotype association analysis of a large collection of germplasm (McNally et al 2006). The project involves partnership with Perlegen Sciences to apply tiling arrays to identify SNP in multiple rice genotypes relative to a reference genome. A collection of 20 diverse varieties/landraces, representing popular donor germplasm in breeding, will be investigated for genome-wide SNP. A pilot experiment has been conducted involving arrays containing 379 kb of unique sequences from a region of 684 kb on the long arm of chromosome 3. DNA obtained from 20 varieties was tested with the arrays. Perlegen finished the resequencing with 259,721 nonredundant SNPs predicted by model-based algorithms. These SNPs have been annotated relative to the TIGR release 5 and Rice Annotation Project release 1 gene models. Version 1 of the SNP annotation database was released to the public on 16 October 2007 via OryzaSNP project pages hosted on the International Rice Functional Genomics Consortium Web site (http://irfgc.irri.org). This public database will provide the foundation for association genetics and identification of alleles in the rich rice gene pool.

CONCLUSIONS

We have identified rice germplasm and mutants exhibiting BSR, which are essential materials for understanding the genetic basis of BSR. We have identified a set of defense genes and favorable allelic combinations based on converging evidence of QTL mapping, allelic variation of individual genes, expression analysis, and gene silencing. The use of different kinds of genetic resources and experimental evidence appears essential for validating the roles of defense genes with small but important effects. A SNP database is being developed as a platform for finding new genes and alleles. New candidate genes can be identified by transcriptome analysis. Unlike qualitative resistance where a major gene often confers a clear-cut phenotype, quantitative resistance could be mediated by different alleles of multiple loci. The *OsOXL* gene family may provide a case to test whether allelic composition across multiple genes is important in conferring the target phenotype.

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Comparative Analysis of Rice and Wheat Genomes as a Tool for Gene Discovery

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Complete genome sequences of model species such as rice and *Arabidopsis* are being compared with those of other plant species largely based on the available expressed sequence tag (EST) information. Apart from the evolutionary significance, such studies are important for gene discovery and genetic improvement of crop plants. Early comparison of rice genome sequences with those of bread wheat showed complex patterns of synteny (gene content) and colinearity (gene order). The large-size wheat genome appears to have evolved through extensive duplication and divergence of genes and noncoding repetitive sequences. These duplications and rearrangements pose a real problem in the analysis of synteny and colinearity, which is required for the transfer of information from model species to other economically important crop species. We found presence of the same ancient polyploidy in wheat that was first identified by the computational analysis of rice genome sequences. We also found that single-copy rice genes have a much higher conservation of synteny and colinearity with wheat than multicopy genes. A large proportion of the single-copy rice genes is still distributed randomly to all the nonsyntenic wheat groups and this could be explained only by a background dispersal of genes in the genome through transposition. The breakdown of rice-wheat synteny was much greater near wheat centromeres, suggesting wheat-specific transposition activity. The single-copy rice genes reveal a conserved primordial gene order that gives clues to the origin of rice and wheat from a common ancestor through polyploidy and aneuploidy followed by chromosome fusions. On the basis of conserved colinearity of 1,244 mapped single-copy rice genes, we predicted the location of 6,178 unmapped single-copy rice gene homologs in the wheat genome and experimentally validated the location of a random set of 213 of these. More than 50% of the single-copy genes do not have any known protein functional domains, and hence represent an important but yet underexplored category of genes.

Genome sequencing has added a new dimension to our understanding of evolution in plant species. But so far, only two plant genomes, *Arabidopsis* and rice, have been sequenced to completion (AGI 2000, Goff et al 2002, Yu et al 2002, 2005, IRGSP 2005). Comparisons with other plant species are based largely on the available genetic and expressed sequence tag (EST) information (Fulton et al 2002, Vandepoele et al 2003, Bowers et al 2003, Sorrells et al 2003, Paterson et al 2004). Such comparative studies are important for the practical use of the knowledge of genomics (Appels et al 2003, Gill et al 2004, Sasaki et al 2005). Large genomes appear to have evolved through extensive duplication and divergence of genes and noncoding repetitive sequences (Lynch and Conery 2000). Duplications are present in all genomes as tandem arrays of individual genes and chromosome segmental duplications resulting from aneuploidy and polyploidy (Ohno 1970, AGI 2000, Paterson et al 2004, Cannon et al 2004, Yu et al 2005). Transposition of DNA segments to multiple locations in the genome is another common mode of duplication (Bennetzen 2000).

Duplications and rearrangements pose a real challenge in the analysis of gene synteny and colinearity, which is required for the transfer of genome information from model species to other economically important crop species. Except for the well-established colinearity among the closely related members of tribe Triticeae (wheat, barley, and rye) and that between rice and sorghum (Paterson et al 2004, Devos et al 2005), previous studies have shown definite but limited conservation of gene order among rice, maize, and wheat (Song et al 1995, La Rota and Sorrells 2004, Singh et al 2004, Munkvold et al 2004, Gustafson et al 2004). A sequence-based approach has also been used by the TIGR (www.tigr.org/tdb/e2k1/tae1/wheat_synteny.shtml) and Gramene (www.gramene.org/) for rice-wheat synteny. Here, we review the results of our study on filtering out the noise due to genome-wide duplications on rice-wheat synteny and colinearity.

RICE GENE PREDICTION AND FUNCTION ANNOTATION

The sequences of 3,343 BAC/PAC clones in the minimum tiling path of 12 rice chromosomes were downloaded using the "Batch Entrez" tool of NCBI (www.ncbi.nlm.nih.gov) in August 2003. Each clone was checked for its orientation with respect to its neighbors and incorrect orientations were corrected by reverse complementation to bring all the BAC/PAC sequences into a uniform north-south orientation. Gene prediction was performed on individual BAC/PAC clones using FGENESH (www.softberry.com) for monocots (Salamov and Solovyev 2000), and gene information including cDNA sequences (CDS) and protein sequence was extracted in a separate set of files using an in-house Perl script "fgenex" (unpublished). The predicted CDS were used for mega BLASTX search (Altschul et al 1997) with an nr-protein database to check for similarity with known proteins (www.genome.

ad.jp). The mega BLASTX output was saved in text format to serve as an input for another Perl script "annotate" (unpublished), to automatically classify these genes into three functional categories: exact/putative, unknown, and hypothetical, as per the International Rice Genome Sequencing Project (IRGSP) guidelines (www.rgp.dna.affrc.go.jp). The overlap between neighboring BAC/PAC clones was removed manually. Each gene from the 12 rice chromosomes was assigned a unique number to indicate its chromosomal location and relative position, for example, gene numbers 01-0001 to 01-6737 were assigned to the 6,737 genes predicted for rice chromosome 1 according to their physical order in the chromosome beginning from the short arm end. The database is available at www.nrcpb.org/rgp/VanshanuDhan.html.

HOMOLOGY BETWEEN RICE AND WHEAT GENES

A total of 56,298 genes were predicted and predicted CDS of these genes were compared against 39,813 wheat EST contigs developed by the international wheat SNP mapping consortium (build 3, Dec. 2002, http://wheat.pw.usda.gov/ITMI/2002/WheatSNP), using an optimized set of search parameters (Singh et al 2004). All the rice CDS showing matches with the wheat EST contigs at a cutoff bit score of 100 were considered significant, and the output was tabulated on Excel sheets using an in-house Perl script "mblastex" (unpublished). In addition, the 56,298 rice CDS were also compared with a database of 3,792 wheat EST contigs (ver. Aug. 2003) containing bin-mapped ESTs (http://wheat.pw.usda.gov). An AQL query, "aql_retrieve" (unpublished), was used to extract the bin information and other details for these contigs directly from the GrainGenes database of bin-mapped wheat ESTs. This information was used as a base to calculate different statistics regarding the conservation of gene synteny between rice and wheat at different cutoff bit scores and to find out the rice gene copy numbers by sorting and filtering tools in Microsoft Excel. The location of each rice gene homolog was plotted onto the 21 wheat chromosomes and their bins using a combination of automated and manual steps and cross-checked at least three times by different individuals (Singh et al 2006).

An optimized BLAST search of the CDS of 56,298 rice genes with the consensus sequences of 39,813 wheat EST contigs showed 24,209 matches at a cutoff bit score of 100. A further search against 3,792 bin-mapped wheat EST contigs revealed that 8,834 rice genes matched with bin-mapped wheat EST contigs. Genes from each of the 12 rice chromosomes mapped predominantly to a syntenic wheat group (Table 1). The proportion of rice genes mapping to the syntenic wheat groups increased from the 28.4% at a 100 cutoff bit score, to 33.9% and 38.2% at cutoff bit scores of 200 and 300, respectively, but the total number of matches dropped concomitantly from 8,834 to 5,840 and 4,238, respectively. Therefore, an intermediate cutoff bit score of 200 was used as a compromise between the need for higher stringency

Table 1: Genome-wide analysis of homology between 56,298 rice genes predicted from the IRGSP sequence build 3 and 39,813 wheat EST contigs (international wheat SNP consortium, build 3) and 3,792 bin-mapped wheat EST contigs (USDA-NSF wheat genome project, version Aug. 2003), at a cutoff bit score of 200.

	All rice genes			Single-copy rice genes			
Rice chromosome	Total no. of genes	No. (%) mapping to syntenic wheat groups	Syntenic wheat group	Total no. of genes	No. mapped in wheat	No. (%) mapping to unique wheat groups	No. (%) mapping to syntenic wheat groups
1	6,737	391 (44.9)	3	1,152	192	173 (90.1)	137 (71.0)
2	5,501	228 (33.8)	6	929	155	131 (84.5)	94 (60.6)
3	5,590	207 (26.6)	4[a]	1,091	216	173 (80.1)	106 (47.1)
4	5,383	215 (41.3)	2	707	103	82 (80.7)	69 (66.9)
5	4,482	161 (31.2)	1	608	105	93 (88.5)	63 (60.0)
6	4,871	159 (34.5)	7	580	88	74 (84.1)	56 (63.6)
7	4,594	135 (30.0)	2	592	91	79 (86.8)	46 (50.5)
8	4,352	93 (26.3)	7	492	81	68 (83.9)	42 (51.8)
9	3,624	101 (33.3)	5	377	45	42 (93.3)	24 (53.3)
10	3,122	105 (33.8)	1	313	56	52 (92.8)	31 (55.4)
11	3,945	85 (29.4)	4	278	49	38 (77.5)	21 (42.0)
12	4,097	103 (32.1)	5	331	63	58 (92.0)	42 (66.7)
Total	56,298	1,983 (33.9)		7,450	1,244	1,063 (85.4)	731 (58.7)

[a] Part of rice chromosome 3 is syntenic to wheat group 5.

and allowing for retention of distant matches between rice and wheat genes for further analysis.

A graphical depiction of the location of each of the 5,840 rice gene homologs onto 21 wheat chromosomes revealed many interesting patterns of rice-wheat synteny (Fig. 1). We compared individual rice genes against a set of presumably nonredundant wheat EST contigs, and hence did not expect more than one match for a single rice gene. However, more than one rice gene may hit the same wheat contig due to the presence of gene duplications in the rice genome. Thus, 5,840 rice genes matched with only 1,896 wheat contigs, as quite often the same wheat EST contig did match with two or more rice genes. Since these matches were at a very high stringency (bit scores of 200 or above and E values of 10^{-40} or less), this reflected the existence of extensive gene duplications in the rice genome. The multiple rice genes matching with the same wheat EST contig were quite often located consecutively in a rice chromosome, indicating tandem gene duplications.

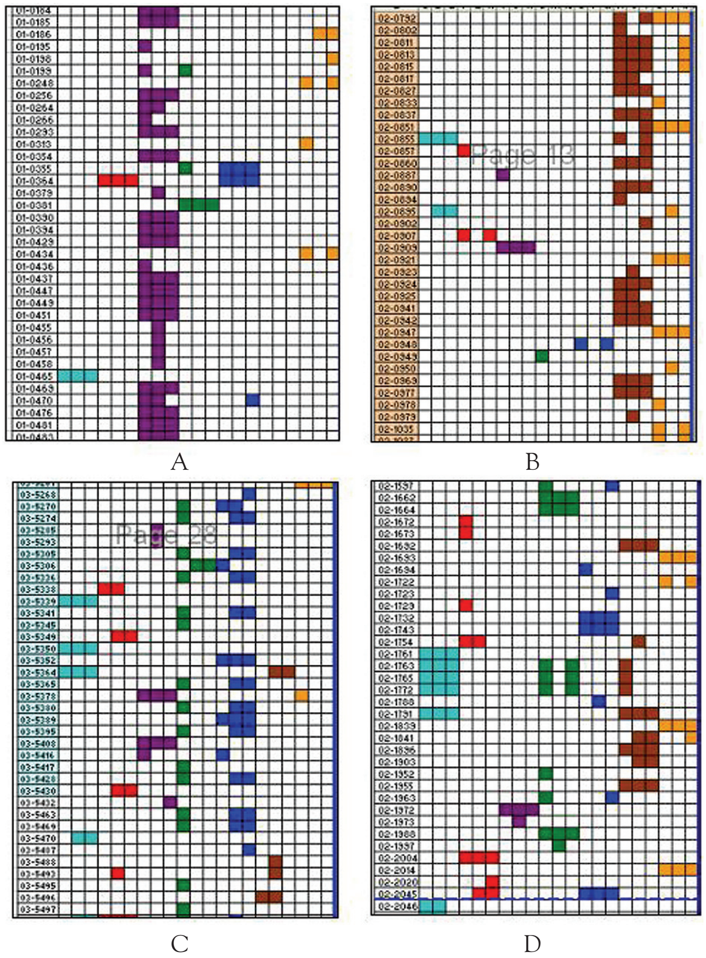

Fig.1: Screen shots from homology plots showing the location of wheat EST homologs of physically ordered rice genes (shown in the extreme left column) on 21 wheat chromosomes (1A, 1B, 1D, … up to 7D, from left to right). To create this map, the individual cells on an Excel sheet were color-filled whenever a rice gene matched with bin-mapped wheat EST, at a bit score of 200 or higher (see Singh et al 2006 for details). Seven wheat groups are color-coded to visualize the syntenic relationship between individual rice chromosomes and wheat chromosomes. Rice genes are numbered consecutively according to their physical order in the rice chromosome, beginning from the short arm end. (A) A region from rice chromosome 1, showing synteny with wheat group 3 (purple color), with significant dispersal of genes to another six nonsyntenic wheat groups. (B) A region of rice chromosome 2 corresponding to the ancient polyploidy-related duplication (orange shade), showing synteny with two different wheat groups, group 6 (main synteny) and group 7 (duplicate synteny). (C) A region of rice chromosome 3 matching with 4A (instead of 5A), 5B, and 5D, indicating translocation between 4A and 5A. (D) A part of rice chromosome 2 lacking synteny with any specific wheat group.

The homology plot showed that 79.7% of the 5,840 rice genes mapped to unique wheat groups, but only 33.9% of the genes mapped to the respective syntenic wheat groups (Table 1). In all, four distinct patterns of synteny were observed. The first pattern showed a majority of the rice genes mapping to a syntenic wheat group, while the remaining genes were distributed over all the six nonsyntenic wheat groups (Fig. 1A). The second pattern was typical of the regions of rice chromosomes involved in an ancient polyploidy where two-thirds of the rice genes were located on just two wheat groups (dual synteny) and one-third were distributed on the remaining five wheat groups (Fig. 1B). The third pattern clearly identified chromosomal translocations within the specific wheat genomes and therefore must have occurred after the divergence of wheat from rice (Fig. 1C). The fourth pattern represented regions of the rice genome that did not show synteny with any wheat group (Fig. 1D).

EVIDENCE FOR ANCIENT POLYPLOIDY IN RICE AND WHEAT GENOMES

Paterson et al (2004) identified large segmental duplications covering 62% of the transcriptome predicted from the genome sequence of japonica rice variety Nipponbare (IRGSP 2005). These duplications were also found in the genome of indica rice line 93-11 (Yu et al 2005) and their origin has been dated to a time about 70 million years ago, well before the divergence of rice and wheat, and they are thought to have resulted from an ancient polyploidy in the ancestral grass genome (Paterson et al 2004). Much earlier, Nandi (1936) concluded that *Oryza sativa* is a balanced allopolyploid originating from an ancestral grass species with basic chromosome number five. Since rice and wheat diverged from a common ancestor long after this event, the signs of ancient polyploidy must be present in the wheat genome also. Segmental duplications corresponding to this ancient polyploidy were clearly visible in our rice-wheat homology plot showing the location of all the 5,840 rice gene homologs in wheat. The rice chromosome segments corresponding to ancient duplication showed a high number of gene matches with two different wheat groups (dual synteny), which was at the same time consistent with the pattern of rice-wheat synteny for the individual rice chromosomes (Fig. 1B). A pattern of duplication and postduplication conservation of lineages between rice and wheat was present for all the large segmental duplications in the rice genome (Singh et al 2006). In the ancient duplicated segments, 64% of all rice gene homologs (2,339 out of 3,651 genes) were mapped in the two syntenic wheat chromosome groups, while the remaining 36% of the genes were distributed over five nonsyntenic wheat groups (Singh et al 2006). This provides independent evidence, in addition to the high K values of the duplicated gene pairs in rice, that the origin of these segmental duplications must predate the divergence of rice and wheat. Subsequent diploidization of these duplications in wheat was evident from the fact that 96% of the mapped rice gene homologs in these regions were present in only one of the two syntenic wheat groups. The existence of ancient polyploidy in the rice genome has been a subject of debate (Moore et al 1995, Vandepoele et al 2003, Paterson et al 2004) but it is consistent with our observations showing corresponding duplications in the wheat genome also in the form of dual synteny patterns (Singh et al 2006).

SINGLE-COPY RICE GENES SHOW CONSERVED SYNTENY AND COLINEARITY WITH WHEAT

Rice genes showing unique matches with wheat EST contigs were identified as single-copy (SC) genes. Two or more rice genes matching with a single wheat contig represented duplicated multicopy (MC) rice genes. La Rota and Sorrells (2004) used single-bin wheat genes for the synteny analysis but these were not necessarily SC genes. This is possible from the rice side only after the availability of complete genome sequence information. Frequency distribution of the copy number of genes in a genome follows a power law equation due to inherent control on the amplification of gene copies (Huynen and van Nimwegen 1998, Cannon et al 2004). In a power law distribution, as the number of genes in a gene family increases, the frequency of such gene families in the genome will decrease. The frequency distribution of genes with different copy numbers among the 4,659 rice genes mapping to unique wheat groups was consistent with this pattern. The highest frequency of 1,063 was for the SC genes, and there was a stepwise reduction in the frequency of genes with higher copy numbers. While only 27.2% of the MC genes mapped to their syntenic wheat groups, the proportion more than doubled to 58.7% for the SC rice genes, showing striking conservation of synteny of the SC genes.

With SC rice genes, each of the 12 rice chromosomes showed synteny with only one wheat group, except for rice chromosome 11, which showed a significantly high number of matches with wheat groups 4 and 5. This appeared to be due to an exchange of segments between wheat groups 4 and 5 in the region corresponding to the long arm of rice chromosome 3 (Singh et al 2006). This exchange was common to all the three wheat genomes and therefore must have occurred quite early in the progenitor of the A, B, and D genomes of wheat. There was random distribution of a large number of gene homologs from each rice chromosome to all the nonsyntenic wheat groups. A plausible explanation for this is background movement of genes in the genome through infrequent transposition or ectopic recombination (Bennetzen 2000, Goldman and Litchen 2000). The role of transposition in the breakdown of synteny was further highlighted by disproportionately high movement of genes near the wheat centromeres from a syntenic wheat group to nearly all the nonsyntenic wheat groups (Fig. 2). The breaks in

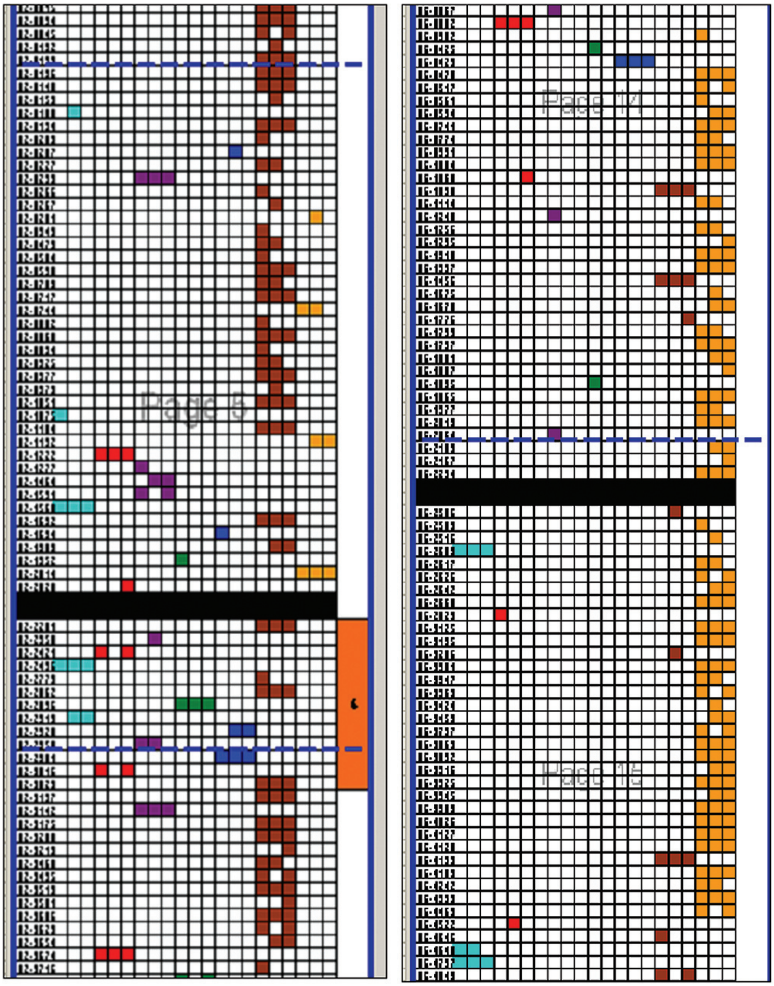

Fig. 2: Highly conserved synteny of rice and wheat chromosomes based on single-copy rice genes: (A) between rice chromosome 2 and wheat group 6 showing transposition of genes to nonsyntenic wheat chromosomes near rice (black shade) and wheat (orange shade) centromeres; (B) between rice chromosome 6 and wheat group 7 with no transposition of genes in the absence of association with a wheat centromere.

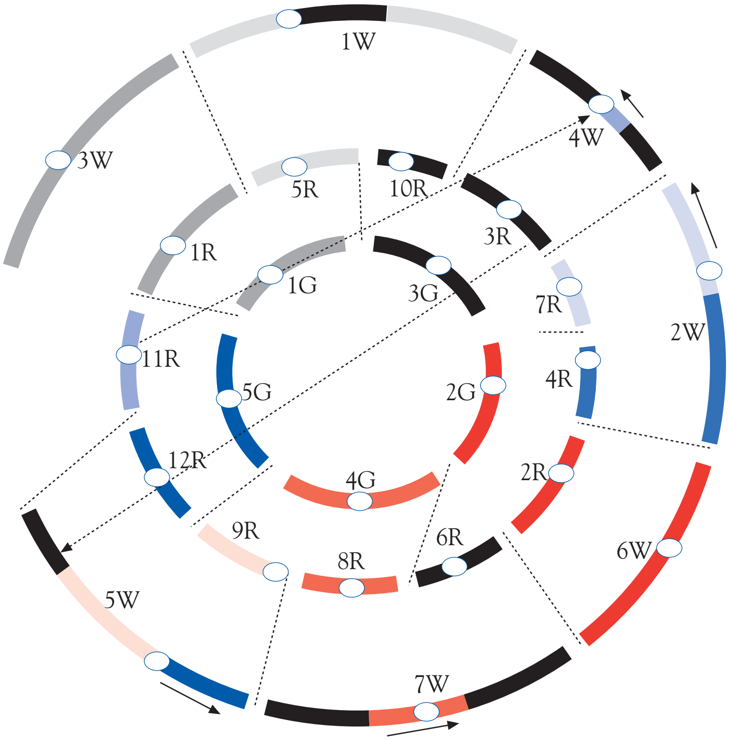

Fig. 3: Origin of rice and wheat chromosomes from a common grass ancestor with five pairs of chromosomes (1G to 5G, central circle). Polyploidy and aneuploidy events about 70 million years ago resulted in 12 pairs of chromosomes (5 + 5 + 2) in rice (1R to 12R, middle circle). Rice and wheat shared a long common lineage before the evolution of diploid wheat by fusions between two or three of the 12 chromosomes, thus reducing the number to seven pairs (1W to 7W, outer circle). Circles are drawn based on observed colinearity of single-copy rice genes with seven wheat groups. Orientation of the chromosomes in the three circles is clockwise beginning from the short arm ends. Reverse orientation of four wheat chromosome segments with respect to their rice counterparts is indicated by arrows on the wheat circle.

synteny due to transposition were associated with the wheat centromeres rather than rice centromeres (Singh et al 2006). Wheat chromosomes have a large amount of repetitive sequences near their centromere and a detailed characterization of these may elucidate the exact mechanism of transposition (Li et al 2004).

Based on the conserved colinearity of SC rice genes across the wheat bins, we reconstructed how the karyotypes of rice and wheat relate to a common ancestral karyotype (Fig. 3). Nandi (1936) concluded from his detailed study of several hundred prophase I nuclei that both aneuploidy (two separate duplications of individual rice chromosomes) and polyploidy (created by hybridization between two related species) have contributed to the origin of *Oryza sativa*, and he suggested a haploid chromosome formula for rice as AA_1A_1, BB_1B_1, CC_1, DD_1, EE_1. The simplest explanation as to how multiple ancestral chromosomes of rice are arranged in a single wheat chromosome group is by fusion of the ancestral chromosomes leading to the evolution of larger-size wheat chromosomes. The presence of seven basic chromosomes in wheat compared with 12 in rice could be explained by two centromeric fusions in wheat groups 1 and 4, and seven translocations, one each in wheat groups 1, 2, and 4, and two each in wheat groups 5 and 7 (Fig. 3). It is well known that the failure of meiotic chromosome pairing in the interspecific hybrids (polyhaploids) leads to chromosome breakage and fusion. Cereals with divergent basic chromosome numbers, for example, 7 in wheat, barley, and rye; 10 in sorghum, maize, and sugarcane; and 12 in rice, could have originated in such polyhaploid(s). Such chromosomal rearrangements were seen in synthetic polyploids of mustard and wheat (Song et al 1995, Ozkan et al 2001). Although the outcome of synteny studies may be influenced by the choice of genes (Gaut 2002), our conclusions are based on a comprehensive analysis of all genes rather than a selected set of genes (Singh et al 2006).

PREDICTING THE LOCATION OF WHEAT GENES USING RICE GENOME INFORMATION

High-resolution molecular maps are an essential resource for structural and functional genomics in crop plants. Assignment of a large number of ESTs to specific wheat chromosome bins will reduce the time and cost of developing high-resolution maps (Gill et al 2004, Qi et al 2004). Based on the conserved colinearity of 1,063 SC mapped rice genes, we predicted the wheat bin location of 6,178 unmapped SC rice gene homologs (Singh et al 2006). To validate these predictions, we designed forward and reverse PCR primers for a set of 213 wheat EST contigs predicted to map in the telomeric bins of 21 wheat chromosomes, and used genomic DNA of Chinese spring wheat and its telomeric segmental deletion lines for our validation studies. Forward and reverse primer pairs were designed using Primer 3 software (http://frodo.wi.mit.edu) from consensus sequences of the 213 wheat EST contigs predicted to map in the telomeric bins of 21 wheat chromosomes, and 164 of these amplified DNA fragments in the expected size range. Sixty-nine of these amplified a single-size DNA band but, in 49 of these instances, the single-size amplified band could not be assigned to the predicted wheat bin, probably because of lack of polymorphism or in some cases because of their location on nonsyntenic wheat chromosomes. Nonetheless, 58 genes (35.4% of the amplified genes) were located in the predicted telomeric bins of the seven wheat chromosome groups (Singh et al 2006). This is a conservative estimate, as more primers are likely to be validated at their predicted locations using

CAPS (cleaved amplified polymorphic segments) and SNP (single nucleotide polymorphism) genotyping of the single monomorphic-size PCR bands. Only 1,244 of the 7,540 SC rice gene homologs are bin-mapped in wheat.

RICE AND WHEAT SHARED A LONG COMMON LINEAGE AFTER ANCIENT POLYPLOIDY

The coding sequencese of a random set of orthologous pairs of rice-wheat genes, at cutoff bit scores of 200–400, 401–600, 601–800, 801–1,000 and more than 1,000, were extracted. A total of 116 representative gene pairs, including 22–24 genes for each of the five bit score intervals and 8–10 genes from each of the 12 rice chromosome, were aligned using ClustalW in MEGA3 software (Kumar et al 2004). The meg files were then analyzed using DnaSP 4.0 software (www.ub.es/dnasp/) for synonymous (Ks) and nonsynonymous (Ka) substitution rates. We plotted the frequency distribution of Ks values for the 116 gene pairs to see if the bit score cutoff has any influence on the Ks values. The mean Ks values were indeed lower for the highly conserved gene pairs with higher bit scores but the modal Ks values were not much affected by the cutoff bit scores (Fig. 4), and hence provide a better criterion for the phylogenetic dating of duplication events (Paterson et al 2004). The modal Ks values for the 116 syntenic SC rice genes and their wheat orthologs were in the range of 0.2 to 0.3, giving an estimated time of divergence for rice and wheat from 15 to 23 million years ago using the molecular clock of Muse (2000). This is consistent with the idea that the common ancestor of present-day rice and wheat must have followed a common lineage for a long time, somewhere in the range of 20 to 50 million years.

MOLECULAR FUNCTIONS OF THE SINGLE-COPY GENES

Based on the presence of homologous protein functional domains identified by BLASTX search, we classified the SC rice gene homologs of wheat ESTs into two categories: (1) with exact/putative function and (2) with unknown functions. Significantly, 50.2% of the bin-mapped SC rice genes have unknown function compared with only 29.4% of all bin-mapped MC genes with unknown function. The proportion of genes with unknown function was still higher (54.0%) in the unmapped SC rice genes. Thus, the SC genes have lagged behind in both mapping and characterization of their functions, probably because of their poor representation in the mRNA populations. The conserved sequence and single-copy constitution of these genes point toward their vital role in plant biology, which was also supported by the annotated function of these genes (Table 2). The SC rice genes have maintained their single-copy status despite the prevailing forces of gene duplication, including tandem duplication, background duplication, and polyploidy (Yu et al 2005). More than 85% of the SC rice genes mapped

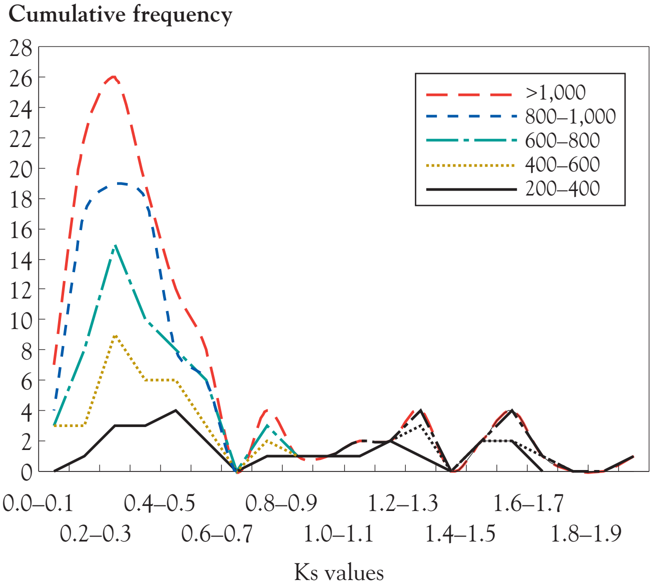

Fig. 4: Cumulative frequency distribution of Ks values for rates of synonymous nucleotide substitutions among 116 randomly selected single-copy rice genes and their wheat homolog pairs, representing all the 21 wheat and 12 rice chromosomes. Rice-wheat gene pairs matching with increasing bit score values are shown in different-color line graphs. The modal Ks values fell in the range of 0.2 to 0.3, indicating divergence of rice and wheat from a common progenitor about 15–23 million years ago.

to unique wheat groups, indicating that duplicate copies resulting from the ancient polyploidy have largely been deleted or diverged beyond recognition in the wheat genomes. More than one-third of the expected triplicate sets of the 1,063 SC rice gene homologs (3,189 genes for the three genomes of bread wheat) have already been eliminated or diverged beyond recognition. Bread wheat has only 2,149 homologs of the SC rice genes, including duplicates and triplicates. A rapid mechanism for the elimination of duplicated loci has been described in synthetic wheat polyploids (Ozkan et al 2001), but other duplicates may take longer for elimination, or may even be tolerated and evolve new functions (Lynch and Conery 2000). Single-copy genes are present in almost all the sequenced genomes despite the increasing evidence that most of the higher species have evolved by duplication and divergence of genes and genome (Dietrich et al 2004). The inferred deletions of SC rice gene homologs in wheat need not have occurred after the formation of polyploid wheat and many of these could have occurred during independent

Table 2: A partial list of highly conserved rice-wheat orthologs of known exact or putative functions, matching with bit score values of 1,000 or higher, and bin-mapped in wheat. Discovery of the function of these genes and their association with agronomic traits in any one species will facilitate their use in another.

Rice gene ID	Molecular function	Wheat contig ID	Bit score
01-2966	Putative heme A farnesyltransferase	16686	1,080
01-4041	Malate dehydrogenase–*Oryza sativa*	18245	1,225
01-6009	Putative signal recognition particle 72 kD	16180	1,466
01-6217	Putative selenium binding protein	18102	1,703
02-34	Ferredoxin-NADP(H)	17968	1,073
02-598	Thiosulfate transferase	15535	1,008
02-1694	Dipeptidyl peptidase IV-like protein	11718	1,144
02-3747	Succinyl-CoA ligase GDP-forming	18522	1,632
03-584	Putative male sterility protein	18118	1,317
03-1281	Beta-galactosidase (EC 3.2.1.23)	17611	1,366
03-1624	Malonyl-CoA:ACP transacylase	13019	1,000
03-2073	Beta-adaptin homolog F8L21.170–*Arabidopsis*	17393	1,627
03-5528	Putative zinc finger protein	17075	1,331
04-45	Arginase (EC 3.5.3.1)	17135	1,214
04-2718	Initiation factor–*Arabidopsis thaliana*	18154	1,247
04-3522	Putative leucine-rich protein	16284	1,431
05-958	2-oxoglutarate/malate translocator	18719	1,047
05-4275	Malate dehydrogenase–*Oryza sativa*	17475	1,201
05-4368	Mitochondrial solute carrier protein homolog	18229	1,248
06-82	Ferredoxin–NADP reductase, leaf isozyme	16485	1,065
06-1310	TF-like protein (fragment)	5897	1,190
06-3424	T complex protein–*Cucumis sativus*	18326	1,941
07-2968	Putative ATP synthase gamma-subunit	17203	1,225
07-3592	Transporter-related-like	17184	1,096
07-4155	Putative NADH dehydrogenase	18648	1,925
08-910	GTP-binding protein	16993	1,356
08-3737	Aminotransferase 1	18199	1,513
08-4242	Peroxisome biogenesis protein PEX1	4849	1,073
09-1576	Cysteine desulfurase, mitochondrial precursor	9841	1,302
09-2478	Aldehyde dehydrogenase	18493	1,678
09-2630	ARP protein–*Arabidopsis thaliana*	16640	1,363
10-2457	Putative glutamyl-tRNA reductase	16934	1,814
10-2572	Putative electron transfer oxidoreductase	15663	1,296
10-2582	Putative gamma-lyase	15531	1,077
11-1233	Chlorophyll a/b-binding protein CP26 precursor	18125	1,069
11-1939	Protein transport protein Sec23	15637	1,291
11-2313	Similarity to enolase-phosphatase	17902	1,524
12-2991	2-oxoglutarate/malate translocator-like protein	8584	1,012
12-3407	Replication licensing factor MCM7 homolog	17513	1,887
12-3955	Methionine synthase protein	18820	2,299

evolution of the diploid progenitor genomes of bread wheat over a period of 2.5 to 7 million years ago (Devos et al 2005).

Tandem duplication of genes (a kind of paralog) is much more frequent than segmental duplication. For example, tandem duplications have played a key role in the rapid divergence of rice disease resistance genes (The Rice Chromosomes 11 and 12 Sequencing Consortia 2005). The tandem-duplicated copies of genes are likely to evolve the fastest, as this represents a more fundamental feature of all the sequenced genomes and is also present within the large duplicated segments of the chromosomes. The orthology must have its origin in the duplication of chromosome segments by translocation, aneuploidy, or polyploidy, whereas transpositions are responsible for moving the individual genes from their orthologous positions (ancestral gene context) to new paralogous positions. After their divergence from a common ancestor, the daughter species are likely to retain the orthologous set of genes in the same order (colinearity), depending on the duration of their separation or adaptation to specific ecological niches, which may lead to loss of colinearity.

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Hybrid Rice in the Tropics: Where Do We Go from Here?

Sant S. Virmani

Following the success of hybrid rice in China and considering the urgent need to increase rice production and productivity, the International Rice Research Institute (IRRI) was encouraged in 1979 to lead the development and dissemination of hybrid rice technology in the tropics. Currently, about 2 million hectares are planted with hybrid rice varieties, primarily under irrigated conditions in India, Vietnam, the Philippines, Bangladesh, Myanmar, and Indonesia, resulting in a yield advantage of 1–1.5 t ha^{-1} over inbred high-yielding varieties. This has encouraged the participation of the seed industry in public, private, NGO, and farmers' cooperative sectors. Experimental evidence has been generated that indicates a proportionately higher yield advantage of rice hybrids over inbred rice under certain unfavorable rice ecosystems having moderate drought, salinity, submergence, etc. The cytoplasmic male sterility system has been primarily used to develop rice hybrids. The future of hybrid rice in the tropics is even brighter. This paper highlights future opportunities for the development of better technology and its faster dissemination.

Rice yields per unit area and per unit time must increase to meet the growing rice demand due to increased population and decreasing land and water availability for rice production as competing opportunities emerge for economic development, including for rice farmers. Since the 1980s, the International Rice Research Institute (IRRI) has been providing leadership to develop hybrid rice technology in the tropics following the success of the Chinese experience in developing and commercializing this technology since the 1970s. Currently, China cultivates about 15 million ha (50% of its rice land) with hybrid rice varieties that yield about 1.5 t ha^{-1} more than the high-yielding inbred rice varieties (HYVs) that average about 5.5 t ha^{-1}. This provides about 22.5 million tons of extra paddy annually to China (valued at US$4.5 billion) and saves the country about 4 million ha of rice land and 2.4 billion cubic meters of water. In collaboration with IRRI and China, several other countries (India, Vietnam, the Philippines, Bangladesh, Myanmar, and Indonesia) have developed and commercialized

Table 1: Area covered by hybrid rice varieties in selected tropical countries (2006).

Country	Hybrid rice area (ha)
India	800,000
Vietnam	600,000
Philippines	325,000
Bangladesh	100,000
Myanmar	45,000
Indonesia	40,000

hybrid rice technology during the past 12 years (Table 1). Currently, about 2 million ha of rice land are covered in these countries using several public and private hybrid rice varieties (Table 2) that outyield inbred HYVs by 1–1.5 t ha^{-1} and result in increased farmer profitability of about \$90 ha^{-1}. The increased paddy production due to rice hybrids is estimated to be about 2–2.5 million t (worth about \$400–500 million). The associated hybrid seed production technology, primarily involving the cytoplasmic male sterility system, has led to the development of a hybrid rice seed industry in the public, private, and NGO sectors. This has helped increase rural employment opportunities and international trade in hybrid rice seeds. This paper highlights some future opportunities for developing and disseminating hybrid rice technology in the tropics.

FURTHER INCREASES IN RICE YIELD

Experimental evidence at IRRI (Khush et al 1998) had indicated that heterosis in rice could be enhanced further in the tropics by using crosses involving indica, tropical japonica, or indica-tropical japonica derivative lines. Using such lines, Chinese scientists have already developed and commercialized super rice hybrids (Yuan 2003). With the availability of molecular tools, it should be possible to identify heterotic gene blocks in rice. The selective deployment of these through parental lines would also help to enhance rice heterosis. With the use of various genetically diverse introgression lines developed through the wide hybridization program at IRRI and NERICA lines from WARDA (The Africa Rice Center), as one of the parents, it should also be possible to enhance heterosis beyond the current levels. The extent of DNA methylation has been found to be lower in hybrid rice than in inbred maize (Tsaftaris and Polidoros 1993, Stuber 1999). Such

Table 2: Names of commercialized rice hybrids in different countries.

Country	Hybrid	Public or private	Source/sponsoring institution/company[a]
India	PA 6444[a]	Private	Hybrid Rice International Ltd., Hyderabad
	PA 6111[a]		
	KRH-2[a]	Public	Karnataka
	Narendra Sankar Dhan-2[a]	Public	Uttar Pradesh
	Pant Sankar Dhan-1[a]	Public	Uttar Pradesh
	PA-6201[a]	Private	Hybrid Rice International Ltd., Hyderabad
	PHB-71[a]	Private	Pioneer Seed Company, Hyderabad
	Sahyadria	Public	Maharashtra
	DRRH-2[a]	Public	DRR, Hyderabad
Indonesia	Maroa	Public	IIRR
	Rokana	Public	IIRR
	Intani 1[a]	Private	PT. BISI
	Intani 2[a]	Private	PT. BISI
	Longping Pusaka 1	Private	PT. Bangun Pusaka
	Longping Pusaka 2	Private	PT. Bangun Pusaka
	Hibrindo R1	Private	PT. Sutowindo
	Hibrindo R2	Private	PT. Sutowindo
Bangladesh	Sonarbangla 1	Private	Mallika Seed Company
	Hira	Private	Supreme Seed Company
	BRRI Hybrid Dhan1[a]	Public	BRRI
	GB 4	NGO	BRAC
	Aftab LP 50	Private	Aftab Bahumukhi Farm Ltd.
	Richer 101	Private	Chens Crop-Science Bangladesh Ltd.
Philippines	Mestizo 1[a]	Public	PhilRice
	Mestizo 2[a]	Public	PhilRice
	Mestizo 3[a]	Public	PhilRice
	Bigantea	Private	Bayer Crop Science, Inc.
	SL-8	Private	SL-Agritech
	Bio 401[a]	Private	Bioseed
	Rizalina 28[a]	Private	HyRice Corporation
Vietnam	Bo you 903	Private	China
	Bo you 253	Private	China
	Er you 838	Private	China
	Er you 63	Private	China
	D you 527	Private	China
	VL 20	Public	Vietnam
	TH 33	Public	Vietnam
	HYT 57[a]	Public	Hybrid Rice Research Center
	HYT 83[a]	Public	Hybrid Rice Research Center
	TN 15		China-Vietnam

[a] Hybrids with at least one parent derived from IRRI-developed germplasm. [b] IIRR = Indonesian Institute for Rice Research, DRR = Directorate of Rice Research, BRRI = Bangladesh Rice Research Institute, BRAC = Bangladesh Rural Advancement Committee.

Table 3: Yield (t ha^{-1}) of 115 elite irrigated lowland lines and 10 hybrids under lowland drought + 0 N, delayed transplanting, and stagnation: IRRI, wet season 2005.

Cultivar type	Irrigated	Drought + 0 N	Delayed transplanting (60 days)	Water stagnation (40–60 cm)
Hybrids	5.0	2.2	2.7	1.0
Inbreds	3.4	1.6	1.5	0.5
Hybrid advantage (%)	47	34	80	92

Source: G. Atlin, IRRI.

a relationship should be studied in rice and, if consistent, it could be used to select heterotic rice hybrids.

Opportunities also exist in the tropics for maximizing the manifestation of yield heterosis by developing and deploying an appropriate agronomic package of practices in target areas. The experience at IRRI (IRRI 1993) and in China clearly indicated that the yield performance of rice hybrids is maximized when agronomic management is somewhat modified to suit their growth and development pattern in comparison with the management commonly recommended and used for inbred HYVs of rice.

RICE HYBRIDS FOR UNFAVORABLE RICE ECOSYSTEMS

Sufficient experimental evidence has been generated at IRRI to indicate equal or higher yield advantage of rice hybrids over inbred rice under moderate drought, submergence-prone (Table 3), salinity-prone (Virmani 2003), and aerobic rice ecosystems. Several rice hybrids developed for the irrigated rice ecosystem have been found to be highly adapted under certain rainfed lowland ecosystems in eastern India and are spreading fast. It is therefore important that intensive hybrid rice breeding programs be undertaken for such ecosystems. Parental lines, adapted to these ecosystems, when used, would result in rice hybrids that are better than currently used hybrids developed for the favorable irrigated rice ecosystem. Also, seed production of such hybrids has to be made more efficient to make the seed more affordable for poor rainfed rice farmers. Appropriate agronomic management guidelines and packages would have to be developed to maximize the expression of a yield advantage of rice hybrids under unfavorable ecosystems.

IMPROVED GRAIN AND NUTRITIONAL QUALITY OF RICE HYBRIDS

The first-generation rice hybrids commercialized in China and outside China did not appeal to rice consumers and millers. One or both parents of these hybrids did not have the desired milling or grain quality. This adversely affected the pace of adoption of hybrid rice technology in parts of India. Studies conducted at IRRI (Khush et al 1988) indicated that hybridity was not associated with poor grain quality. With an appropriate choice of parental lines, rice hybrids of desired milling and grain quality can be developed. Indian hybrid rice breeders have successfully developed a basmati rice hybrid, Pusa RH 10 (Zaman et al 2003), which supports IRRI findings. The grain quality of rice hybrids in a target area should be improved by using parental lines with the required grain quality.

Heterosis also exists for iron and zinc content in rice grain (G. Gregorio, unpublished). Elite rice hybrids should therefore be routinely evaluated for iron and zinc content in their grains to identify whether any of these manifested a higher level of these traits to increase their nutritive value.

RESISTANCE TO BIOTIC STRESSES

Many of the commercialized rice hybrids did not have an acceptable level of resistance to bacterial leaf blight, tungro virus, sheath blight, stem borers, and whitebacked planthopper. This is because the parental lines used to develop these hybrids did not carry any genes with resistance to these stresses. Considering the importance of the specific biotic stresses in a target area, appropriate parental lines possessing the required resistance genes should be used to develop commercial rice hybrids for that area. *Bt* and chitinase genes would also be useful to develop hybrid rice resistant to stem borers and sheath blight, respectively. However, this strategy would be useful only when transgenic rice became accepted by farmers and consumers.

DIVERSIFICATION OF THE MALE STERILITY SYSTEM

Although there is no evidence so far to indicate genetic vulnerability of the widely used wild abortive (WA) CMS system (Faiz 2000), it is always desirable, especially in the tropics, to use diverse male sterility systems to prevent genetic vulnerability of commercial rice hybrids if they are associated with a CMS system. Diverse CMS systems are available, and these should be identified using mitochondrial DNA fingerprinting technology available for the purpose. CMS systems can also be supplemented with a thermosensitive genetic male sterility (TGMS) system to increase the efficiency of hybrid rice breeding and seed production. The transgenic male sterility system (e.g., Exogenous Allelic System, U.S. Patent #6852 911), if found usable in rice, would also be useful for this purpose. Molecular marker-assisted selection of available *tms* genes should help to breed new TGMS lines more efficiently.

MANIPULATION OF FERTILITY RESTORER GENES

Several fertility restorer (Rf) genes, interacting with (WA) Bo and several other CMS systems, have been identified. With the help of molecular markers, several of these have been tagged. Therefore, it is possible to identify restorer lines possessing these genes using specific molecular markers. Molecular markers should be used routinely by hybrid rice breeders to increase their efficiency to select effective restorer lines. These markers would also enable plant breeders to pyramid restorer genes in selected restorer lines to increase fertility restoration ability.

Inhibitory genes present in CMS or restorer lines are also known to reduce their restoration ability (Govinda Raj and Virmani 1988). Molecular markers should be used to identify and tag these inhibitory genes, which can then be bred out from the selected parental lines to obtain heterotic hybrids more frequently, thereby increasing hybrid rice breeding efficiency.

INCREASING HYBRID RICE SEED YIELD

Hybrid rice seed yield is a function of the outcrossing ability of male sterile lines, pollen supplying ability of male parents, and agronomic management in hybrid rice seed production plots. The weather conditions prevailing during the reproductive phase of the parental lines used for hybrid seed production also play an important role in determining outcrossing ability and, hence, hybrid seed yield. During the past 8–10 years, Chinese scientists have developed male sterile lines possessing very high (50–60%) outcrossing compared with tropical CMS lines (such as IR58025A) that can give 20–30% outcrossing. The floral traits imparting high outcrossing can be identified critically and transferred into parental lines using conventional and molecular breeding approaches. A composite population breeding approach using genetic male sterility was started at IRRI to improve outcrossing potential. The population should be useful to extract parental lines possessing higher outcrossing and should also be used and/or be developed outside IRRI. These parental lines, under appropriate agronomic management conditions in a given target environment, should help to increase seed yields significantly to reduce seed cost in the tropics, where high seed cost is one of the major factors limiting the pace of adoption of hybrid rice technology.

APOMIXIS

Apomixis is known to fix heterosis. Therefore, farmers can use the harvest of F_1 rice hybrids as seed for the succeeding crop without facing a problem of yield reduction and F_2 segregation. Several approaches, including polyembryomy (twin seedling), wide hybridization, and mutagenesis, have been tried unsuccessfully during the past 15 years. Currently, a synthetic apomixis approach (Bi et al 2003), involving a genetic engineering strategy, is being tried in a collaborative project between IRRI and the Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia. It has yielded some encouraging results. However, this research still needs several more years to get this phenomenon incorporated in rice. If successful, apomixis will help to revolutionize the use of hybrid rice technology by poor small rice farmers who are currently unable to afford expensive hybrid rice seeds.

PUBLIC-PRIVATE PARTNERSHIP

A good partnership between the public and private sector as well as NGO sector is essential for the expeditious development and transfer of this technology. The public sector is stronger in technology generation whereas the private sector is stronger in developing commercial hybrids and their seed production, processing, and marketing. NGOs are strong in arranging on-farm demonstration and promotion of the technology at the grass-roots level. There are several problems constraining this partnership that have been identified by IRRI in collaboration with some national hybrid rice programs. These problems need to be resolved and models of effective partnership between the two sectors need to be developed for faster development and dissemination of the technology. IRRI, in collaboration with some public, NGO, and private organizations, can play the role of an honest broker to help the interested countries to develop models of this partnership. Once developed, these models would enhance the pace of development and adoption of hybrid rice technology. An effective partnership developed for this purpose may also pave the way for significant financial commitments to support national and international rice research programs, not only on hybrid rice but also on other seed-based technologies.

In conclusion, hybrid rice technology has a bright future in the tropics and elsewhere to contribute toward farmers' income, national food security, rice production efficiency, seed trade, rural employment, and, consequently, global prosperity.

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Physiological and Morphological Traits Associated with High Yield Potential in Rice

Takeshi Horie, Koki Homma, and Hiroe Yoshida

To break through the current plateaus of rice yield potential, it is necessary to understand yield determination processes and identify traits associated with high yield potential. Many previous studies indicate that rice yield is most closely related to spikelet number per unit area (Sn) and then to grain-filling percentage (Fp), both of which are determined through physiological processes of genotype by environment interaction (G × E). The Sn is determined as the difference between spikelet number differentiated and that degenerated. Analysis of data from G × E experiments on nine widely different genotypes grown at eight different locations in Asia, covering cool temperate to tropical climates, revealed that the generated Sn is proportional to plant nitrogen (N) accumulated at 2 weeks before heading and that the degenerated Sn is inversely proportional to crop growth rate (CGR) during the 2-week period preceding heading. There were large genotypic differences in both the generated Sn per unit plant N at 2 weeks before heading and CGR during the 2-week period. Genotypes having higher N-use efficiency in spikelet production tended to have more secondary rachis branches per primary rachis branch with a moderate panicle number per unit area. Genotypes having higher CGR had higher stomatal conductance and higher leaf N per unit area. G × E experimental data indicated that Fp had no clear relation to Sn or to biomass production during the grain-filling period and that Fp was more strongly affected by genotype than by environment. This may agree with the previous findings that two QTLs located on chromosomes 8 and 12 controlled rice grain filling independent of Sn or photosynthetic capacity. Genotypes having higher Fp showed lower leaf N content at heading. However, it is not clear whether the lower N content and the higher grain-filling ability are affected by a single locus with pleiotropic effects. These results suggest that traits associated with higher yield potential in rice are higher stomatal conductance, higher N-use efficiency in spikelet production, a larger number of secondary rachis branches per primary branch, moderate tillering ability, and moderate leaf N content as well as traditional plant-type traits.

Under the increasing demand for food associated with population expansion and economic development in the world, it is obviously necessary to break through the current plateaus of rice yield potential (Horie et al 2003). Recognizing this, intensive work has been done to create new high-yielding rice genotypes, which includes the breeding of new plant types (NPTs, Khush and Peng 1996) and F_1 hybrids (Yuan 2001). 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 (IRRI), but NPTs did not show an appreciable yield advantage over existing elite cultivars (Khush and Peng 1996, Horie 2001). These results indicate that more efforts have to be made to break the barriers to increasing rice yield potential. To surpass the current yield potential of rice, appropriate physiological and morphological traits as well as the traditional plant type (Tsunoda 1959, Yuan 2001) should be incorporated in breeding programs with the aid of molecular markers. For this, it is important to identify yield-limiting processes and associated traits and to quantify their genetic variability.

It is well accepted that rice yield potential is primarily determined by the product of spikelet number per unit area and grain-filling percentage, as the contribution of single grain mass was small (e.g., Matsushima 1976). To quantify the determination processes of these two major yield components of rice, we analyzed extensive data from various field experiments conducted on diverse genotypes under widely different environments in Asia. On the basis of these analyses and a review of relevant studies, this paper describes the physiological and morphological traits associated with high yield potential of rice and their genetic variability.

DATA USED FOR THE ANALYSES

Comparative field experiments on genotypes have been conducted in Kyoto since 1999 to identify yield-limiting processes of rice and associated traits. In 2001 and 2002, multilocational genotype-comparative experiments termed the Asian Rice Network (ARICENET) experiments were conducted at eight locations across Asia. Those sites were located at Morioka (Iwate Agricultural Experiment Station), Ina (Shinshu University), Kyoto (Kyoto University), and Matsue (Shimane University) in Japan; Nanjing (Nanjing Agricultural University) and Yunnan (Lijiang Agricultural Experiment Station, Taoyuan Branch) in China; and Chiang Mai (Chiang Mai University) and Ubon Ratchathani (Ubon Rice Research Center) in Thailand. Widely different genotypes including indicas, temperate and tropical japonicas, new plant types (NPTs) of IRRI, and a *glaberrima* and *sativa* interspecific hybrid (WAB) were used for the experiments. The numbers of genotypes tested each year were four and eight in Kyoto in 1999 and 2000, respectively, and nine common genotypes plus one location-specific cultivar at each of eight locations in ARICENET experiments in 2001 and 2002.

Another field experiment using a Rice Diversity Research Set (RDRS, Kojima et al 2005) of germplasm was also conducted in Kyoto. The RDRS consists of 69 widely different genotypes selected on the basis of cluster analysis on 179 RFLP markers to represent about 31,000 genotypes stored at the gene bank of the National Institute of Agro-biological Resources of Japan (Kojima et al 2005). A genotype-comparative experiment was done using 64 genotypes of RDRS in 2004 and 2005.

Rice crops grown under nearly optimum conditions at those sites and in those years were periodically harvested to determine dry weight and nitrogen (N) content of different organs and leaf area. At maturity, yield and its components were also measured. In Kyoto, leaf photosynthetic rates, stomatal conductance, carbon isotope discrimination rates in the leaves, plant nonstructural carbohydrate content (NSC), and canopy temperature were also measured periodically. For the RDRS experiment, numbers of primary and secondary rachis branches on panicles and spikelet numbers on those branches were also determined. The details of those experiments were described in Yoshida et al (2006) and Homma et al (2006).

The results described in the following sections are based on analyses of the data derived from those experiments.

DETERMINATION OF SPIKELET NUMBER PER UNIT AREA AND ASSOCIATED TRAITS

Plant Factors Determining Spikelet Generation

It is well recognized that the number of spikelets or their potential is proportional to plant N content in the early reproductive period (Wada 1969, Hasegawa et al 1994, Kobayashi and Horie 1994, Horie et al 1997). Spikelet number was given by the difference between the number differentiated and ones degenerated. Wada (1969) suggested that, although the differentiated spikelet number was proportional to plant N content in the early reproductive period, the degenerated spikelet number depended on the availability of carbohydrate during the late reproductive period. On the basis of this hypothesis, we synthesized the following model (Yoshida et al 2006) to explain spikelet number per unit area (S) for different genotypes grown under different environments:

$$S = S_g - S_d \qquad (1)$$

The differentiated (S_g) and degenerated (S_d) spikelet numbers were represented, respectively, by

$$S_g = aN_p + bln(cN_p + 1) \qquad (2)$$

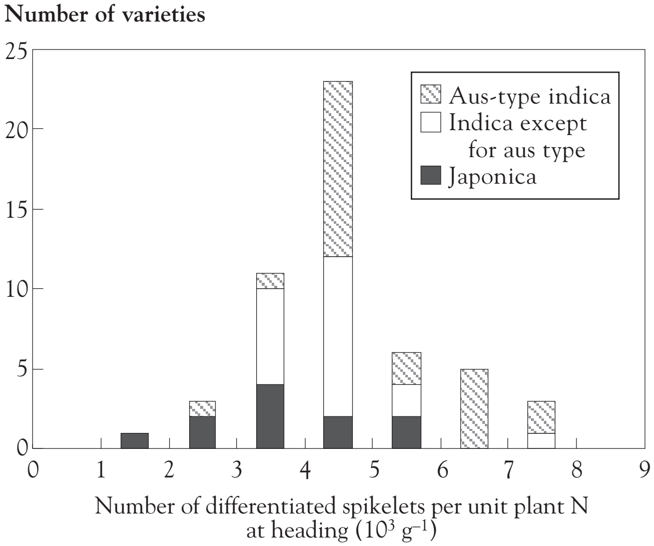

Fig 1: Genotypic variation in spikelet production efficiency per unit plant N for 64 rice genotypes of Rice Diversity Research Set experiment.

and

$$S_d = \exp(-k \times \text{CGR}) \qquad (3)$$

where N_p is the plant N content 2 weeks before heading, CGR is the crop growth rate during the 2-week period preceding full heading, and *a*, *b*, *c*, and *k* are parameters.

Using the ARICENET experimental data, we determined the values of the parameters for each genotype. The value of parameter *a* strongly depended on genotypes but that of the others could be regarded to be common over nine genotypes investigated. This model with those parameter values well explained (R^2= 0.88, P<0.001) the spikelet numbers of nine genotypes grown at eight different locations in Asia for 2 years (Yoshida et al 2006). Parameter *a* represents spikelet production efficiency per unit N_p that a plant accumulated. Quite a large genotypic difference was found in spikelet production efficiency per unit plant N_p in RDRS experimental results (Fig. 1), with higher efficiencies in aus-type indicas and semidwarf indicas and lower efficiencies in japonicas. Higher spikelet differentiation efficiency per unit N_p of genotypes was more strongly correlated with secondary rachis branch number per primary rachis branch and spikelet number per secondary rachis branch than with primary rachis branch number per panicle and spikelet number per primary rachis branch (Table 1).

Table 1: Correlation coefficient between spikelet production efficiency per unit plant N and size of panicle morphological components for 64 rice genotypes.

Panicle	Correlation coefficient[a]
Panicle number per unit area	0.15
Spikelet number per panicle	0.26**
Primary rachis branch number (R_1) per panicle	–0.14
Secondary rachis branch number (R_2) per R_1	0.36**
Spikelet number per R_1	–0.07
Spikelet number per R_2	0.37**

[a]** = significant at $P<0.001$.

Ashikari et al (2005) found a gene to increase spikelet number per panicle through the accumulation of cytokinin in inflorescence meristems. The panicle morphological characteristics of rice genotypes with larger spikelet number are probably regulated by cytokinin dynamics.

Plant Factors Related to Spikelet Degeneration

The model predicted that percentage degenerated spikelets increased exponentially with decreasing CGR during the late reproductive period, which nearly corresponds to the 2-week period preceding heading. It showed that when the CGR is as low as 10 g m^{-2} day^{-1}, about 40% of differentiated spikelets degenerate, which agreed well with the observation that as many as 37% of the differentiated spikelets degenerated in Nipponbare grown under poor environmental conditions (Kobayashi and Horie 1994). This implies that rice has the ability to differentiate an excess number of spikelets that are to be filled so as to regulate the number by “self-thinning” in response to the availability of carbohydrate around the meiosis stage (Horie 2001).

Horie et al (2003) showed that genotypic differences in CGR during the late reproductive period were mainly due to the difference in leaf photosynthetic rate. Significantly different leaf photosynthetic rates at light saturation were observed among genotypes grown under field conditions in Kyoto. The genotypic difference in leaf photosynthetic rate was closely related to the difference in stomatal conductance (g_s) and leaf nitrogen content per unit area (N). On the basis of these results, Ohsumi et al (2007) synthesized the following model to explain gross photosynthetic rate (P_g) of leaves of different genotypes at different development stages as a function of g_s and percentage leaf N content (N, 100 g N m^{-2}):

$$P_g = k(N - N_o)g_sC_a/\{k(N - N_o)(1+g_s/g_m) + g_s\} \qquad (4)$$

where C_a denotes CO_2 concentration in the air, N_o minimum leaf N content for photosynthesis, g_m mesophyll conductance, and k is a parameter. Equation 4 was derived from CO_2 diffusion equations by assuming that carboxylation rate is proportional to CO_2 concentration in chloroplast and N, and that a constant ratio is maintained between g_s and mesophyll resistance (g_m). This equation explained fairly well ($R^2 = 0.85$) the observed leaf photosynthetic rates of different genotypes of ARICENET at different stages by assuming that dark respiration rate of leaves was 5% of P_g (Ohsumi et al 2007). This suggests that genotypic differences in leaf photosynthesis were mainly derived from the difference in g_s and leaf N content.

This analysis implies that genotypic differences in percentage spikelet degeneration are due to the difference in CGR under a given environment, which in turn is mainly determined by the difference in g_s and leaf N.

Overall Process of Spikelet Number Determination and Associated Traits

On the basis of this analysis, the overall process for determining spikelet number per unit area and associated traits is schematized in Figure 2. This suggests that traits required for increased spikelet number per unit area are larger leaf area index (LAI) during the reproductive period, higher leaf N content and g_s, and a larger number of secondary rachis branches per primary branch and spikelets on secondary rachis branches.

PLANT FACTORS DETERMINING GRAIN-FILLING PERCENTAGE

Several plant factors are thought to be involved in the grain-filling process: number of spikelets per unit area, biomass production during the grain-filling period, and amount of nonstructural carbohydrate (NSC) stored in the plant before heading. However, no clear relationship was observed between grain-filling percentage and any single other factor in our genotype by environment (G × E) data sets from ARICENET and RDRS experiments. This result may infer the effectiveness of the previous findings of Nakamura et al (1992) and Tsukaguchi et al (1996) that percentage filled grains in rice does not necessarily depend on carbohydrate supply to spikelets during the whole grain-filling period, but strongly depends on its supply during the initial 10 days of grain-filling, in which endosperm cell number is determined (Hoshikawa 1976). Tsukaguchi et al (1996) suggested that, since photosynthetic production during the initial 10 d of grain-filling is usually not enough to supply the necessary amount of carbohydrates for all the spikelets in a panicle for their full development in endosperm cell number, NSC stored in the plant during

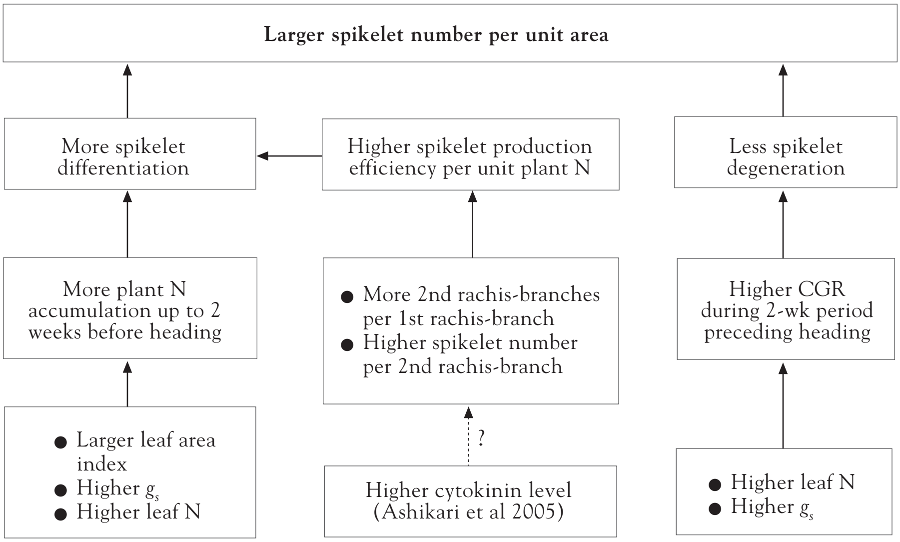

Fig 2: Process and plant factors for increased spikelet number per unit area.

the reproductive period plays an important role. These studies suggest that biomass production during the reproductive to initial grain-filling period has a critical effect on grain-filling by determining endosperm cell number. As already described, genotypic differences in biomass production during this period mainly depend on differences in leaf photosynthetic rate. Thus, the traits associated with higher leaf photosynthetic rate (higher g_s and higher leaf N content) may also contribute to higher grain-filling.

Interestingly, Tsukaguchi et al (1996) indicated that there was a large genotypic difference in grain-filling percentage at a given amount of available carbohydrate per spikelet during the initial 10 d of grain-filling. This and other results (Seo and Ota 1983, Sumi et al 1996, Murchie et al 2002, Takai et al 2005) suggest that rice grain-filling is determined by both carbohydrate supply and the ability of spikelets to pump up carbohydrate from leaves and stems, called sink activity. Takai et al (2005) identified two quantitative trait loci (QTLs) on chromosomes 8 and 12 that control rice grain-filling independently of plant photosynthetic capacity and NSC content. Especially, the QTL on chromosome 8 was closely linked to NSC translocation from stems to spikelets.

Grain-filling percentages of nine genotypes of the ARICENET experiments, averaged over different locations and years, were closely related to their leaf N content at heading (Fig. 3). A negative correlation between grain-filling percentage and leaf N content was also observed for 64 genotypes of the RDRS experiments. These results suggest that, although higher leaf N

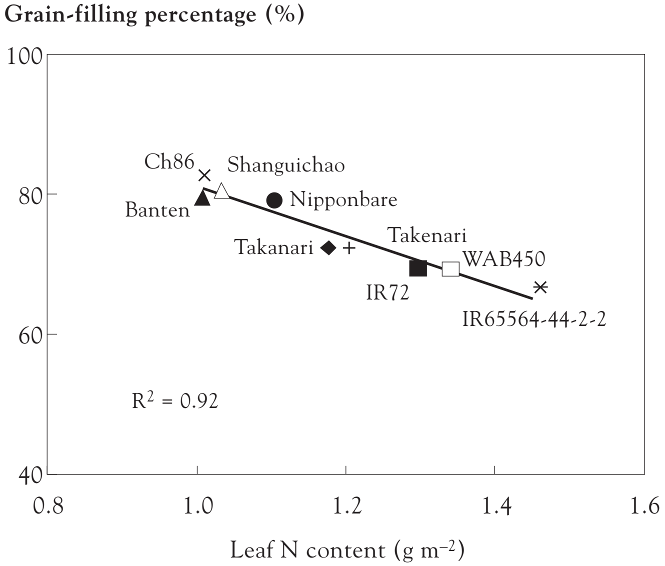

Fig 3: Relationship between leaf N content at heading (g m^{-2} leaf) and grain-filling percentage for nine rice cultivars averaged over eight locations of ARICENET experiments.

content may enhance grain-filling through increased photosynthetic rate, it has a more negative effect on sink activity. Although some reports indicate a negative effect of higher leaf N content on carbohydrate translocation to spikelets (Yamaguchi et al 1995, Ohshima 1962), more research is needed on the mechanism for the negative correlation between grain-filling percentage and leaf N content.

CONCLUSIONS

The above analyses and reviews of relevant work suggest that the following physiological and morphological traits are associated with high rice yield potential:

- High stomatal conductance
- Large secondary rachis-branch number per primary rachis branch
- Large spikelet number on secondary rachis branches
- Intermediate tillering ability
- High and moderate leaf N contents before and after the late reproductive stage, respectively
- High NSC accumulation at the onset of grain-filling

Since genetic variability is large in these traits in existing rice genotypes and their wild relatives, the accumulation of these traits, as well as those traits associated with the classical ideal plant type, will lead to the creation of genotypes that break through the current plateau of rice yield potential.

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NOTES

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