rice breeding

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Foreword

This book is based on papers presented at the Symposium on Rice Breeding held from September 6 to 10, 1971 at the International Rice Research Institute. More than 100 scientists from 26 countries reviewed developments in rice breeding and allied areas of research to identify ways to further increase rice yields and to improve quality features through breeding. The discussions were broadened by the participation of several eminent wheat breeders and plant physiologists.

A total of 64 technical papers were presented and discussed in the conference. Special discussion groups were organized to formulate cooperative plans for conservation of rice germ plasm, testing for reaction to diseases and insects, and procedure of varietal release. General discussion focused on three areas of broad interest: maximizing yield potential, improving upland rice, and training rice breeders for the tropics.

Dr. Lewis M. Roberts, Associate Director for Agricultural Sciences, The Rockefeller Foundation, served as moderator of the symposium and his summary remarks appear as part of this book.

The program of the symposium was planned by a committee composed of D. S. Athwal, H. M. Beachell, S. A. Breth, R. F. Chandler, Jr., T. T. Chang (convener), G. S. Khush, A. C. McClung, M. D. Pathak, S. H. Ou, and S. Yoshida. Dr. Chang coordinated the organizational details of the conference and acted as technical editor of the papers presented. Other members of the board of reviewers were D. S. Athwal, R. Barker, H. M. Beachell, R. F. Chandler, Jr., R. Feuer, B. O. Juliano, C. Kaneda, H. K. Krupp, A. C. McClung, S. H. Ou, M. D. Pathak, F. N. Ponnamperuma, B. S. Vergara, G. S. Khush, R. K. Walker, G. L. Wilson, and S. Yoshida. Dr. Chang summarized the various discussion sessions. Editorial work and publication arrangements were handled by S. A. Breth and the staff of the Institute's Office of Information Services. Mrs. Lina Vergara and Mrs. Nancy Perez verified and corrected the literature citations in each paper. Mrs. Perez also prepared the index.

We believe that this book represents the most comprehensive treatment of rice breeding activities in major rice producing countries of the world. We hope that its publication and distribution will make a significant contribution to our knowledge of this important but poorly documented subject. Through this book and the Institute's earlier volumes on rice genetics and cytogenetics, the rice blast disease, the mineral nutrition of the rice plant, the major insect pests of rice, and the virus diseases of rice, we believe that useful information is being assembled on the rice plant and its culture.

The Ford Foundation, The Rockefeller Foundation, and the U.S. Agency for International Development provided financial support for the symposium. Several international and national institutions also contributed to the conference by funding the participation of their leading researchers.

ROBERT F. CHANDLER, JR.
Director

Advances in rice breeding

Rice breeding in tropical Asia up to 1960

N. Parthasarathy

Early breeding work in most countries of tropical Asia aimed at improving popular local varieties, mostly by pure-line selection and in a few instances by hybridization. The rediscovery of Mendel's laws of heredity diverted the attention of rice breeders in some countries to the study of the inheritance of qualitative characters. Because of a narrow germplasm base, the concept of limited adaptability of varieties, little use of fertilizers, the multiplicity of varieties without regional testing, poorly organized extension, and lack of trained personnel and of a multi-disciplinary approach to breeding only marginal gains were made. Although rice research suffered a setback during World War II, the post-war period has been marked by great awareness of the disparity between population increases and rice supplies. The founding of the International Rice Commission and its working parties ushered in several regional projects, such as cataloging and maintenance of genetic stocks, japonica-indica hybridization, cooperative variety trials, wide adaptability tests, variety-fertilizer interaction in the indicas, and uniform blast nurseries. These projects provided an international approach to the basic problems of low rice yields in the region and prepared the ground for the major gains of the 1960's.

INTRODUCTION

Nine-tenths of the world's rice is produced and consumed in the Far East. This review is confined to varietal improvement in the countries of tropical Asia that, excluding mainland China, contain over 90 percent of the rice area of the Far East.

At the beginning of the century, population increase was not given much thought, but the colonial administrations of the Indian subcontinent, Burma, Ceylon, Malaya, Indonesia, and Indo-China, recognized the importance of agricultural development, particularly the production of rice, the staple food of these countries.

A review of the trends in the area, production, and yield of rice from 1934 to 1960 shows that the increased production in the major rice-producing countries of tropical Asia more or less kept pace with the population increase, but the change in yields has been negligible (Table 1). Apparently rice breeding had no significant impact on yields during this period. The breeder's effectiveness

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Table 1. Annual growth in population, rice production, area, and yield in Asia, 1934-38 to 1956-60.

Country	Annual growth (%)			
	Population	Rice production	Rice area	Rice yield
Japan	1.3	1.1	0.1	1.0
S. Korea	1.8	0.5	−0.5	1.0
Taiwan	2.8	1.6	0.8	0.8
Burma	1.1	−0.6	−0.9	0.3
Cambodia	2.1	2.7	2.3	0.4
Ceylon	2.4	3.2	1.1	2.1
India	1.7	1.0	1.2	−0.2
Laos	2.5	2.5	1.8	0.7
W. Malaysia	2.3	2.0	0.9	1.1
Pakistan	1.2	0.8	1.0	−0.2
Philippines	2.1	2.1	2.0	0.1
Thailand	1.9	2.0	1.8	0.2

Source: FAO Production Yearbooks.

was limited by the variable conditions under which rice is grown, the small number of varieties available as parents, inadequate research facilities, the lack of trained personnel, the failure to recognize the importance of an interdisciplinary approach to breeding, and, above all, the preference of farmers for varieties with specific grain features rather than for high-yielding types.

Rice breeding in tropical Asia can be divided into three phases: 1) work up to World War II, 2) the revival of progress in the countries affected by war with the start of international cooperation through the establishment of the International Rice Commission and its working parties, and 3) work after 1960. The third phase is not within the scope of this review. Cooperative research during the third phase led to the recognition and the understanding of the type of tropical varieties required for high fertilizer response. Within 4 years after the International Rice Research Institute started its research activities in 1962, it was able to produce tropical types with a high yield potential.

EARLY BREEDING WORK

Rice breeding at the beginning of the century was based on varieties selected for local adaptation by farmers who had no knowledge of genetic principles. During the first two decades of the century, agricultural experiment stations were established in almost all rice-growing countries of tropical Asia.

The rediscovery of Mendel's laws of inheritance in 1900 did not change selection methods, but it may have set back selection activities. It diverted the attention of some workers, especially in Indonesia and India, to the study of the inheritance of qualitative characters. Much time and labor was devoted to Mendelian ratios and the genetic factors controlling the inheritance of characters, such as anthocyanin pigment in the various plant parts, awning, and other mutant traits. Initially, however, this type of work involved the study of anthesis, time of flower-opening, and emasculation and hybridization procedures.

Rice is grown mostly in the monsoon seasons from June to December in the tropics north of the equator and from November to April south of the equator. In Ceylon, the east coast of India, the Philippines, West Malaysia, Indonesia, and East Pakistan, rice is also grown in the so-called off-seasons, though to a much smaller and limited extent. Monsoon varieties have the longest maturity period, from 160 to 200 days, while the limited number of varieties grown in the off-season have shorter maturity periods, from 90 to 130 days. Most of the latter varieties have little sensitivity to photoperiod changes, e.g. the aus and boro varieties of East Pakistan, the Kuruvai and Kars of India

Early selection work was limited to purification by removal of off-types in the varieties popular with farmers. The next step was mass selection in such varieties. Most varietal collections were limited to varieties grown in the lowlands in the monsoon. Varietal collections were not systematically evaluated in this early period.

Farmers in the tropics usually transplant bunches of several seedlings, the number per bunch depending on the size of the seedlings. Breeders first planted individual plants in rows spaced uniformly to facilitate the identification of superior lines. But the ultimate varietal evaluation depended on replications and breeders aimed for at least 10-percent yield increase over the local standard. The concept of variance and standard error determinations advanced field testing technique. The initial conduct of uniformity trials led to the determination of the size and shape of plot for experimentation. The second stage in the more advanced field plot technique came with the principles of randomization and analysis of variance advanced by Fisher (1960) during the mid-thirties. Plot designs based on the above principles helped the breeders evaluate varietal performance more accurately.

A country-by-country review of rice breeding in tropical Asia, below, shows that in most countries rice breeding work was started in a single experimental station and local varieties provided material for selection work, though critical tests on the range of adaptability of these varieties were not done. Moreover, the great diversity of rice varieties was considered to be due to their narrow adaptability, so in most countries several stations were eventually established, each in a known ecological area. Breeding work in the regional stations reduced the number of recommended varieties somewhat but the hope of finding the best varieties for smaller geographic units persisted. As a result, too many recommended varieties existed to permit practical seed multiplication and distribution programs to be established.

The idea that regional stations could be used for breeding more widely adaptable varieties—ones that could be grown in an area larger than a single region, was first conceived in Java. Selection work was made from a common hybrid material at each of six regional stations as well as at the central station at Bogor. The selections made at all the stations were tried at each station. Numerous trials followed in farmers' fields all over Java. This procedure led to the evolution of varieties adapted to the whole of Java, covering different soil types and climates (H. Siregar, *personal communication*).

In rice exporting countries like Burma and Thailand, the breeding objectives, in addition to yield, are particular grain types and milling quality. These objectives have restricted the number of varieties farmers plant.

But before the war in most countries too many varieties were developed, most of them pure-line selections, thus preventing the effective implementation of seed multiplication programs. Breeders concentrated on selecting the longer duration varieties of the monsoon season which occupied the largest land area. Breeders held the idea that longer maturity varieties were better yielders.

The limited work on breeding for resistance to rice blast during the late twenties was largely done in India. One of the earlier releases by pure-line selection, CO 4 from Anaikomban, was identified as resistant to blast. It was crossed with Korangu Samba, the popular variety in the Tanjore delta, which was highly susceptible and suffered extensive damage in that area. Selection work from the hybrid progeny was concentrated at that location. The first resistant hybrid releases for the delta were CO 25 and CO 26. CO 25 is still a popular variety in the monsoon season in Tanjore (Tamil Nadu) and Palghat (Kerala).

The earliest reference to breeding for resistance to insect pests is from India. In Uttar Pradesh, the rice bug (*Leptocorisa varicornis*) was causing extensive damage to rice at ripening stages. A cleistogamous variety, whose ripening grain was protected by a leaf sheath enclosing the panicle without emergence, was crossed with a local variety but the resulting strains had enclosed panicles and were not well accepted by farmers (Sethi, Sethi, and Mehta, 1937).

Apart from these exceptional cases, progress was not achieved in breeding for insect resistance because of the lack of cooperation between entomologists and pathologists who were mostly concerned with studying the life history of insect pests and the epidemiology of diseases.

Seeds of GEB 24 were exposed to X-rays of different intensities during 1932 (Ramiah and Parthasarathy, 1938). A number of mutations with a wider range of variations in chlorophyll deficiencies, leaf and grain characters, and height were isolated. The economic type selected was shorter with better tillering than GEB 24 and adapted to fertile soils. Because fertilizers were not commonly used at that time, critical tests of fertilizer response were not conducted until later. This variety was not popular with farmers who preferred longer straw for animal feed (Ramiah, 1953).

Breeding for rice improvement had insufficient impact because the breeders produced too many varieties, because the adaptation of varieties to particular regions was not studied, and because of the negligible use of fertilizer.

This was the situation in 1949. Previousl the countries engaged in rice breeding had practically no contact with one another except through literature on rice improvement. Exchanges of seed material were rare.

INTERNATIONAL COOPERATION

Immediately after World War II, the shortage of food supplies and the immediate threat of population increase directed world attention towards finding ways to increase the production of the most important staple food of the Far East. The founding of FAO and the establishment of the International Rice Commission (IRC) in 1949 within the framework of FAO was a milestone in the advance of cooperative rice research.

The first meeting of the Working Party of IRC held at Rangoon in 1950 emphasized that the primary aim of rice improvement was increased yield through selection and breeding (IRC, 1950). While this had been the objective from the early period of rice improvement, it was pointed out that yield was almost invariably low due to limitations of the varieties under cultivation: susceptibility to diseases and insect pests; late maturity; lodging; shattering of grain; lack of tolerance to drought, salinity, and flooding; and a narrow range of adaptation. In addition, the importance of milling and grain quality for the rice exporting countries was emphasized. As early as 1950, bacterial leaf blight was listed as one of the important diseases along with blast and helminthosporium.

The IRC Working Party meetings recognized the importance of early maturing varieties for double cropping and minimum use of water and the absence of a correlation between late maturity and high yields. These observations pointed out the need for breeding for early maturity. Furthermore, some of the early maturing varieties were heavier yielders than the late ones. Non-lodging varieties were urgently needed, so short stature and stronger straw became important breeding objectives. The nucleus of international cooperation started with the cataloging of major rice varieties of the world, and the establishment of centers for maintaining these stocks and for the exchange of seed. An indica-japonica cooperative hybridization project was worked out as a promising means of combining the valuable characteristics of each variety group. Attention was also focused on breeding for widely adapted varieties though the importance of insensitivity to photoperiod was not given attention.

The first working party recommended that the full-time services of an experienced rice breeder be made available to coordinate the comprehensive rice improvement programs outlined above (IRC, 1950). K. Ramiah was appointed as FAO Rice Consultant in 1951.

FAO international training courses in rice breeding

In some countries of tropical Asia, personnel were not sufficiently trained in rice breeding. Two training courses, the first in 1952 and the second in 1955, were conducted at the Central Rice Research Institute in India. Most countries of tropical Asia sent one or two trainees to attend the courses which focused on selection procedures, field plot techniques, and principles of genetics and breeding.

IRC working party on rice breeding

The IRC Working Party on rice breeding held eight meetings from 1950 to 1959. During this period, projects were begun on the introduction of fertilizer response in the indicas through the international cooperative project on indica and japonica hybridization, on variety-fertilizer interaction in indicas, on compilation of world genetic stocks of rice, on reduction in the number of varieties through regional trials and selection of the best varieties with wider adaptation, and on international cooperative variety trials and, later, trials of varieties with wider adaptability in the countries of the region.

Indica-japonica hybridization project

All the countries of tropical Asia participated in the indica-japonica hybridization project by sending the seeds of their best varieties for crossing with japonicas at the Central Rice Research Institute (CRRI), Cuttack, India. CRRI was selected as the center for making the crosses and the growing of the F_1 plants. F_2 seed from the crosses were dispatched to participating countries for further selection work. In addition a parallel project was begun with funds from the Indian Council of Agricultural Research to serve the several rice-growing states of India.

Japonica parents were early, taking 58 to 70 days to flower at Cuttack, while indicas took from 95 to 100 days. Restricting day length to 8 hours in 30-day-old seedlings of indica parents for 3 weeks and planting japonicas all the year round enabled breeders to synchronize the flowering of both parents so they could make crosses.

The final report was compiled by me (Parthasarathy, 1960): 1) F_1 hybrids had a high degree of heterosis in the expression of such characters as height, tillering, and single-plant yield when the percentage of sterility was low. 2) F_1 sterility did not prove disadvantageous, since selections could be made for increased fertility in the succeeding generations and fully fertile pure-breeding lines could be obtained later. 3) In no country was selection in the F_2 generation made under high fertility. 4) The average F_2 population grown from each cross-combination was small in Burma, India, Pakistan, and the Philippines. 5) The F_2 generation was rigorously selected in India, Indonesia, and Burma. Selection was based on individual plant yield from the F_2 plants in India, Pakistan, and Malaya. 6) Except for India, no country has conducted experiments to determine the response of final selections to different levels of fertility as compared with the corresponding indica parents. 7) The final promising strains were from crosses involving the following japonica parents: *Burma* Norin 6, 8, 18, Rikuu 12, Asahi; *India* Norin 6, 17, 18, 20, 36, Rikuu 132, Asahi; *Philippines* Norin 1, 16; *Thailand* Rikuu 132. 8) Rikuu 132 had a great potential as a parent. 9) The following good qualities were introduced into the selections: non-shattering, high tillering, non-lodging habit, good quality grain, early maturity, low sensitivity to photoperiod, and higher response to medium levels of fertilization.

The selection methods did not lead to outstanding results because the breeders knew little about the type of plants to select. In retrospect, it is interesting that short-statured types were identified during the 1950's especially in Orissa State of India (Orissa Department of Agriculture, *personal communication*), but perhaps these types were not followed up adequately.

The largest number of short, early segregates in the F_4 generation were identified in the following cross-progenies in descending order of importance in Orissa: Norin 6 x T 1145, Gimbozu x T 812, Norin 6 x T 812, and Asahi x T 812. The combination in the first three cross-progenies gave the largest number of short plants with yields of 50 g and above, while tall plants with 90 g and above predominated in the cross Asahi x T 812. As these plants were collected and individual yields were recorded in the segregating lines of the F_4 generation, the competition effect of tall plants might have led to the incorrect evaluation of the short plant types, and perhaps because of poor grain quality, they were discarded. At Maligaya Experiment Station (Philippines) among the 25 F_4 lines tested, a few short-strawed, high yielding lines were selected for testing in the different rice regions of the country (Umali et al., 1956).

Only in India and Malaysia were early-maturing, nonseasonal commercial varieties derived from the indica-japonica project distributed for cultivation. In India, ADT 27, which is suitable for the early monsoon season (Kuruvai), replaced the earlier varieties, ADT 3 and ADT 4, in the Tanjore delta. In Malaysia, Malinja and Mashuri were found adapted to the second crop season in the irrigated areas in Province Wellesley and had the preferred grain quality. They replaced Bir-me-fen and Taichung 65 introduced by the Japanese during the war. Recently Mashuri has gained ground in Andhra Pradesh, India.

Hybridization between indica and japonica varieties was attempted as early as 1928 in Burma (Kirk and Silow, 1951). Variety D17-88 was crossed with Shinriki but the work was discontinued because the progeny were sterile. Although progeny with better grain quality were available in the cross D17-88 x Aikoku, no pure-line selection was obtained from it.

Variety x fertilizer interaction

Closely related to the production of varieties highly responsive to fertilizer was the possibility that varietal differences may be present in indica varieties. This led to the testing of improved varieties under different levels of nitrogen in several countries. The earliest report of the detection of such differences was from the Punjab in 1954 (Silow, 1954). Coarse-grained Jhona 349 produced twice the yield of fine-grained Basmati 370 in an unfertilized plot, but Basmati 370 outyielded Jhona 349 at 80 kg ha N. Baba (1954) pointed out that varieties highly responsive to fertilizer invariably had shorter straw with short panicles and they tillered profusely. The grain-to-straw ratio declined in low-response varieties, but was relatively constant in highly responsive varieties.

Although several countries reported negative results in the variety x fertilizer interaction, Ceylon (IRC, 1957, 1960) pointed out two important features of fertilizer response in the indicas. One was the time of nitrogen application. While japonica varieties used nitrogen at any stage of their growth, indicas responded best to nitrogen applied 2 months before harvest. Ptb 16 gave the best response among a number of varieties from Ceylon, India, Indonesia, and Malaysia. Lodging due to early application of nitrogen in indicas kept highly responsive varieties from being identified. Another feature reported by Ceylon was that there was a better chance of identifying highly responsive varieties in crosses among indicas. 114, isolated from the cross of Murungakayan 302 x Mas, was cited as an example of a responsive variety.

The lack of encouraging results in the indica-japonica hybridization project turned breeders' hopes to crosses between indicas and intermediate varieties which were expected to combine japonica and indica characters, like the bulus of Indonesia and varieties from Central and South America. Fifty to sixty varieties were distributed to the countries that desired to use them in hybridization after intermediates which give high fertilizer response were identified. No successful results were reported from this project, however.

The earliest hybridization work between indigenous varieties and American varieties was in Burma about 1928 where crosses gave somewhat better results than indica-japonica crosses, but they yielded no useful strain.

FAO catalog of genetic stocks

To facilitate the exchange of seeds, collections of rice varieties from different countries were registered in the FAO catalog of genetic stocks with their known characteristics. The collections of indica varieties were maintained in duplicate, one at Cuttack, India, and the other at Bogor, Indonesia. Japonica varieties were maintained both at Hiratsuka, Japan, and in the U.S. The floating types were maintained at Habiganj, East Pakistan. By 1962 eight supplements to the catalog were issued, listing a total of 1,344 varieties.

Cooperative variety trials

As information on successful introductions from one country to another accumulated, the idea of cooperative trials in different climatic regions was developed. The accessions in the FAO catalog were used in the selection of varieties for the trials. Although the effect of photoperiod response was recognized, the varieties were grouped mainly according to season and maturity.

At the 1959 meeting of the IRC Working Party (IRC, 1960) the following varieties from India were reported to be adapted in the different countries: MTU 19 (Andhra) in Burma and Indonesia, BAM 6 (Orissa) in Malaya, CO 14 (Madras) in Burma, and ADT 5 (Madras) in Malaya.

The following varieties from outside India tested in six out of 11 states in India gave promising results: Milfor (Philippines), Murungakayan 302 (Ceylon), and A 29-20 (Burma) in Andhra; H. Sinchu (Japan) and CH 1039 (China) in Kashmir; Ramadja (Indonesia) in Kerala; Bengawan, Intan, and Thahaya (Indonesia) in Madras; A28-8 (Burma) in Orissa; B43-11, A28-8, B24-92, D25-4, D17-18 (all from Burma), and Apostol (Philippines) in West Bengal.

During the same meeting of the IRC Working Party the trials were modified (IRC, 1960). Only varieties that were widely adapted in the individual countries were included. About 70 varieties were exchanged between countries and the trials started in 1960. During 1961 and 1962 at the Maligaya Experiment Station in the Philippines, D52-37 (Burma) gave high yield and UPCA A29-20 had short and stiff straw. UPCA A29-20 was proposed for use as a parent in crosses with BPI-76. The Maligaya station reported in 1962-63 that C15-10, A29-20, B43-11, from Burma, Radin-kling from Malaysia, and Srivimankoti from Surinam were promising materials. In Hong Kong, Taichung Native 1 was found unsuitable in the initial tests because of spikelet sterility, but it gave higher yields than local varieties. It was discarded, however, because of its susceptibility to diseases.

Reduction in the number of recommended varieties

The importance of regional trials to reduce the number of recommended varieties and limit the number in each ecological zone was brought out by Love (1955) in Thailand. The use of varieties with low photoperiod sensitivity to permit wide adaptability was exemplified by breeding procedures adopted in Indonesia. The IRC Working Party in 1955 emphasized reducing the number of varieties recommended for cultivation through regional trials and introducing insensitivity to photoperiod changes to facilitate seed multiplication and distribution (IRC, 1956; Parthasarathy, 1959).

Breeding for resistance to blast

The increased use of fertilizers aggravated blast incidence, prompting the IRC Working Party on rice breeding in 1954 (Silow, 1954) to suggest that all the available information be pooled and presented at the next meeting. Cooperative testing was recommended for which a uniform methodology for testing had to be evolved. A committee established for this purpose adopted a testing procedure based on the type of nursery tests conducted by S. H. Ou in Thailand. The essential features of the nursery are its simplicity, the comparatively small field space required, and the feasibility of repeating the experiments throughout the year. The essential criterion for scoring depended on the complete killing of the susceptible variety interplanted between the test varieties. The report of the committee was adopted by the IRC Working Party in 1961 (IRC, 1961).

The importance of this international approach needed no emphasis in regard to selection of resistant parents and screening hybrid progenies in the early stages of breeding.

In 1958, the IRC member-governments called for an international rice research institute in the tropics not only for achieving the identified objectives in rice breeding, but also for training personnel in the different disciplines (IRC, 1958). The establishment of IRRI in Los Baños in 1960 by The Rockefeller Foundation and the Ford Foundation was a significant event in the progress of rice breeding in the tropics.

RETROSPECT

One might wonder why, although rice breeding work was started in the early decades of the century in the tropics and international action during the 1950's gave it impetus, the impact was not great enough to raise the average yield in most of the countries of tropical Asia. The traditional belief that indica varieties have a lower yield potential than japonicas and are not suitable for high levels of fertilizer application persisted. This observation, however, does not deprecate the work of the early rice breeders, who had to depend on the natural populations of rice for breeding material; it must be mentioned that the importance of using fertilizers was realized only in the 1950's in tropical Asia.

Through centuries of rice cultivation, soils have come to a state of low fertility. When breeding began at the start of the century, varieties cultivated by the farmers were perhaps the best competitors under the primitive conditions of rice culture. The types that prevailed under conditions of high soil fertility have been eliminated through the centuries by gradual depletion of soil fertility, by diseases and pests, and by human selection. Varietal collections cataloged by FAO are mostly of pure breeding lines of the varieties grown over large areas and selected by the rice breeders. Even though the traditional varieties gave significant yield increases with moderate application of fertilizers up to 40 kg/ha N, with the price levels of fertilizer and rice, farmers did not find fertilizers profitable. At best 1 kg N gave only an average of 10 kg of grain.

In spite of the response of short, stiff-strawed varieties to higher levels of fertilizer, identifying such types in the world collection was like finding a needle in a haystack. The fact that Taichung Native 1 and its parent Dee-geo-woo-gen were the only semidwarf sources available for breeding of high-yielding rice varieties in the 1950's proves that such high yielding types had been eliminated by the tall, leafy varieties adapted to the conditions that prevailed at the beginning of the century.

Restricted or small parcels of rice areas, especially the uplands, to which rice breeders had paid little attention, include varieties that are sources of widely variable plant stature and resistance to diseases and pests. From the collection made recently in Assam, India, a number of semidwarfs with resistance to blast and bacterial blight have been obtained. U.S. breeders successfully produced indicas that had much higher yields than those of the countries of the Asian tropics because they came from crosses between upland varieties from the Philippines and Taiwan japonicas. These facts emphasize the need for exploring rice areas not yet much influenced by civilization.

IRC greatly influenced the breeding program of countries by emphasizing the importance of regional trials, nonsensitivity to photoperiod for wide adaptation, screening for blast resistance, resistance to lodging, and early maturity.

COUNTRY-BY-COUNTRY SUMMARY

Most of the information in this summary is drawn from the unpublished reports by K. Ramiah and later by me on field visits during the tenure of our assignments with the Food and Agriculture Organization.

INDIA

In India rice breeding started in 1911 in East Bengal (now East Pakistan). An economic botanist took up selection work at the Dacca research station. Rice breeding soon followed in Madras at the Coimbatore station. The other rice growing states did not have a full-time botanist to deal with the crop, but in places where there was a botanist, he worked on improvement of several crops, including rice. Recognizing the significant role played by rice in the economy of the nation and the need for stimulating research on the crop, the Indian Council of Agricultural Research (ICAR) has, since 1929, sponsored and aided rice breeding projects in the various states. With its help other states like Bihar, Orissa, Madhya Pradesh, and Uttar Pradesh hired a special staff to institute rice breeding work. A detailed account of rice breeding work in India is given by Ghose, Ghatge, and Subrahmanyan (1960).

Rice breeding is conducted at 69 research stations throughout India. These stations are maintained and operated by the state governments. Problems of national significance received the attention of the Central Rice Research Institute (CRRI), Cuttack, founded by ICAR in 1946. The work was organized into different sections such as agronomy, breeding, soil chemistry, plant pathology, and entomology. The programs in these sections are fully coordinated. CRRI also undertakes post-graduate training. It is a center for maintaining indica varieties included in the FAO World Catalogue of Genetic Stocks of Rice.

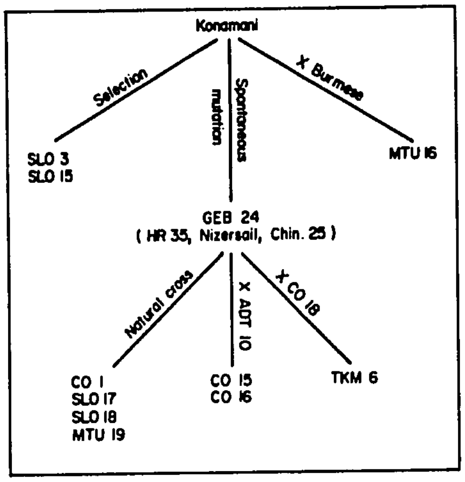
The principle of having regional stations represent ecological rice regions was first recognized by Madras and Bombay states, which have a larger number of new improved varieties than elsewhere. In states that have several stations, one station is treated as a central station where work is more intensive.

At the various rice experimental stations 430 improved varieties have been evolved, 27 by hybridization. The varieties most widely grown received earlier attention, but there are still areas where natural variability remains to be exploited. High yield was the most important objective in all breeding programs and additional objectives such as early maturity, strong straw, and resistance to diseases and adverse environmental conditions were also included in the projects. The improved varieties gave an average of 10 to 20 percent higher yields than the varieties grown by farmers.

The improved varieties are usually tested in the region for which they are intended before they are released for general distribution. This regional testing has not been sufficiently extensive in all states, however, because of lack of facilities.

Rice is grown in the country under widely varying conditions with maturation periods ranging from 90 to 200 days. It is grown in three main seasons; each season has its own set of varieties. New objectives that are assuming importance (e.g. higher response to fertilization) require that breeding projects be intensified in all states. Even among the available improved varieties only some are important and grown extensively. Some of the most outstanding of the existing improved varieties are MTU 1, MTU 15, and HR 19 of Andhra Pradesh, Chinsura 7 of West Bengal, Kolamba strains of Bombay, Hybrids 2 and 18 of Madhya Pradesh, GEB 24, CO 2, CO 25, CO 26, and ASD 1 of Madras, T 141 and SR 26B of Orissa, Basmati 370 of Punjab, and T 136 of Uttar Pradesh. The variety GEB 24 was obtained as a spontaneous mutant in a traditional variety, Konamani. It proved to be a useful variety which spread far from its native habitat and contributed towards the development of several varieties (fig. 1).

Varieties of India are broadly divided into four maturity groups: very early — 110 days and less; early — 110 to 140 days; medium — 150 to 170 days; and late — more than 170 days (the least important, since it is confined to flooded areas). Early maturing rices are especially important to India because water supply is uncertain. They are also required for areas with multiple cropping.



1. Contribution of Konamani to improved rice varieties in India.

Early maturing rices are generally insensitive to photoperiod and are therefore adapted to a wider range of planting times. Breeding for earliness has been an important item for many experiment stations. Nearly 40 percent of the improved varieties belong to the very early and early maturity groups. The only other country in Asia where early maturity is important is China. Varieties introduced into India from China have been systematically tried in many states, and some were found suitable to Indian conditions. The area under these varieties expanded rapidly. In Kashmir State, the Chinese variety CH 1039 almost completely replaced the local varieties. This is a good example of a successful introduction.

Some rice areas are subject to intermittent floods, the depth of water rising to about a meter. Floating rices suitable for greater depths of water have no use in these conditions. Breeding for such good conditions has been pursued successfully in some states. Varieties Ar. 1, Ar.C.353-148, and Ar. 614-250 of Assam, Ar. 108-1, DWP-1311 of Andhra, CO 14, ADT 17, Ptb 15, Ptb 16 of Madras, FR 13A and FR 43B of Orissa, and Hybrid 84 of West Bengal were found suitable for these conditions.

Rice areas close to the sea are subject to inundation by saline water. Special experimental stations are now breeding for salinity resistance, an important problem in these areas. Some varieties obtained by selection, such as SR26B of Orissa, Kalarata 1-24 and Bhura Rata 4-10 of Bombay, and Chin. 13 and Chin. 19 of West Bengal are tolerant to saline conditions, and are grown extensively in these states. Variety SR26B because of its medium maturity and good-quality rice has spread to several states outside Orissa.

Breeders are also trying to develop drought-resistant varieties, badly needed under uncertain and bad distribution of rainfall. Among the existing improved varieties, the following have proved somewhat tolerant to drought: AKP 1, AKP 2, BCP 2, and BCP 5 of Andhra Pradesh; ASD 4, ASD 18, and Ptb 18 of Madras; BAM 15 of Orissa; N. 22, N. 32, and A 64 of Uttar Pradesh; and Chin. 25 and Chin. 27 of West Bengal.

Almost all varieties grown in India have weak straw and lodge badly even under fair management. Lodging of the crop after it is fully ripe does not cause much yield loss unless the variety has the grain shattering character. Since most varieties do shatter to some extent, loss due to lodging cannot be completely avoided. Varieties which have straw that is somewhat resistant to lodging have been bred, but even these cannot stand high rates of fertilizer. Varieties unusually resistant to lodging are often poor in tillering and yield.

All Indian varieties shatter to some extent. The estimated loss in yield due to shattering may vary from 5 to 12 percent. Shattering is also influenced by environment, chiefly climate. For example, varieties that do not shatter when grown in the plains shatter badly when grown in Kashmir Valley at an altitude of 1,500 meters. Bulus of Java and many japonica varieties do not have the shattering character. In fact breeders in Andhra Pradesh and Orissa states obtained progeny from the indica x japonica hybridization project with the non-shattering character of japonicas. Among the improved varieties of India, the following are non-shattering: S 22 of Assam, MTU 27 of Andhra Pradesh, Hybrid No. 2 of Madhya Pradesh, and Ptb 9, CO 12, GEB 24, and CO 25 of Madras.

In some states, such as Madhya Pradesh, Bombay, Bihar, and Punjab, the wild rice, "*O. sativa* f. *fatua*," occurs as a weed. Because it crosses freely with cultivated rice, its presence in the field is a continuous source of contamination. It results in yield losses because all hybrids carry the extreme grain shattering nature of the wild parent. The natural hybrids cannot be distinguished in the early stages, so no roguing can be done. By hybridization breeders have produced varieties with satisfactory yield and deeply pigmented foliage. Since the wild rice and the crosses between wild and cultivated rice do not show the pigment, they can be easily identified and removed by weeding. This is one instance where a character of no economic importance – presence of anthocyanin pigmentation in the leaf – has been used for economic ends.

The drive to intensify rice cultivation and increase production involves the use of fertilizers. Varieties that respond to high levels of fertilization were rare among the indicas. Among the improved varieties of India, those that respond somewhat to fertilization are MTU 2 and MTU 10 of Andhra Pradesh, CO 20 of Madras, and S. 601 of Mysore.

Breeding for blast resistance has been an important program of Madras State. CO 25 and CO 26 are outstanding varieties evolved for resistance to blast through a successful cooperative research between the breeder and the pathologist in the early thirties. India has reported that MTU 15, TKM-6, SLO 12, and CH 47, are less susceptible to stem borer infestation (IRC, 1961).

PAKISTAN

Breeding in Sind (now part of West Pakistan) began in the early twenties when Sind formed part of the Bombay State. In 1936 Sind became a separate state of colonial India. Rice research was shifted from Larkhana to Dokri in 1937. Two of the important varieties evolved were Kangini 27, a selection from a local variety, and Silver Jubilees, a hybrid strain. These were distributed to rice farmers for several years. Kangini 27 was the only improved variety grown on any scale in Sind.

In the Punjab, rice breeding was undertaken at the Kalashakaku research station which was established in 1926. Seven improved varieties were being distributed to farmers. Jhona 349 and Basmati 370 occupied large areas. The Punjab grows both coarse and fine rices, the former being more common on alkaline soils. Basmati is a high-quality table rice, with long grain and a pleasant aroma. It is highly prized for its cooking and eating quality. Attempts to shorten the maturation period of Basmati 370 by suitable crosses were unsuccessful.

Rice grown in East Pakistan is classified into four groups: the early maturing aus harvested in September, the transplanted aman harvested in December and January, the boro or spring rice harvested in April, and the deep-water aman (floating rices) harvested in January. Breeding was undertaken in all four groups. Before partition, the headquarters of the rice botanist was at Dacca, and breeding was in progress at two other stations, Chinsurah and Bankura in West Bengal. After partition, Dacca remained the major rice research center for Pakistan. The research station at Habiganj (formerly in Assam) for the study of deep-water rices is also in East Pakistan.

Rice improvement work, which started in Dacca nearly 60 years ago, produced useful contributions to the genetics and agronomy of rice. The results achieved in breeding were also substantial. There were 62 improved varieties in the approved list, 17 in the aus group, 29 in the transplanted aman group, eight in the boro group, and eight in the floating rice group. Since many were evolved before partition, they are common to West Bengal and Assam in India and East Pakistan. Of the several improved varieties only five in the aus group and five in the aman group are grown on a large scale, though no regional trials were undertaken to identify the areas for which they were suitable. The list includes some varieties of hybrid origin but their suitability to different areas was not critically determined.

The Habiganj station maintains the floating rices included in the FAO Catalogue of World Genetic Stocks of Rice. This station also maintains a good collection of boro rices.

Among the improved aman rices popular with the farmers, the most important are Nizersail introduced from Nigeria, and Latisail. Nizersail is actually GEB 24 of Madras, which was introduced to Nigeria about 20 years ago from Madras.

Pure japonicas can be grown successfully with satisfactory yields in the boro season, January to April, in East Pakistan. They respond better to fertilization than indicas. They lose seed viability very soon, however (Alim, [1956]). The japonica Norin 1 gave high yields in boro season, but farmers did not like the stickiness of cooked rice.

Under the Ganga-Kobatek irrigation project, two experimental farms were established during the mid-fifties. One was at Amla, which was typical of the area coming under irrigation in Jessore and Kushtia districts, and another at

Bonapetta in Kulna district, which were representative of the areas subject to salinity because of tidal action.

At Amla, eight varieties from Indonesia were planted in 1957 during the aus season and harvested in September. The varieties Ramadja, 3478, and Sigadis yielded 5.9, 5.5, and 5.6 t/ha. However, the maturity periods ranged from 175 to 180 days. During 1959, Sigadis and Untung (bulu), both from Indonesia, gave consistently high yields during the same season. Among the early maturing varieties tested during the aman season, the hybrid T 1145 x Satika, evolved at Cuttack, and the Taiwan varieties, Frost, I-kung-pao, and Taichung Native 1 yielded from 4.0 to 4.5 t/ha; however they were not tested in the aus season.

BURMA

Burma was a province of India until 1937. The first rice experimental station was opened in Mandalay in 1907 where rice work for upper Burma was started. The rices of lower Burma, which contributed the largest exports, started receiving attention when an experimental station was established in 1914 at Hmawbi. Three more stations were started subsequently. By 1932, 19 improved varieties had been distributed in lower Burma and eight in upper Burma (Grant, 1932).

The breeding program in Hmawbi was strengthened in 1932 by a grant from the Indian Council of Agricultural Research. At this time Burma was losing her market in Europe which preferred a fairly translucent grain that glazes well. Milling quality was therefore an important objective and varieties were not released till they conformed to the milling and trade system of varietal classification. The classification consisted of five groups, A to E, based on grain length and length-to-breadth ratio. The grading and marketing organizations were disrupted during World War II and the export trade was mostly confined to the C group among which C14-8, C15-10, and D17-88 were a few of the more popular varieties.

The nucleus stock of the improved varieties was saved by being sent to India until the war was over. By the end of the war the number of improved varieties rose to 36 in lower Burma and 22 in upper Burma. Considering the volume of trade apart from the difficulties involved for seed multiplication and distribution, so many varieties might have presented difficulties for marketing as well as for seed multiplication and distribution but only a few varieties became popular in each ecological zone. Each of these zones had one main variety, for instance C28-16, for the Tennesserim area, XQ4 (hybrid between A and C type) for the Rangoon area, D17-88 and D25-4 for Bassein, A29-20 for the lower middle area north of the delta.

Among the five class groups, the C and D are the predominating types for export from lower Burma. The D type is just like the short and broad type of Japan and was intended mainly for Japanese consumption.

One of the D types, D25-4, which was popular in Bassein, has a chalky and opaque kernel, but when cooked the grain elongates to three times its raw length and has good eating quality. Another export type, XQ4, called the "pearl of Hmawbi" grown mainly in Rangoon and Pegu area has the particular defect of white belly which the breeding program sought to eliminate by crossing XQ4 with other varieties with better grain quality, like C28-16 and C24-102.

Late-maturing varieties (170 to 200 days) are generally grown in lower Burma. Varieties of less than 150 days maturity cannot be grown because of the rainfall distribution.

CEYLON

Ceylon is divided into dry and humid regions according to the amount of rainfall received. The dry area, the northern and eastern two-thirds of the island, is not really dry. It gets most of the 175 cm of rainfall from the northeast monsoon with a peak in October. This season is called "maha." The humid or wet zone in the south central highlands and the south western coastal region receives more rain from the southwest monsoon with peak rains from May to June. This season is referred to as the "yala" season. Rice is grown throughout the year because the maha and yala seasons overlap.

The main rice station is located at Batalagoda on the border of the dry and wet zone about 40 miles north of Peradeniya. Besides Batalagoda, there are several smaller rice stations scattered in different parts of the island, but selection is done in only two or three of these testing stations.

The rice growing conditions of the wet zone are not very different from those in Java and Kerala (India), and some varieties like Ptb 16 from India, Mas from Indonesia, and Siam 29 from Malaya became popular.

Breeders concentrated on incorporating low sensitivity to photoperiod, less grain shattering, strength of straw, high tillering, milling quality, and resistance to blast into the existing varieties. Like consumers in Kerala (India), and unlike in those other rice-growing countries in tropical Asia, Ceylonese prefer red rice and this is an important consideration in breeding work.

Nearly 20 varieties were recommended for growing in different districts. Three are from introductions from India and Indonesia and the rest are local selections. The most popular and widely adapted were Murungakayan 302, grown in both seasons, and Pachaiperumal for the yala season. These varieties mature in 4 to 4.5 months. Murungakayan 302 is insensitive to photoperiod under Ceylon conditions. This variety is high yielding and responsive to high levels of fertilizers. It displaced the previously popular Vella-illankayan which was poor in fertilizer response. Among the local varieties, Dovareddere was selected for resistance to floods and Pokkali for tolerance to salinity.

A separate rice improvement unit in the Department of Agriculture was established on the recommendation of a Colombo Plan mission in 1954 and two Japanese scientists were associated with the rice improvement program.

Only indicas were used in breeding for varieties highly responsive to fertilizer because the japonica x indica program did not yield expected results. The cross between Murungakayan 302 and Mas gave rise to H4 (red rice) and H5 (white rice). H5 gained ground and in Ceylon it gave good response to high levels of nitrogen. It was also resistant to blast.

MALAYA

In Malaya, study on rice formed an important activity of the Agricultural Department which started in 1915. Selection work was first started in Krian, District of Perak, in a special rice breeding station at Titi Serong. Several pure lines were established in important local varieties like Seraup Ketchil, Seraup Bessar, Radin, and Padi Pahit (Jack, 1923). Before World War II, the political set-up of the country was not conducive to coordinated breeding work because of the existence of several semi-independent states. Moreover, the rice area, except in the western coastal tract, was scattered in patches and the rice-growing conditions and water facilities varied markedly. For these reasons seven breeding centers were set up. About 50 small testing centers are located in the eight main ecological regions.

World War II halted rice improvement work. Many of the pure lines selected before the war were lost or became contaminated. Varietal improvement work had to be started anew in 1947. The initial program assessed local varieties, and introduced and identified the best adapted ones to each of the ecological regions. Well-established pure lines were also included in these tests (Larter, 1955). A further selection program based on these tests was confined to a few varieties adapted to different areas. During 1958 about 20 varieties including nine pure lines and the regions to which they were suited were listed. Siam 29, recommended for four out of 10 states in Malaya, appeared to have great adaptability. Tankai Rotan, which later proved to be a very good parent for evolving high yielding varieties, was recommended for Johore State.

Malayan rices were similar to those of the Philippines in that most were highly sensitive to photoperiod and had a long maturation period, 180 to 220 days. No variety matured earlier than 140 days.

The Japanese during the war introduced Bir-me-fen from Taiwan (called Pebifun in Malaya) in Province Wellesley. After the war the japonica x indica selection work in the FAO project, intensively carried out with the help of Japanese breeders, resulted in the release of Malinja and Mashuri for the second crop area. Mashuri is now being grown in Andhra Pradesh in India.

Grain type, cooking quality, and resistance to penyakit merah, then thought to be a physiological disease, received the attention of the breeders in addition to yield and resistance to lodging.

INDONESIA

In Indonesia, breeding work in rice was started in 1905 with the establishment of the General Agricultural Research Station at Bogor (then named Buitenzorg) in Java. The first reports on the genetics of rice were from Java, by Stok (1908), but rice improvement was limited to the testing of varieties from different regions of the country and of introductions from other countries. Until 1926, the progress was slow and work was confined to the purification of the popular bulu varieties and to selection of pure lines. One of the earliest introductions, the indica variety Tjina, received from China in 1914, spread over a substantial area because of its photoperiod insensitivity, yield, and quality. Koch (1930) developed a pure line from the same variety in the late twenties.

The varieties grown in Indonesia belong to two groups, the tjereh (indica) and the bulu or javanica. On the island of Bali and Lambok where there was a high standard of cultivation the bulus are grown exclusively. On the island of Java, the southern provinces of the island of Sumatra, and the southern provinces of the island of Celebes, tjerehs and bulus are planted in almost equal areas (H. Siregar, *personal communication*).

The origin of bulus in Indonesia is interesting. Varieties belonging to this group are grown nowhere else except the mountain terraces of Banaue, Philippines, and Java or Bali, Indonesia. The presence of bulus in Indonesia and in the rice terraces of the Philippines suggests that ancient communication took place between these areas.

The bulus as a group are distinguished from japonicas and indicas by their low tillering habit, stiff straw, non-shattering grains, wide leaves, and low sensitivity to photoperiod. In other characters, such as texture of leaf, pubescene of glumes, and stickiness of cooked rice, they are intermediate between japonica and indica. Practically all bulu varieties are awned and those that are short-awned or awnless are classified as gundils.

Rice is harvested and planted during all months of the year. The peak period is in the west monsoon season (November to April) and hence, the need for varieties insensitive to photoperiod, so bulus and insensitive indica varieties like Tjina are cultivated. Except for Tjina the rest of the 10 recommended indica varieties were photoperiod sensitive. The bulus are grown under good cultivation conditions; they yield up to 10 t/ha (H. Siregar, *personal communication*). The whole breeding program in Indonesia was later reoriented for improving indica varieties with greater adaptability to the diverse soil and climatic conditions prevailing in the country.

Six regional stations were therefore established from 1926 to 1945, each located in one major soil type. The regional set-up combined with the breeding procedures to evolve nonseasonal varieties with wider adaptation and to meet the quality requirements of the farmers was successful.

Among the three groups of crosses made — bulu x bulu, bulu x indica, and indica x indica — only the last succeeded in producing useful selections of which Bengawan was the leading variety in the late fifties. These strains from the cross Tjina x Latisail, are referred to as 40C selections. The cross was made at Bogor and after three generations of bulking, seeds were sent to all the regional stations and line selections were made in F_4. After the lines were tested for 2 or 3 years, all the selections made in all the seven stations (including Bogor) were tested for 3 years in all the stations. The well-adapted lines were again tested in numerous locations in farmers' fields. Though time-consuming, this procedure gave successful results. Among the varieties derived from this cross, Mas, Intan, and Peta spread to the Philippines and Ceylon. Although the bulu x indica crosses were not successful because of sterility in the hybrid progeny, the cross of the bulu Benong with Bluebonnet (a U.S. selection) evolved Sigadis, which has the desirable characteristics of the bulu and the increased tillering capacity of the indica. Although it had a shorter stature and an earlier maturation period than Bengawan and a fairly erect habit, Sigadis had inferior grain quality. Nevertheless, this variety is now being used as a parent by breeders at IRRI and in Thailand and India for its resistance to some isolates of bacterial leaf blight and races of blast. Another leading variety, Ramadja, was derived from the double cross (Baiang x Tjina) x (Tjina x Latisail), all indicas.

All rice improvement work was confined to Java. The other islands did not receive much attention due to lack of technical staff. Indonesia also has a large area under upland rice and the improvement of these rice varieties has not received adequate attention.

PHILIPPINES

Before 1960, the Philippines had never been self-sufficient in rice except during 1950 when a bumper crop reduced imports to nothing. From 1910-14 to 1930-34 production increased 250 percent with the imports dropping from 3 million cavans (1 cavan = 56 kg) to 220,270 cavans.

Rice improvement work began as early as 1902 by the then Bureau of Agriculture, now the Bureau of Plant Industry. Introduction of foreign varieties, selection, and later hybridization were undertaken. Before World War II, there were 61 varieties in the approved list with detailed information on the suitability of these varieties to different regions, on maturation period, on yield, and on milling quality.

Some of the outstanding introductions were Khao Bai Sri and Kra Suey from Thailand, and Ramai, Seraup Ketchil 36, and Seraup Besar 15 from Malaya. Selection work produced the important popular varieties, Apostol, Inastila IV, Sipot, Guinangang, Continedo II, Macan 1, Cruz, Pinili, and Wagwag. Rice hybridization work was started in 1920. Of the several crosses studied, two strains, Ramelon 12 from Ramai x Elon-elon and Raminad Str. 3 also called Quezon rice, from Ramai x Inadhica, were among the approved varieties. In the recommended list, 27 varieties were lowland, 23 were upland, and 10 were suitable for double-cropped areas. Twenty-two of these standard varieties were considered as nationally important and could be grown in many parts of the country. Two important varieties of the last group were Apostol and Elon-elon.

World War II disrupted rice improvement programs and even the nucleus of the standard varieties was lost. Seed schemes were again started after the war because the seed stocks had become impure. In 1952, with the cooperation of the Technical Cooperation Administration of the U.S., a program was set up to build up pure nucleus stocks of the more important standard varieties and to multiply the seed.

Because of concern over the "stunt virus disease" or "accep na pula" (probably tungro), which was destructive throughout the Philippines, a regular program of hybridization was begun, using Ketan Koetoek (a glutinous bulu variety) and two standard varieties, Milagrosa and Kasungsong, and later the progenies of their crosses: Milketan, from Milagrosa x Ketan Koetoek; Bueukitan, from Buenavista x Ketan Koetoek; Milfor, from Milketan x Fortuna; Milbuen, from Milfor x Bueukitan; and Rammil, from Milfor x Raminad 3 (Serrano, 1952).

Field trials with seven of the homozygous selections were undertaken in 1952, one at Guiginto Experimental Station, Bulacan, and the other at the Quezon City station. These strains are erect, nonlodging, and resistant to stunt. One of them, Milfor, though it did not outyield Raminad 3, Elon-elon, and Wagwag, matured early (in about 130 days) and was nonseasonal, while the standard varieties took more than 150 days to mature (Borja, Torres, and Octubre, 1952).

The year 1952 is a landmark for rice improvement in the Philippines. The Bureau of Plant Industry (BPI), University of the Philippines College of Agriculture (UPCA), Bureau of Agricultural Economics (BAE), and International Cooperation Administration under the Rice and Corn Improvement Project participated in a modest coordinated program of regional variety trials. In 1954, a memorandum of understanding was signed covering four projects which included improvement of lowland rice, improvement of upland rice, and seed production and distribution (Hayes, 1954; Umali et al., 1956). An evaluation of the commercially grown varieties (122 upland and 119 lowland) established that a number of early maturing varieties (130 to 150 days) could give significantly better yields than varieties of 160 days maturity. Some of these early varieties were best suited to rainfed areas (Cada, 1962).

The Seedboard with members from BPI, UPCA, and BAE was established to recommend varietal releases for multiplication and distribution of seed.

The world collection of 2,362 varieties received from the U.S. Department of Agriculture were grown in observational nurseries in both UPCA and the Maligaya Experiment Station.

The Seedboard approved and released for multiplication 10 lowland and eight upland varieties. In regional adaptability trials of both upland and lowland rice from 1953 to 1959, however, no one variety performed well at all experiment stations. The upland varieties that showed a wide range of adaptation were Dinalaga, Azucena, and Palawan; the lowland varieties were Bengawan, BPI-76, BE 3, Raminad Str. 3, and Seraup Ketchil 36 Str. 482.

By 1960, the Seedboard varieties, as estimated by the Rice and Corn Coordinated Council covered 150,000 hectares in the regular season and 33,000 hectares in the dry season out of the goal of 300,000 hectares under the Rice and Corn Program.

In the breeding for disease resistance, 1,205 varieties maintained at UPCA were evaluated for natural infection by stem rot, root rot, rhizoctonia, cercospora, helminthosporium, and bacterial blight. Artificial inoculation for blast and stem rot indicated that Texas Patna, 3821A, Peta, FB 12, FK 128, and AC 440 were resistant to blast; Paimat, Magnolia, AC 435, T/W 43, Norelon Str. 340, Peta, and Seraup Ketchil 36 Str. 482 were resistant to stem rot.

THAILAND

Thailand specializes in growing varieties with fine-quality, long and slender grain. These varieties form the bulk of her exports. For over 20 years before World War II, all selection work was confined to improving the quality of grain. As a result practically all the commercially important varieties had long and slender grain. In spite of variations in maturation period, morphological characters, and adaptability to different ecological conditions, grain size and shape were kept more or less uniform. Even the floating rices which usually have poor grain quality elsewhere have better grains in Thailand.

The Rangsit experimental station was established in 1916, but large-scale scientific breeding work was begun only in 1950 with technical aid from the U.S. (Love, 1955). In 1954 the Ministry of Agriculture established a separate Rice Department. A complete picture of rice growing conditions, breeding, and results achieved has been presented by Dasananda (1960).

An important feature of the comprehensive project was the training of staff through special short courses. Although the staff who took the training belonged to the junior non-technical cadre of the Rice Department, actual experience has shown that with such training, these junior cadre staff could be depended upon for the breeding work under the supervision of senior technical staff.

The project consisted of three phases: variety evaluation, selection in the local material, and hybridization. Several hundred varieties were carefully tested at locations in the three important regions, the North, the Northeast, and Central Thailand. This regional testing brought out clearly that about 10- to 20-percent increases in yield over the local varieties could be obtained.

Panicle selection in local varieties was done on a scale not attempted before in any country of tropical Asia. Over 200,000 panicles per year were selected initially and up to 600,000 in subsequent years. To facilitate regional testing, the two experimental stations were increased to eight and during 1969, two stations in North, three stations in Northeast, and seven stations in Central plus one for the floating rice and one in South were in operation in addition to the Central Rice Experiment Station at Bangkhen.

The strict demands of the rice trade in Thailand for high-quality grain naturally imposed some restrictions on achieving other objectives in breeding. For commercial purposes and also for local consumers in the Central Plain and a portion of the Northeast, non-glutinous varieties of the grain type mentioned earlier were needed. In the North and some of the Northeast, glutinous types are in demand for local consumption and for export to Laos. In the glutinous varieties, two types of grain are predominant, one broad and round for North and the other slender and long for the Northeast. The hybridization program from 1950 to 1954 was confined to selection work in indica x japonica material supplied by FAO; later the work was extended to hybridization between promising local varieties to introduce the non-lodging habit, high yield, and better grain quality with good milling quality and milling recovery. During the late fifties an intensive breeding program for screening for blast resistance was started with the assistance of FAO.

Floating rice occupies nearly 800,000 hectares in the Central Plain. Suitable varieties for different depth conditions are needed. Out of the varieties evolved for the North, Northeast, and Central Plain, five floating varieties were released for cultivation.

In early reports on varietal resistance to gali midge, Ptb 21 was identified as a resistant variety in India, and Muey Nawng 62 M as resistant in Thailand (IRC, 1961).

CAMBODIA

Rice development work started with the establishment of the Battambang rice genetic station as a central station for the whole of Indochina in 1928 (Coyaud, 1950). A small central laboratory with special irrigation facilities was built. It was not further expanded because Indochina was eventually divided into three independent states.

Early work on rice improvement was confined to mass selection of the more important varieties in the non-irrigated areas, but the material was lost during the war. Work had to be started anew after the war. Three principal groups of varieties needed attention: varieties of medium to long maturation period in irrigated areas, early-maturing varieties for well-drained high-level lands, and floating rices which occupy a considerable area in the country. Pure-line work was started in 1949, and a small amount of hybridization was taken up. Some of the old varieties, along with a few of the introduced ones, were put under comparative trial.

It is not certain if the progeny selection started in 1949 was sufficiently comprehensive. For 50 varieties, only 2,500 progeny were studied. Several crosses were also studied. Of these, the hybrids between local lowland and upland varieties showed promise. They had a preponderance of upland characters, including resistance to drought, and the desirable features of good tillering and fine grain characteristic of lowland rice.

Neang Mas, the leading variety during 1958 and 1959, and five varieties (mass selections) with different maturity periods were distributed. But Neang Mas grows 6 to 7 feet tall under high fertility and it lodges prematurely, so the need was felt for non-lodging, short-statured varieties.

The primary objective of breeding in Cambodia is the improvement of the export quality of the prominent variety Neang Mas suited to Battambang conditions. To improve the rices in the other provinces about 300 varieties have been collected from these areas which require early-maturing varieties.

VIETNAM

Breeding work in Vietnam was started in 1920, but it was not until 1950, when the Rice Office in Saigon was set up, that the work was placed on a national basis (Coyaud, 1950). Earlier work involved purifying certain important commercial varieties by mass selection and in propagating the mass-selected seed at a large number of seed farms scattered throughout the rice regions.

Before World War II there were 16 rice stations. Work that was disrupted during the war began again afterwards, but lack of technical staff and adequate facilities slowed down progress. The internal political difficulties and lack of security also hampered development. The chief rice station was located in Phu My, near Saigon, but the area was not suitable for rice research. The central rice research station was shifted to Mytho, and a substation was established at Canto. There is also a substation at Longxuyen in the center of the floating rice area, where work was confined to floating rices.

Pedigree selection and secondary selection were practiced (Coyaud, 1950). Perhaps the large quantities of uniform grain suitable for milling and export that were obtained in a short time were responsible for this change. Even mechanical graders were used to separate the main types from the mixture of varieties grown by the farmer. The most suitable type for the market was taken out and given to farmers for multiplication.

Besides purifying the older varieties, breeders began pure-line selection in 1953, and several progeny reached yield trials. A small amount of hybridization work was undertaken before World War II, but almost all the material was lost during the war. A few of the hybrid cultures were observed, but were not very promising. The chief breeding objectives were high-yielding, stiff-strawed varieties with good grain milling quality suitable for export. The breeders also tried to develop varieties suitable for acid-sulfate soils. At Mytho station, rice breeding work focused on maintaining local and foreign collections grouped according to maturity and testing them with adequate checks; trial of varieties from the local and foreign collections that had yielded more than 3 t/ha; and conducting three series of trials according to maturity groups in three representative locations to reduce the number (over 100) of varieties in general cultivation. As in Malaya, most Vietnam varieties had a long growth duration. Only 10 percent of the rice area is cropped with varieties that mature in 120 days; 50 percent of the area is grown to varieties that mature in 200 to 225 days. Varieties must have a specific maturation period. In floating rice areas and in areas where double transplanting is practiced, varieties must be late in maturity. The possibility of growing varieties that mature in less than 150 days and of double cropping rice is limited by poor drainage. The potential for improving local varieties by pure-line selection, so well established in Thailand, also exists in Vietnam. The only obstacle to launching a similar project is the lack of technical staff. Regional experimental stations are also lacking.

A small part of the rice area is under glutinous rice which is mainly used for the manufacture of alcoholic drinks. No improvement program has been undertaken to improve glutinous rice.

LAOS

The chief feature of rice cultivation in Laos is the growing of glutinous varieties. Before 1960 no complete survey of the varieties grown in Laos had been made. The first rice station was established at Salakom, near Vientiane in 1956. The rice season is from June to December and 50 percent of the area is under varieties that mature in October and 30 percent is under varieties that are harvested in September, while the rest are long maturity varieties that are harvested in December.

Since North and Northeast Thailand adjoin Laos, glutinous varieties developed for these regions were sent to Laos for trial.

Rice breeding work at Salakom was started with panicle selections made in local varieties. During 1959, 29 lines, each representing a local variety, were maintained at the station. Thirteen of these lines were grouped into three classes (four in short maturity, 150 to 157 days; five in medium maturity group, 160 to 172 days; and four in the late group, 175 to 185 days) and tested both in the station and in three other locations in the Vientiane plains.

Ten tons of pure lines, Pong Eve and Deng Tom, were distributed to selected farmers in the Vientiane region, though no previous experiments had been conducted to compare these with the local varieties, from which these selections were made.

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Discussion: Rice breeding in tropical Asia up to 1960

D. S. ATHWAL: Why did the induced dwarf mutant from GEB-24, fail to spread on farms?

N. Parthasarathy: Farmers did not prefer this mutant because they wanted more straw for fodder and also chemical fertilizers were not commonly used then.

W. H. FREEMAN: How short was the induced GEB mutant?

N. Parthasarathy: It was a semidwarf about 100 cm.

T. T. CHANG: Referring to the indica-japonica hybridization project, it was rather unfortunate that the Republic of China was not a member of the International Rice Commission and, as a result, the promise of using the ponlais (japonicas) from Taiwan in the crossing program was not appreciated. Only Taichung 65 was included, while most of the japonicas came from Japan which are poorly adapted to the tropics. For this reason, we have attempted to include rice breeders from all major rice producing areas in this symposium so that the genetic diversity of breeding materials will be adequately covered.

R. F. CHANDLER: Breeding work in those early days was important in sorting out the promising sources of germ plasm. This phase laid the foundation for today's breeding work.

E. CADA: Norelon Strain 340 was another product of the indica-japonica project selected at the Maligaya Station from the cross of Norin 1 and Elon-elon. It became a Philippine Seed Board variety in the early 1960's.

Ponlai varieties and Taichung Native 1

C. H. Huang, W. L. Chang, T. T. Chang

The ponlai varieties of Taiwan represent genotypes of largely japonica parentage that have been successively selected, hybridized, and re-selected under two different crop seasons to recombine a high yielding plant type with low sensitivity to variations in daylength and temperature. Early transplanting, close spacing, and heavy fertilization made possible the full expression of superior performance and seasonal stability in yield. Recent breeding efforts were directed toward further increasing nitrogen responsiveness, shortening the growth duration, reducing the rate of leaf senescence, and incorporating resistance to blast and leafhoppers. The development and subsequent improvement of the ponlais accelerated the intensity of multiple cropping and greatly improved farmers' income. Taiwan's native varieties of the last 3 centuries suffered from the common drawbacks of traditional, unimproved indica types: tall stature, leafy growth, poor straw strength, and, often, photoperiod sensitivity. The breeding of the first semidwarf hybrid variety, Taichung Native 1, enhanced the yield potential of the native type to a level similar to that of the ponlai varieties. Taichung Native 1 and related semidwarfs represent a giant stride in enhancing grain productivity mainly by reducing plant height. Further refinements are needed to enhance their yield potential and seasonal stability and improve grain quality. The ponlai varieties and Taichung Native 1 were bred under a subtropical environment. Those superior morphological and growth characteristics that contribute to their high productivity in Taiwan operate well under tropical environments. The recessive gene from Taiwan's semidwarfs has proved its value in the accelerated breeding programs of several countries in the tropics including the development of the worldwide IRRI varieties and their derivatives.

INTRODUCTION

The rice varieties of Taiwan belong largely to two groups: the "ponlai" (synonym: "keng" or japonica) varieties and the "tsailai" or "native" (synonym: "sen" or indica) varieties. "Ponlai" rice originally referred to the Japanese varieties grown in Taiwan early in the 20th century. It is now used to include all japonica-type varieties developed in Taiwan. The "native" group includes varieties of the indica type brought by Chinese farmers from their homeland in southern China, mainly Fukien and Kwangtung provinces.

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Table 1. Early trials of Japanese varieties in Taiwan.

Location	Period	Grain yield (t/ha)			
		Japanese varieties		Native varieties	
		Average	Range	Average	Range
Taichung	1908-14	2.25	0.02 to 3.04	2.98	2.95 to 3.18
Tainan	1908	2.67	2.11 to 3.31	3.10	—
Pingtung	1908-14	1.89	0.58 to 3.31	2.83	2.30 to 3.23

"Native" was first used to distinguish the Chinese varieties from the Japanese introductions. A third group of minor importance is the "mountain rice" grown by aborigines of the island, most of whom now live in mountainous areas. This group probably came from the Philippines and Indonesia.

EVOLUTION OF THE PONLAI RICES

During the early period of the Japanese occupation of Taiwan, which began in 1894, the colonial government studied at length the alternatives between the continued production of the native varieties and the use of Japanese introductions. It decided to keep the tsailai varieties and these were planted on about 450,000 hectares during the period 1907 to 1912. Although Japanese varieties were not commercially grown during this period, they were tested at different experiment stations.

The average brown rice yield obtained by the Taiwan Agricultural Research Institute from 1909 to 1912 was 2.86 t/ha for the Japanese varieties and 2.79 t/ha for the native varieties when seedlings were transplanted from March 22 to 28 at an age of about 50 days. In trial plantings at 39 locations in the hilly areas of Taipei during 1912 and 1913, the Japanese varieties gave an average yield of 2.55 t/ha brown rice, or 27 percent more than the native varieties.

But, in trial plantings with 40- to 70-day-old seedlings in the lowlands of central and southern Taiwan in the first crop season, the Japanese varieties gave much lower yields than the native types. Moreover, the Japanese varieties differed widely in yield performance (Table 1). Trial plantings of Japanese varieties in the second crop season were conducted throughout the island but they produced disappointing results. This led the Taiwan Rice Production Committee to recommend in 1924 that Japanese varieties be grown only in the mountains to meet the needs of Japanese residents who consumed about 5,600 tons of rice a year.

Among the many technical improvements for the successful planting of Japanese varieties in the subtropical climate of Taiwan, the lowering of the seedling age for transplanting is the most important (Iso, 1954). Conventionally, the native varieties were transplanted at the seedling age of about 50 to 60 days for the first crop and 30 to 40 days for the second crop. Experimental results showed that the yields of the Japanese varieties planted on the hills of northern

Taiwan were low and fluctuated widely if the seedlings were more than 40 days old. In the central and southern regions or on the lowland of northern Taiwan, the yields of Japanese varieties transplanted at a seedling age of 40 days were still low compared with those of the native varieties. In the second crop, the 30-day-old seedlings of the Japanese varieties decreased significantly in plant height, and heading was hastened and irregular; thus yield was extremely low (Iso, 1968).

Further testing led to the official recommendation of the following seedling ages to the farmers: 30 to 40 days for the first crop and 15 to 20 days for the second crop. Other cultural improvements, such as thin seeding in seedbed, shallow transplanting, heavy fertilization, and closer spacing in a rectangular pattern, also contributed to the improved performance of the ponlai varieties (Iso, 1954, 1968; Chu, 1957). Improved cultural practices and the stimulus of high prices led to the rapid expansion of the area planted to the adapted Japanese varieties. In 1926, the Japanese varieties planted on 119,600 hectares produced 186,700 metric tons of brown rice. In May 1926, at the Japan Rice Production Conference held in Taipei the Japanese varieties planted in Taiwan were named "ponlai rice" (meaning heavenly rice, synonymous to "horai" in Japanese).

Before 1926, the varietal improvement mainly involved screening introduced Japanese varieties that were adaptable to the subtropical conditions of Taiwan and comparable in yield capacity to high yielding native varieties. Among the 752 early introductions, 97 varieties for the first crop and 44 for the second crop were selected because they produced more than 3 t/ha of brown rice. This standard was based on previous experimental results in which about 130 varieties among 236 native varieties, and one Japanese variety, Nakamura, produced yields of more than 3 t/ha. None of the 135 varieties introduced from the southern parts of mainland China and the southeast Asian rice-producing countries produced yields comparable to those of the tsailai varieties in screening tests. Nakamura led all the introduced Japanese varieties (total: 1,256) and their progeny-selections made in Taiwan (Iso, 1947).

In the late 1920's, the rice blast disease became prevalent on the island. After 1926 varietal screenings therefore emphasized blast resistance. To check the spread of blast disease, seed disinfection and field sanitation practices were adopted in addition to the planting of disease-resistant varieties. As a result, the blast disease was gradually brought under control, especially after the release of Chiayi-Late 2, a selection from Iyosengoku made in the early 1930's (Iso, 1954).

From 1931 to 1943, new ponlai varieties were developed that had yielding abilities and grain qualities like those of japonica varieties introduced from Japan. Most of the new varieties that were recommended and released were derived from crosses made in Taiwan. Additional parents came from the native group, from other introductions from the China mainland, and from foreign introductions. The outstanding ponlai varieties developed in this period are shown in Table 2.

Taichung 65 was the most prominent pre-war variety for both the first and second crop seasons. It was adaptable to all rice areas of the island and tolerant of both dry and wet seasons. It yielded well on a wide range of soil types. This variety rapidly replaced other ponlai and many native varieties. It was also planted on nearly 250,000 hectares in the Ryukyu Islands during the Japanese era (Iso, 1947). Taichung 65 remained the leading variety until 1959 when it was surpassed in area by Chianan 8.

Taichung 65 is a short-grain type with medium plant height and intermediate tillering ability. It matures in about 120 days after transplanting in the first crop and in 100 days in the second crop. It was intensively used as a parent in hybridization for the development of many other ponlai varieties. It was also often used in yield contests and won the first prize many times in both crop seasons. In 1949 it yielded 9.8 tons of grain in the first crop and 7.6 tons in the second. Huang and Chen (1961) computed the coefficients of relationship between Taichung 65 and each of the 96 commercially grown ponlai varieties and found that 79 varieties were related to Taichung 65. The other 17 varieties were developed before the release of Taichung 65.

POST-WAR EFFORTS TO IMPROVE THE PONLAI TYPE

In the early years after World War II, the main objective of the japonica rice improvement program was to breed for nitrogen responsiveness, high yielding ability, and blast resistance. In 1949, the first blast-resistant variety, Kwangfu 1, was released by the Chiayi Agricultural Experiment Station. Kwangfu 1 was shortly replaced by Kwangfu 401 and then by Chianung 242.

Table 2. Parentage of 12 important ponlai varieties developed during 1931-1943.

Variety	Parentage
Tainung 16	Shimehari x Iyosengoku
Tainung 18	Iwata-asahi x Iyosengoku
Tainung 23	Iyosengoku x Aikoku
Taipei 8	(Kyonishiki x Osaka Asahi) x (Meijiho x Yokichisen)
Hsinchu 4	Tainung 16 x Taichung 65
Taichung 65	Kameji x Shinriki
Taichung 150	Taichung 65 x NC 4 (Italian variety x Japanese variety)
Taichung Glut. 46	(Miyako x Chengtou O-luan-chu[a]) x (Shinriki x Taichung 65)
Chianan 2	(O-luan-chu[a] x Shinriki Aikoku) x Taichung 65
Chianan 8	(O-luan-chu[a] x Shinriki Aikoku) x Taichung 65
Kaohsiung 10	Kairyo Aikoku x (Takenari x Kinaichusei 76)
Kaohsiung 18	Kaohsiung 10 x (Taichung 65 x NC 4)

[a]Indica type (Miu, 1959).

Chianung 242 was developed by crossing (Hsinchu 4 x Taichung 150) x (Taipei 7 x Tainung 45) and was released for extension in 1955. This variety was highly resistant to blast and also high yielding at many locations, especially in the first crop season. In island-wide rice yield contests, Chianung 242 obtained the first prize in the first crop from 1956 through 1963, except for 1960. In the second crop, Chianung 242 also obtained the first prize in 1955, 1957, 1958, and 1960. The highest yield for the first crop was 11.23 t/ha rough rice in 1962 and for the second crop, 8.11 t/ha in 1957. Chianung 242 is a panicle-weight type and it has high fertilizer response. It matures in about 125 days in the first crop and in 105 days in the second crop; the plant height ranges from 110 to 120 cm. Being rather tall, it often lodged in the second crop, especially under heavy nitrogen fertilization. The area planted to Chianung 242 reached 51,000 hectares in 1962 and was only behind Chianan 8 and Taichung 65. This variety was gradually replaced by other new ponlai varieties. Less than 12,500 hectares was planted to it in 1969. The lodging susceptibility of Chianung 242 prompted rice breeders to develop shorter varieties that are highly responsive to nitrogen.

Another important breeding objective was earliness: 100 days from transplanting to harvest in the first crop and 80 days in the second to fit into the multiple cropping system in which a winter or a summer cash crop, or both, could be grown between two rice crops. The first early-maturing ponlai variety, Taichung 180, was released in 1956. Because it had narrow adaptability, it was soon replaced by Taichung 186, another early variety developed from Taichung 65 x Kanto 55 (a Japanese variety). Taichung 186 was resistant to blast and possessed the same yielding ability as Taichung 65 at many locations.

Other outstanding high yielding ponlai varieties possessing intermediate resistance to blast were Hsinchu 56, Kaohsiung 53, and Tainan 1, 3, and 5. Hsinchu 56, developed from Tainung 44 x Chianan 2, is highly responsive to nitrogen. Tainan 3 showed stable yield performance at 14 testing sites in both seasons.

Some other post-war innovations in breeding ponlai varieties were the coordinated regional testing of promising selections at all experiment stations (Shen and Kung, 1958), the establishment of blast disease nurseries (Ou and Ling, 1959; Chang et al., 1965), coordinated efforts in planning crosses, testing and exchanging of breeding lines (Chang, 1961*a*), the initiation of cooperative testing for resistance to blast and to sheath blight (Chang, 1962; Wu, 1971), and the search for high yielding varieties in the second crop (Huang, 1956; Chang, 1961*b*).

An outstanding ponlai variety of recent origin is Tainan 5, selected from Kaohsiung 18 x Chianan 8. Tainan 5 matures in about 120 days in the first crop and in about 95 days in the second crop. It is between 100 and 110 cm tall. It has narrow leafblades and maintains more green leaves at the ripening stage. It has moderate blast resistance in the second crop season, but is moderately susceptible in the first crop season, especially in southern Taiwan. Therefore, a much larger area is planted to it in the second crop than in the first crop. During 1970, Tainan 5 was planted on 302,000 hectares or 39 percent of the total rice area, an outstanding record for any rice variety.

Table 3. The relationship between area planted to outstanding rice varieties and the island-wide unit yield increase in Taiwan.

Year	Area planted ('000 ha) Chianan 8	Taichung 65	Hsinchu 56	Chianung 242	Tainan 1	Tainan 5	Taichung Native 1	Taichung Sen 2	Total	Proportion of total rice area (%)	Island-wide yield (t/ha)
1961	106	85	76	45			34		287	37	2.58
1962	107	90	37	51			49		302	38	2.66
1963	122	50		41	35		77		324	43	2.82
1964	130	44	35		53		75		337	44	2.94
1965	142	35	43		66		79		366	47	3.04
1966	129		47		72	40	78		365	46	3.02
1967	104		51		51	112	64		383	49	3.07
1968	83		47			199	63	42	429	54	3.19
1969	64		47			275	55	39	480	61	2.95*
1970	49		46			302	50	35	482	62	3.17*

*Typhoon damage in the second crop season.

Over the past decade, rice production in Taiwan has increased about 50 percent although the planted area has remained almost unchanged. This achievement was partly the result of improved cultural practices including heavy fertilization, pest control, and irrigation facilities, but the extension of outstanding ponlais and semidwarf indica varieties is undoubtedly the most important factor. Table 3 indicates the relationship between the area planted to outstanding varieties and the per-hectare yield increase.

IMPACT OF PONLAI VARIETIES ON THE MULTIPLE CROPPING SYSTEM IN TAIWAN

Farmers in Taiwan grow a short-duration crop between two rice crops on the same piece of land in summer or in winter. Although this intensive crop production system had been practiced since the end of the 19th century, the area devoted to it did not increase significantly until 1926 when ponlai varieties were planted on a large scale for the first time. The average multiple cropping index during the period from 1911 to 1925 was 118 and 130 from 1926 to 1945 (Taiwan Provincial Department of Agriculture and Forestry, 1970).

The establishment of the improved relay type of interplanting a cash crop between rows of rice 2 weeks or more before the harvest of rice, and the development of early-maturing ponlai varieties further accelerated the adoption of the multiple cropping system. The multiple cropping index soared to 188 in 1968. Statistics indicate that practically all the flax, tobacco, and wheat, over 80 percent of the soybeans, 40 percent of the maize, and about 50 percent of vegetables produced in 1968 were grown by the multiple cropping system in the rice fields. The estimated net returns of various multiple cropping patterns ranged from 125 to 206 percent when compared with that of growing only two rice crops a year (Joint Commission on Rural Reconstruction, *unpublished*).

Selection for several desirable agronomic features in the development of ponlai varieties contributed to the efficient operation of the multiple cropping system in Taiwan.

Nonsensitivity to photoperiod and temperature variations

Ponlai varieties were developed through continuous selection in both the first and second crop seasons during segregating generations. This breeding procedure permits the elimination of thermo- and photoperiod-sensitive genotypes. Thus, in contrast to many native varieties, nearly all the ponlai varieties are insensitive to photoperiod. This characteristic has made it possible to grow the same variety twice a year. Insensitivity also eliminates the trouble of multiplying separate seed stocks for different seasons.

Desirable plant type

Ponlai varieties generally have shorter plants than the native varieties, they are moderate in tillering, and have dark-green, narrow, erect leaves. Because they are relatively short, ponlai varieties under proper fertilization seldom grow tall enough to cause serious lodging. The short, narrow, and erect leaves allow sufficient amounts of sunlight to reach the ground level, even as rice plants approach full maturity, and this reduces mutual shading. The rather elastic culms permit gentle pressing and bending when the companion crop is interplanted between rows of maturing rice plants.

Early maturity

Early maturing rice is the pre-requisite for a successful multiple cropping system in rice fields. Since the release of ponlai varieties, the growing period of rice from transplanting to harvesting has been shortened to about 120 days in the first crop and about 105 days in the second crop. This also means that in the summer there will be about 40 days, and in the winter fallow, 100 days available for growing the cash crop. In recent years, the development of early-maturing ponlai varieties, such as Taichung 180 and Taichung 186, has further shortened the growth period of rice from 120 days to 100 days in the first crop and from 105 to 85 days in the second crop, thus resulting in a higher multiple cropping index.

STAGES IN IMPROVEMENT OF NATIVE RICE

From 1624 to 1682, Chinese immigrants crossed the Taiwan straits and settled on the island. Many varieties from mainland China were introduced during this period, most of them sen or indica type. They comprised the so-called native varieties. These early introductions were briefly described in Volume 6 of an official history of Taiwan, *Taiwan Fang-Chih*, dated 1717 (Bank of Taiwan, 1958).

Volume 1 of the 1871 edition of *Taiwan Fang-Chih* (Bank of Taiwan, 1956) described such non-glutinous varieties as Chan-tao, Ko-san-hsian, Yuan-li, Pu-chan, and Ta-pai-mu, and such waxy types as Chan-tze-chu and Chu-shi-chu, all of which had appeared in the earlier version, suggesting that many varieties had been continuously grown by farmers on the island for more than 150 years. Semidwarf types were not mentioned (C. S. Huang, *unpublished*).

Early in the Japanese administration (1894 to 1945), Taiwan had nearly 2,000 native varieties. To limit the number of native varieties, 390 were selected and recommended to be grown by farmers. Later, the recommended varieties were reduced into 175 varieties, most of which fell into two groups. The first group consisted of 72 varieties suited for the first crop (photoperiod-insensitive); the second group consisted of 57 varieties adapted to the second crop (photoperiod sensitive). Studies from 1906 to 1913 by Iso (1954) showed that only half of the 175 classified varieties had practical or commercial value because many of them could have had the same pedigree if based on the characters of rough rice and other features.

In 1939, a survey was made of the areas planted to Taiwan native rices. The varieties that were planted on 1,000 hectares or more in various districts for the first and second crops are listed in Table 4.

The lack of hybridization work to further improve the tsailai varieties during the Japanese occupation could be traced to the colonial government's support for ponlai rice production. A substantial amount of the ponlai rice was exported to Japan, especially during World War II.

The native varieties retained a substantial proportion of the rice area throughout the colonial period in spite of the administration's efforts to encourage the production of ponlai rice. Although most of the tsailai varieties are tall, leafy, susceptible to lodging and low in yield potential, many farmers persisted in planting the indica types because they have one or more of the following merits: low sensitivity to seedling age at transplanting, when irrigation water becomes limiting; high resistance to the blast disease, sheath blight, and insect pests; a wide range of maturities to suit different needs; tolerance to drought; competitiveness with weeds; and a dry cooking quality.

DEVELOPMENT OF TAICHUNG NATIVE 1 AND OTHER SHORT-STATURED INDICA VARIETIES

After World War II, the Chinese government gave limited encouragement to the improvement of native varieties. The first phase of the program for the improvement of native rice was aimed at reducing the number of cultivated rice varieties. In 1951 and 1952, Taiwan Agricultural Research Institute surveyed the Taiwan native rices and collected 114 cultivated varieties, of which 75 were classified as first-season varieties and 39 as second-season varieties, according to the degrees of photoperiod sensitivity. As a result, the leading varieties such as Pai-mi-fen, I-kung-pao, Liu-chou, Dee-geo-woo-gen, Wu-chien, Tuan-kung-hua-lo, Ai-chueh-tze, and Liu-tou-tze in the first crop, and Min-tang, Keh-tze, Chin-kuo-chan, Shuang-chiang, Dee-geo-min-tang, Pai-eo, Yuan-li, and Chu-tze of the second crop were selected, purified, and recommended for commercial planting (Huang, 1957).

Table 4. Leading native varieties in 1939.

District	Crop	Varieties
Taipei	1st	Hsia-chueh-liu-chou, Wu-chung, Tuan-kung-hua-lou, Ti-chueh-hua-lou[a], Hsiao-wu-ko, Kao-chueh-liu-chou
	2nd	Pai-ko, Pai-mi-chih-hou
Hsinchu	1st	I-kung-pao, Pai-mi-fen, Chin-yu, Dee-geo-woo-gen[a], Wu-chien
	2nd	Pai-ko, Shui-chin
Taichung	1st	Pai-mi-fen
	2nd	Shuang-chiang, Min-tang, Man-tzu, Hsien-lo, Keh-tzu, Chin-kao
Tainan	1st	Wu-chan, Wu-ko-chin-yu, Chiu-wei-pai
	2nd	Pai-ko-yuan-li, Min-tang, Niao-yao, Pai-keh-tzu, Tien-lai, An-tzu, Kang-san-ta-pai, Wu-ko-chin-yu, Hung-chueh-chin-liu
Kaohsiung	1st	Wu-ko-chin-yu, Ai-chueh-chin-yu[a], Ta-li-chin-yu, Pai-ko-chin-yu, Wu-li
	2nd	Ching-kuo-chan, Liu-chan, Pai-ko
Taitung	1st	Wu-li
	2nd	Wu-li

[a]Semi-dwarf varieties.

Hybridization among native varieties as well as between the native type and other introduced indica varieties began at the Taichung District Agricultural Improvement Station and the Taiwan Agricultural Research Institute. The first semidwarf hybrid variety, Taichung Native 1, was developed by the Taichung station in 1956 and small amounts of seed were given to nearby farmers for trial planting. This variety was selected from a cross of Dee-geo-woo-gen x Tsai-yuan-chung made in 1949. Dee-geo-woo-gen is a semidwarf that tillers profusely while Tsai-yuan-chung is a tall, disease-resistant variety.

Although the government had long preferred the ponlai type of rice for export, it officially sanctioned the large-scale multiplication and distribution of Taichung Native 1 as late as mid-1960, after the variety had undergone extensive regional testing in three districts by the staff of the Provincial Department of Agriculture and Forestry with financial assistance from the Joint Commission on Rural Reconstruction. This step represents a major policy decision in revitalizing the improvement of native rice (JCRR, 1960).

In 23 of the 26 field trials conducted during the first crop season of 1960 in Hsinchu, Taichung, and Tainan districts, Taichung Native 1 outyielded the best local tsailai variety. The highest yield of 6.05 t/ha was obtained in one trial. This compares favorably with the yield of a superior ponlai variety. Only in Hsinchu district did another semidwarf variety, I-geo-tze, equal the yield of Taichung Native 1 (Chang, 1961*a*). When farmers applied more than the recommended rate of fertilizers in the 1961 first-crop season, Taichung Native 1 produced 6 t/ha in many trials and a top yield of 8.08 t/ha (C. P. Cheng, *unpublished*). Nevertheless, Taichung Native 1 was recommended for commercial production in the first crop only because of its susceptibility to bacterial leaf blight, sheath blight, and leafhoppers (Chang, 1961*a*).

Taichung Native 1 is short statured and high tillering. It responds well to nitrogen fertilization up to 100 kg/ha. Under Taiwan's climatic conditions, it matures in about 123 days after transplanting in the first crop and in about 97 days after transplanting in the second crop. It measures about 83 to 85 cm tall at ripening. It bears an average of 19 panicles per hill; each panicle is about 20 to 22 cm long. The grains are long (7.5 mm) and medium in shape. The rice cooks dry. In fertilizer experiments conducted at the Taichung station in 1955-57, Taichung Native 1 showed a higher response to nitrogen than several ponlai varieties (Table 5).

Taichung Native 1 was rapidly accepted by farmers and 79,000 hectares were planted by 1965, which was 36 percent of the total area under native rice, or 10 percent of the total area planted to rice. Taichung Native 1 became the second most popular variety in Taiwan in that year. Subsequently, the area planted to Taichung Native 1 gradually decreased. It was replaced by Taichung Sen 2 and Ai-chueh-chien in many locations. In 1970, only 50,000 hectares were planted to Taichung Native 1, but it remained second only to Tainan 5 among all the cultivated varieties.

Taichung Sen 2 is another semidwarf indica variety from the cross Dee-geo-woo-gen x Pai-mi-fen. It was developed almost at the same time as Taichung Native 1. It possesses the plant type and growth characteristics of Taichung

Table 5. Grain yield of Taichung Native 1 and three leading ponlai varieties at three fertilizer levels, Taichung District Agricultural Improvement Station, 1955-57.

N-P_2O_5-K_2O applied (kg/ha)	Crop	Yield (t/ha) Taichung Native 1	Taichung 65	Chianung 242	Taichung 178
42-27-25	1st	3.83	3.44	3.66	3.83
	2nd	3.31	2.84	3.19	3.07
63-40-37	1st	4.37	3.8[illegible]	3.93	4.10
	2nd	3.75	3.26	2.89	3.20
84-54-50	1st	4.77	3.81	3.43	4.07
	2nd	3.30	3.29	2.70	3.07

Native 1, but its grains are shorter and broader. It matures a little earlier and occasionally yields better than Taichung Native 1. Taichung Sen 2, however, is not only susceptible to both sheath blight and bacterial leaf blight diseases, but also to blast. For this reason, the release of this variety was delayed until 1966. Because it is early maturing and yields well, Taichung Sen 2 was nevertheless planted by many farmers, especially in the second crop season. In the early 1960's, more than 11,000 hectares a year were planted to Taichung Sen 2. Since then its planted area expanded every year and reached the record of 41,400 hectares in 1968.

The largest areas, next to those planted to Taichung Native 1 and Taichung Sen 2, were under the improved semidwarf varieties, Kaohsiung Sen 2 and Ai-chueh-chien. Kaohsiung Sen 2 was developed by the Kaohsiung District Agricultural Improvement Station by crossing Taichung Native 1 and Pai-mi-fen. Ai-chueh-chien was a pure line selection from a native variety. Kaohsiung Sen 2 was released in 1968 for southern Taiwan. Ai-chueh-chien is popular with farmers in the northern part of Taiwan and yields better than Taichung Native 1 in many cases. At the Kaohsiung station two semidwarf strains selected from crosses

Table 6. Grain yields obtained at Kaohsiung District Agricultural Improvement Station in the first rice crop of 1969.

Variety	Yield (t/ha) High fertility level	Low fertility level
Kaohsiung-yu 52 (ponlai)	7.60	6.28
Kaohsiung-yu 755 (ponlai)	8.71	7.22
Kaohsiung Sen-yu 11 (from H-105 × Dee-geo-woo-gen)	10.04	8.08
Kaohsiung Sen-yu 12 (from Peta × Ai-chueh-chien)	8.92	7.01

made at IRRI between Taiwan's semidwarfs and tropical indicas, Kaohsiung Sen-yu 11 and Kaohsiung Sen-yu 12, showed promising yield performance at high soil fertility (Table 6).

IMPROVEMENT OF QUALITY AND RESISTANCE TO DISEASES AND PESTS OF SHORT INDICA RICES

Although the short-statured indica varieties developed in Taiwan have a high yielding capacity that is at least equal to that of the ponlai varieties, such indica varieties have a poor grain appearance, susceptibility to the bacterial leaf blight disease, low resistance to cool temperatures, easy shattering, and susceptibility to some pesticides. In recent years, various agricultural agencies have tried to improve the short-statured tsailai varieties with emphasis on resistance to bacterial leaf blight disease and to green leafhoppers and brown planthoppers, tolerance to low temperatures, and improved grain appearance and eating quality.

Chung Hsing University, and the Kaohsiung station have evaluated and verified resistance to bacterial leaf blight in most ponlai varieties. The researchers also found resistant sources among foreign introductions from the U.S., India, Pakistan, and the IRRI. The backcross method is also being used to transfer the resistance of varieties such as TKM-6 into the semidwarfs.

Of the major insect pests that have become prevalent in recent years, the brown planthopper (*Nilaparvata lugens*) and the green leafhopper (*Nephotettix cincticeps*) are the most damaging to rice, especially in the southern and central parts of Taiwan. To develop resistant varieties, intensive screening tests have been carried out at the Chiayi station. Under projects supported by the Joint Commission on Rural Reconstruction from 1969 to 1971 more than 1,500 varieties, including local rices and foreign introductions, were screened for resistance to the two insects. Unfortunately, not a single Taiwan commercial variety was resistant to the insects, although several foreign introductions were satisfactory. The screening tests also disclosed that several varieties resistant to *N. impicticeps* were also resistant to the widely distributed *N. cincticeps* and *N. apicalis*. Furthermore, some of the leafhopper-resistant varieties were also resistant to the planthoppers.

Breeding for insect resistance is carried out at the Chiayi station. The donor parents having resistance to brown planthoppers are Mudgo, ASD-7, IR9-60, IR747B2-6-3, and IR1154-243, and those resistant to green leafhoppers are DM-27, DS-1, DK-1, and DNJ-27. The recurrent parents include Tainan 5, Chianan 8, Taichung Native 1, IR8, IR20, and Kaohsiung Sen 2. Besides backcrossing, pedigree selection was also made among progenies of the above crosses. Inheritance studies indicate that the resistance of Mudgo to the planthoppers is controlled by one pair of dominant alleles (Chen and Chang, 1971).

The grains of native varieties generally have low translucency; often they have a white belly and a white core which cause low recovery of head rice. A modern rice quality laboratory for testing breeding lines has been established at the Taichung station.

TAICHUNG NATIVE 1 AND THE PONLAIS OUTSIDE TAIWAN

Under a policy designed to facilitate the international exchange of germ plasm, seeds of Taiwan's improved rice varieties were freely supplied to interested researchers in foreign lands (JCRR, 1961). A group of 15 ponlai and four semidwarf native varieties sent to a University of Missouri team in Calcutta during 1960 resulted in the release of two ponlais in West Bengal under the names, Kalimpong I and Kalimpong II, in 1965. Taichung Native 1 and several ponlais were entered in the cooperative variety trials sponsored by FAO and the International Rice Commission. The trials conducted from 1961 to 1963 in Hong Kong, the Philippines, Sierra Leone, and Surinam indicated the wide adaptability and promise of the Taiwan entries (N. Parthasarathy, *unpublished*). The most significant contribution was the usefulness of the ponlai varieties, Taichung Native 1, Dee-geo-woo-gen, and I-geo-tze in the early studies of IRRI that established the improved plant type for the tropics. Taiwan's semidwarfs were used later in the development of IR8 and other semidwarf types (IRRI, [1963, 1964]; Chandler, 1963, 1968; Tanaka et al., 1964). Taichung Native 1 and several ponlai varieties were among the highest yielding entries in IRRI experiments on nitrogen response and cultural practices (IRRI, [1964], 1966).

With IRRI serving as an international center for the exchange of germ plasm, seeds of Taichung Native 1, Tainan 3, Taichung 65, and other ponlai varieties were re-introduced into India in 1964. This triggered the series of exciting events that led to their large-scale cultivation in several states of India (Chalam, 1965; Shastry, 1966). The area planted to Taichung Native 1 in India reached a peak during 1968/69 of 810,000 hectares (Dalrymple, 1969). Taichung Native 1 also established new yield records in the southern United States (Bollich et al., 1969). Inspite of its susceptibility to bacterial leaf blight, the virus diseases, and the leafhoppers, Taichung Native 1 has established yield records at several sites (Chandler, 1966).

Through the 21 Chinese agricultural demonstration teams stationed in Africa, one of which began in 1960, the ponlais and Taichung Native 1 provided the experimental evidence that high yield levels similar to those produced in tropical Asia are obtainable under African conditions (Chang, 1967). Under intensive cultural management, yields ranging from 4 to 8 t/ha were readily obtained with Taichung Native 1; Hsinchu 56; Chianung 242; Tainan 3 and 5; and Kaohsiung 53, 136, and 137; while the mean of local varieties seldom exceeded 4 t/ha. In many experiments, the Taiwan varieties doubled the yield of the best local variety (Sino-African Technical Cooperation Committee, *unpublished*). Data from 15 African countries for the period 1965-69 are summarized in Table 7. Some deficiencies which have prevented Taiwan's varieties from being produced on a large, commercial scale are poor grain quality, lack of dormancy, and susceptibility to blast or bacterial leaf blight.

Perhaps the improved types from Taiwan, particularly those with the recessive semidwarf gene, will contribute to increased world rice production through their role as parents in the development of future varieties. Dee-geo-woo-gen, I-geo-tze, and Taichung Native 1 have already made their impact in the breeding programs of Ceylon, IRRI, India, Thailand, Republic of Korea, and Surinam.

Table 7. Mean grain yield of selected Taiwan varieties and the representative local variety in 15 African countries during the period from 1965-1969.

Variety	Countries[a] included (no.)	Yield (t/ha) Range	Yield (t/ha) Mean	Percent of local check
Taichung Native 1	14	2.95 to 7.69	5.83	182
Hsinchu 56	5	4.05 to 8.27	6.08	189
Taichung 65	9	3.77 to 5.73	4.48	140
Taichung 180	3	2.41 to 3.57	2.91	91
Chianan 8	10	3.91 to 7.03	5.18	161
Chianung 242	12	2.19 to 9.94	5.26	164
Tainan 3	11	3.30 to 7.42	5.65	176
Tainan 5	5	4.74 to 9.71	6.71	209
Kaohsiung 53	4	5.41 to 6.10	5.75	179
Kaohsiung 136	4	5.29 to 6.93	6.30	196
Kaohsiung 137	5	4.74 to 7.89	6.02	188
Local check	13	1.60 to 4.22	3.21	100

[a]Not all varieties tested in all locations in each year.

One of the ponlai breeding lines, Tainan Yu 487 (PI 215936), has often served as a parent in the breeding programs of Colombia and the United States.

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Discussion: Ponlai varieties and Taichung Native 1

B. R. JACKSON: Taichung Native 1 has been mentioned extensively but not much has been said about I-geo-tze and Dee-geo-woo-gen. Why did I-geo-tze and Dee-geo-woo-gen not become popular in Taiwan?

C. H. Huang: Because Taichung Native 1 and several newly developed semidwarf indicas outyielded Dee-geo-woo-gen and I-geo-tze at many locations except for I-geo-tze in small areas of northern Taiwan. To reduce the number of rice varieties, Dee-geo-woo-gen and I-geo-tze were not recommended to the farmers.

A. O. ABIFARIN: What are the characteristics of the "mountain rice"? Have they been used in the breeding program? What are the months for the first and second crops?

C. H. Huang: Mountain rice is the upland type: long awns, big panicles, suitable for direct planting. A few were used as blast-resistant parents in crossing programs in Taiwan. The first crop is sown from December (in southern Taiwan) to February (in the north). Harvesting begins in May and ends in early July. The seeding of the second crop begins in June and ends in July. Harvesting extends from October to December.

H. L. CARNAHAN: Since the improved plant type is being introduced into both indica and japonica varieties, does any feature other than grain shape and quality distinguish improved indicas from japonicas?

C. H. Huang: Yes, some differences still exist between the improved indicas and japonicas, such as leaf color in the seedling stage, tolerance to low temperatures, and sensitivity to pesticides.

R. F. CHANDLER: As more distant crosses are being made, the two names, indica and japonica, will disappear in 20 years.

C. KANEDA: Please name some varieties which are described in your paper as resistant both to brown planthopper and green leafhoppers.

W. L. Chang: Samba and H-105, among others, showed resistance to both brown planthoppers and green leafhoppers in our screening tests at Chiayi.

E. A. SIDDIQ: Taichung Native 1 is suited for rainfed and upland culture in India. The leaves turn yellow early.

C. H. Huang: Because of the susceptibility of Taichung Native 1 to bacterial leaf blight and leafhoppers, it was recommended for growing in the first crop season only.

T. T. CHANG: How much area in India is now planted to Taichung Native 1?

W. H. FREEMAN: Only a small amount in Madhya Pradesh State.

R. F. CHANDLER: Taichung Native 1 has had a significant impact on rice improvement. It is deficient in grain quality and in disease and insect resistance. But it is very useful as a germ plasm source. It pointed the way for tropical rice breeding.

Breeding for high-yielding varieties in Japan

Shiro Okabe

The rice breeding organization of Japan is characterized by two features: a breeding network consisting of small breeding stations, located in different environments, and a limited but well-defined set of breeding objectives which are allotted to each station. In recent years, the organization has been consolidated into four macro-ecological districts to achieve nation-wide breeding objectives. Breeders in Japan have always stressed high yielding varieties. Most leading varieties have been derived from previous leading varieties and all parents for crossing have come from domestic materials, with a few exceptions, in breeding for disease resistance. Recently, however, breeders have become interested in using exotic materials for other purposes as well. The bulk method with shortened breeding cycle in greenhouses is generally adopted. A close communication among breeders, extension workers, and farmers has greatly helped breeding activities. High yielding varieties have evidently made a great contribution to rice production in Japan. However, the importance of favorable socio-economical and cultural conditions should also be considered in interpreting the nation's rapid increase in rice yield.

INTRODUCTION

The annual rice production in Japan reached around 14 million metric tons in brown rice in the late 1960's; it was only 7.5 million tons 50 years ago. During that period, an 85 percent increase in rice production has been achieved, while the area planted to rice increased only 10 percent. In other words most of the increase in production can be attributed to higher yields per unit area. In fact, the rice yield has increased to 4.3 t/ha from 2.5 t/ha (brown rice), or about 70 percent, during the 50 years. A noticeably rapid increase in yield occurred in the last 20 years.

It is difficult to separate the effect of varietal improvement from complicated effects of many other important contributing factors. But there is no doubt that high yielding varieties have been a major cause of the great progress of rice production in Japan.

Socio-economic factors and changes in agronomic practices played an important role, too, in raising yields. Two particularly important socio-economic factors were that all farmers owned their land and that the price of rice was high. Both encouraged farmers to concentrate their efforts to improve their agronomic practices. The spread of new agronomic practices, like heavy

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application of fertilizer accompanied by deep plowing or transplanting of vigorous young seedlings grown in semi-irrigated nursery beds, also had a large effect on yields. Nevertheless, without the high yielding varieties which were developed through breeding work, the great increase in yields could hardly have been achieved in Japan in such a short period.

ORGANIZATION OF BREEDING PROGRAMS BASED ON ECOLOGICAL CONDITIONS

Wide adaptability of breeding materials is, in general, a major concern of breeders. Breeders can adopt either or both of the following approaches for breeding widely adaptive and high yielding varieties: 1) evaluation of the adaptability of the introduced materials in the area concerned, and 2) evaluation of the adaptability of the breeding populations by subjecting them successively to natural and artificial selection within the area beginning from early generations. In the second approach, each breeding population is directly selected so as to be highly adapted to each local condition.

Rice breeding in Japan was organized in 1927 around the second approach, called "ecological breeding." This step resulted from the greatly diversified ecological conditions within Japan. The country needs different types of rice varieties that are well fitted to different environmental conditions. To provide each region in Japan with varieties well adapted to their ecological conditions, a breeding station was established in each region. The country is divided into 12 ecological regions for rice breeding. Furthermore, four additional breeding stations were established to breed for early-season varieties, late-season varieties, upland varieties, and short growth-duration and cold-tolerant varieties. Breeding for late-season varieties has recently been replaced by the breeding objective of blast disease resistance.

Of the 16 breeding stations distributed over the country, seven stations are national and nine are prefectural organizations. The nine prefectural stations are partly subsidized by the national government for their breeding work. Under these breeding stations are more than 50 local stations which test local adaptability and other special characteristics. Performance tests are carried on by each prefecture. For such performance tests, more than 90 prefectural and branch experiment stations and 100 farmers' fields are used every year.

From 1927 to about 1949, the Central Agricultural Experiment Station at Konosu, near Tokyo, was responsible for making crosses and the first selection for distribution of the F_2 selections to regional breeding stations. Selection and purification in later generations was conducted at each regional station. The most promising materials were tested in the systematic national breeding network. Since about 1950, however, each regional breeding station has been making its own crosses. The coordination for testing promising materials is unchanged.

Besides this national network for rice breeding, eight prefectural stations conduct breeding work to serve the specific needs of their areas.

Thus in Japan, the breeding network consists of small breeding stations located in different environments. Each station has limited but specific breeding objectives. This system allows each station to provide varieties well fitted to regional conditions.

The system has some disadvantages, too. First, it is difficult to breed widely adapted varieties because breeders tend to concentrate on their own regional problems. Second, for nationwide common breeding work, the separate organizations require special coordination to integrate their activities. Third, some breeding work at one station sometimes overlaps work at other stations, which is not economical.

To improve this situation, changes were made in 1962. The 12 ecological regions were consolidated into four macro-ecological districts: a cold weather district (Hokkaido island), a cool weather district (northern part of Honshu island), a warm weather district (southwestern part of Honshu, except Seto Inland Sea coastal areas), and a hot weather district (Kyushu, Shikoku, and Seto Inland Sea coastal areas). In each district one of the existing national agricultural experiment stations is designated as a central station.

The reorganization was based on work of Akemine and Kikuti (1958) who investigated adaptive changes in the genetic constitution of two rice hybrid populations that had been grown for several years in different localities in Japan. They found that marked changes occurred within a short period in nearly all characters in both populations. The mean values for flowering time, culm and panicle length, and yield were correlated with the mean temperatures during the rice growing period at each site. It was noticed that the variability within the population was greatly changed as well as the population means. The populations that had been subjected to natural selection in the central region retained a greater variability than those in northern and southern regions. These experimental results suggest that ecological regions of Japan could be reasonably grouped into three or four masses for rice breeding.

Basic studies on rice breeding are conducted by the National Institute of Agricultural Sciences. The institute has a long-term seed storage facility for genetic stocks of economic plants including rice and other cereal crops. The permanent maintenance and distribution of seeds for genetic resources are its responsibility. Basic studies are also conducted by national agricultural experiment stations and universities, though to a lesser extent.

Rice breeding activities in the whole country are supervised and adjusted by a coordinator of the Research Council of the Ministry of Agriculture and Forestry, with the cooperation of the Central Agricultural Experiment Station and also of the National Institute of Agricultural Sciences.

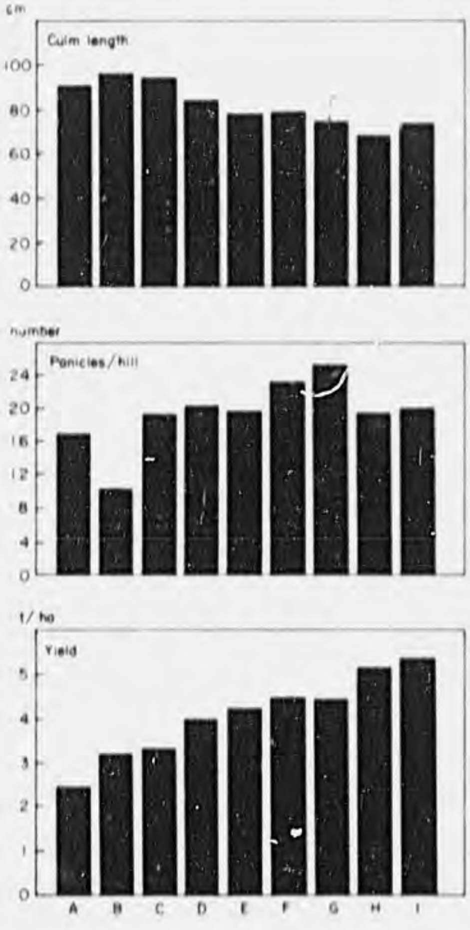
BREEDING OBJECTIVES

During the last 60 years, rice breeders in Japan have placed major emphasis on breeding for high yield under heavy application of fertilizer; resistance to blast, Akiochi, bacterial leaf blight, and stripe virus; short culms for lodging resistance; high tillering; cold weather tolerance in low-temperature regions; and improved grain quality. Breeding for high yields has been the pre-eminent goal. Breeding for resistance to Akiochi, bacterial leaf blight, and stripe virus have been chiefly concerns of the southwestern region.

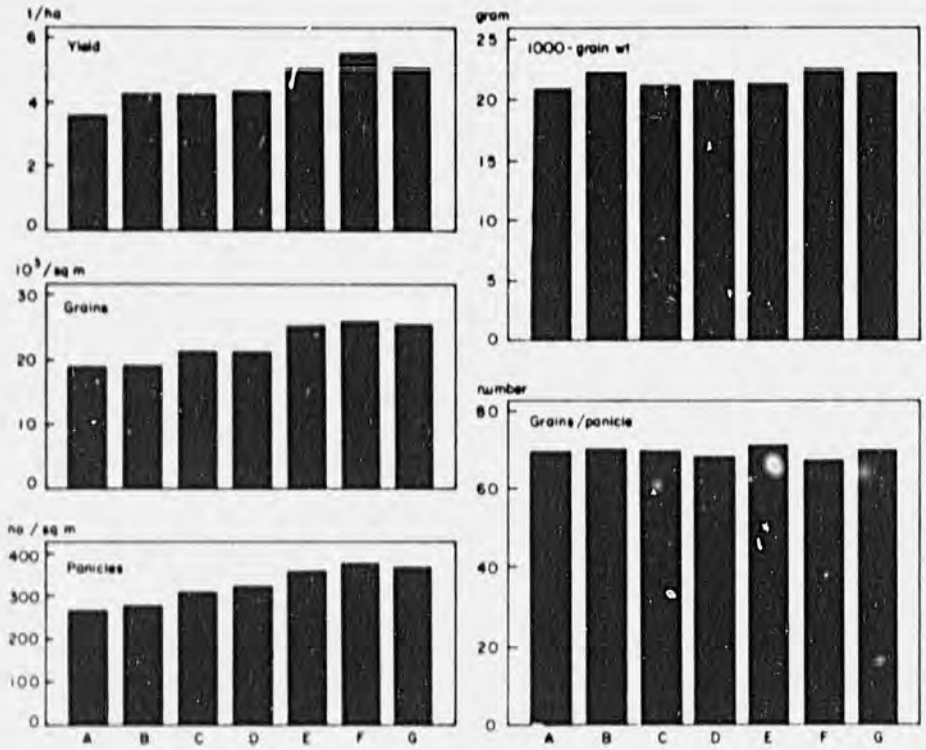
Because of the urgent need for agricultural modernization in recent years rice breeders since 1962 added three new goals to the major breeding purposes mentioned above: breeding for suitable growth characters for direct sowing, breeding for short growth duration, and breeding for wide adaptability.

Breeding for short growth duration is aimed at allowing more intensive use of paddy land. To establish beneficial cropping patterns with rotations of rice and other crops, rice varieties that have a short and stable growth duration must be developed. With surplus production and decreasing domestic demand for rice, improvement of quality and taste is now an important problem for rice breeders.

In Japan, breeders have always emphasized "plant type." This term includes not only the so-called "type" itself (i.e. panicle-, tillering-, or medium-type) but also culm and panicle length and uniformity of panicle height within a plant or hill. Figure 1 shows the general trend in the plant type of old and new rice



1. Trends of agronomic characters of old and new rice varieties in Hokkaido, Japan (Samoto, 1971). Variety and year of release. A) Akamuro, local and very old variety, B) Bozu 5, 1900, C) Kitami-Akage, 1929, D) Fukoku, 1935, E) Eiko, 1940, F) Toyohikari, 1953, G) Mimasari, 1959, H) Sasahonami, 1961, I) Yuhkara, 1962



2. Varietal differences of yields (of brown rice) and related characteristics of rice in Saga Prefecture, Kyushu (Japan Ministry of Agriculture and Forestry, Statistics and Survey Division, 1966). A) Norin 22 (early), B) Norin 18 (late), C) Ariake (middle), D) Kinmaze (early), E) Tachikara (late), F) Kokumasari (middle), G) Hoyoku (middle)

varieties in Hokkaido island: More tillers, more grains per hill, shorter plant height, and shorter panicle length. These changes were highly correlated with yield increase. After 1960, the situation changed in Hokkaido and in other areas of Japan.

In recent years, high grain number with high tiller number has been rather negatively correlated with high yield. Longer panicles accompanied by fewer tillers are likely to produce higher yield, since this combination gives a large number of grains with better filling.

Figure 2 shows the features of varietal differences in yields and other related characteristics of rice plants in Saga Prefecture, the highest yielding district of western Japan. Clearly, the high yielding ability of varieties Hoyoku, Kokumasari, and Tachikara is closely associated with number of grains and panicles per unit area.

In the last 20 years, breeders have recognized that erect leaves are a major factor in achieving high yields and that plant type in a broad sense has a close relationship to yield ability and response to cultural conditions such as fertilizer application levels and soil fertility.

In establishing breeding objectives in Japan, breeders place great importance on improving defects of the leading local varieties. This is understandable since leading varieties have basically favorable genotypes, in general, that are highly adapted to local conditions. This basis for establishing breeding objectives has some disadvantages, however. If the objectives are tied to a few leading varieties in a region, rapid progress in raising yielding ability will be difficult because the breeders' choice of breeding materials will inevitably be narrow. Furthermore, breeders are apt to adopt rather conservative breeding methods.

For efficiency in achieving long-term breeding goals, breeding work for short-term objectives should advance in parallel with work for long-term objectives. It should be noticed that no promising lines have been developed in Japan from several crosses in which IR8 and Hoyoku were used as one of the parents, though they are both outstanding varieties in the areas to which they are adapted.

BREEDING MATERIALS

In Japan in recent years the 16 breeding stations made a total of more than 800 crosses a year, aside from crosses for basic research work. Some crosses are duplicated among stations, but no less than 200 different varieties are annually used as parents for hybridization in the whole country. Before 1950 about 300 crosses were made each year.

Table 1. Coefficients of relationship of leading rice varieties[a] between the period of 1908-1963 and 1963 (Ito, 1966).

Leading varieties in 1963	Leading varieties in the period of 1908-1963[b]							
	Aikoku	Seki-tori	Ohba	Take-nari	Shin-riki	Asahi	Norin 8	Norin 22
Towada						37.5		
Fujiminori	12.5					25.0		
Sasashigure	12.5					50.0	50.0	
Hatsunishiki	12.5					18.8	25.0	50.0
Koshijiwase	12.5					18.8	25.0	50.0
Honenwase	12.5					18.8	25.0	50.0
Koshihikari	12.5					18.8	25.0	50.0
Norin 22	12.5					25.0	50.0	100.0
Norin 29	12.5					25.0	50.0	
Tozan 38	12.5					25.0	50.0	
Manryo	12.5					25.0	25.0	
Kusabue	6.3		6.3			12.5	25.0	
Yamabiko	6.3			3.1		29.7	25.0	50.0
Nakate-Shinsenbon	6.3					12.5	25.0	50.0
Kinmaze				12.5		25.0		
Akebono	12.5				25.0	50.0		
Hoyoku		25.0						
Norin 18	25.0				50.0			

[a] Rice varieties planted on more than 30,000 ha. [b] Five leading varieties of 1908, Ishijiro, Shirozasa, Miyako, Omachi, and Shirotama, had no relationship with leading varieties in 1963.

Although so many varieties have been used as parents every year, almost all leading rice varieties during the past 50 years have been derived from crosses among leading varieties or from hybrids of which at least one of the parents was a leading variety. Exotic varieties have been used only in breeding for disease resistance. Ito (1966) developed a table relating the 18 leading rice varieties of Japan in 1963 with the leading varieties from 1908 to 1963. Of the 18 varieties, 10 were developed from the hybrids among the four old leading varieties and six were from crosses in which one old leading variety was used as a parent (Table 1). Only one leading variety in 1963 was unrelated to these old leading varieties. This variety, Hoyoku, which is one of the highest yielding varieties in Japan, was short-statured and highly resistant to lodging. These characteristics had never before been seen in a recommended variety in the country.

Table 1 shows that in Japan most leading varieties have been developed by crossing previous leading varieties and that only a few foreign introductions were used as parents, for disease resistance breeding.

Rice plants have been cultivated for more than 2,000 years in the mild and humid growing season of Japan with shallow plowing, transplanting, and irrigation. H. Akemine (*unpublished*) discussed the effect of this situation on genetic diversity of breeding materials. He suggested that the genetic constitution of rice populations in Japan, which has been subjected to natural and artificial selection in this area for 2,000 years, is "narrow and shallow." Consequently, useful genes seem to have been accumulated in the existing varieties that have been developed through the decades by repeated mating within domestic germ plasm.

Breeders are now faced with new problems. Breeding for mechanized farming, short and stable growth duration, and high resistance to blast, bacterial leaf blight, and virus diseases is urgent. Breeders have recognized that new genes are needed from exotic materials or from mutants, since few such genes exist in domestic materials. So in recent years, breeders have started to use exotic materials as parents for crossing. Breeding activities at IRRI and in the U.S. and other countries and also close communication with foreign breeders have stimulated Japanese rice breeders to use exotic materials in their breeding work. Japanese rice breeders and research workers are now much interested in introducing useful germ plasm, which exotic varieties may have, to their breeding programs for heading behavior and panicle features, vigorous germination and growth in the seedling stage, higher lodging resistance, higher disease resistance, high grain filling, and adaptability to water stress. This situation has been making great changes in Japan's breeding organization, methods, and scale.

The present leading varieties and their parents are shown in Table 2 with brief descriptions of their characteristics.

BREEDING PROCEDURES

Bulk method with shortened breeding cycle

For 15 years after the systematic breeding program started in 1910, the pure-line selection method was used in Japan with great success in increasing yield.

Table 2. Leading rice varieties in Japan in 1970, their parents and characteristics.

Name	Parents	Planted area: Area (000 ha)	Main region	Varietal characteristics
Nihonbare	Yamabiko x Sachikaze	210	From Kanto to Kyushu	Lodging resistance, high tillering, high yield, susceptibility to brown spot
Honenwase	Norin 22 x Norin 1	166	Hokuriku and Tozan	Good grain quality, susceptibility to germination on panicle
Koshihikari	Norin 22 x Norin 1	150	Kanto and Hokuriku	Good grain quality, susceptibility to lodging, resistance to germination on panicle
Reimei	Mutant from Fujiminori	136	Tohoku and Hokuriku	Lodging resistance, high yield, poor grain quality
Sasanishiki	Hatsunishiki x Sasahigure	128	Tohoku	Good grain quality and high yield, susceptibility to lodging, blast disease, and cold
Fujiminori	Norin 17 x Fujisaka 5	114	Tohoku and Kanto	Lodging resistance, high yield, cold tolerance, poor grain quality
Reiho	Hoyoku x Ayanishiki	92	Kyushu	Lodging resistance, high yield, susceptibility to stripe virus
Kinmaze	Ryosaku x Aichi-Nakate-Asahi	56	Kyushu and southwestern regions	Lodging resistance, high yield, poor grain quality, susceptibility to bacterial leaf blight
Nakate-Shinsenbon	Norin 22 x Hayabusa	53	Chugoku	Lodging resistance, susceptibility to bacterial leaf blight
Shiokari	Meguro-mochi x Kyowa[2]	46	Hokkaido	Very early, cold tolerance, leaf withering

From 1927 to about 1950, the pedigree method of cross-breeding was a major procedure with the exception that the backcross method was used to breed for resistance to blast disease. The pedigree method is still important for certain breeding objectives and with certain materials. But this method has been rapidly replaced by the bulk method since Sakai (1949) and Akemine (1958) emphasized the latter's superiority.

The bulk method of breeding has been widely and rapidly adopted in experiment stations because, in general, the effectiveness of selection in early generations of rice hybrids is very low for quantitatively inherited traits, including yield, particularly in individual plant selections. Thus, selection in advanced generations that have been purified somewhat is effective for such traits. For these reasons the bulk method without any plant selections in early generations seems to be more suitable to breeding for yield increase than the pedigree method, particularly on a small scale. In addition labor can be saved because no human selections are made in early generations. Labor saving is a great concern of rice breeders in Japan because they usually handle a large number of crosses in their breeding programs and labor costs are high. Finally, procedures for shortening breeding cycles in a greenhouse are practicable only by means of the bulk method.

Under natural conditions rice cannot be double cropped in Japan. Therefore, greenhouses or warm-winter localities are widely used for accelerating breeding cycles. Akemine (1959) developed a model of breeding procedures for shortening cycles, which has been widely used in Japan for breeding rice. I have previously reviewed several ways of shortening breeding cycles which are used in Japan, and discussed the problems and future prospects of this procedure (Okabe, 1966, 1967). The rapid turnover technique is not only important to shorten the breeding cycle, but also to develop an artificially controlled procedure of rice breeding from this technique in the future.

With expansion of the use of the bulk breeding method, some modified procedures have been devised. The derived-line method and the bulk method with mass selection or with mass-grouping selection are being adopted. The method used by Chugoku National Agricultural Experiment Station in breeding for high yielding varieties adapted to direct seeding (Yamamoto and Shinoda, 1967; Toriyama and Sakamoto, 1968) involves raising bulk hybrid populations in greenhouses for several early generations (F_1 to F_4) and selecting on a line-basis generally in the F_5 generation in fields. Each line, having five plants in the F_5 generation, is derived from each F_4 panicle grown under extremely close seeding density, i.e. 3.0 cm x 2.5 cm. This means that all of the F_5 lines come from different plants in the F_4 generation, since few F_4 plants have tillers due to the extremely high seeding density. This breeding procedure has the following features:

1. Owing to limited number of plants per line, five individuals on the average, a large number of lines can be grown in the F_5 generation, to be subjected to artificial selection.
2. For succeeding breeding materials from generation to generation, masses of the plants derived from one-plant/one-grain culture are used from the F_2 to the F_4 generation.
3. Selection on line-basis in middle generations, not on individual-basis in early generation, gives higher selection efficiency and preliminary information on the purity of each line.
4. Breeding cycles are shortened by 3 years compared with ordinary procedures.

Some rice breeding stations in Japan are using similar types of breeding methods to that in the Chugoku station. Relative to the breeding procedures in a greenhouse, Yamamoto and Shinoda (1967) pointed out that seed dormancy should be eliminated with heat treatment, favorable environmental conditions should be provided to protect rice seedlings in the seedboxes from fertilizer damage, and the promise of each bulk hybrid population should be evaluated in early generations.

Breeding in Aichi Prefectural Agricultural Experiment Station

Many prefectural agricultural experiment stations have their own rice breeding programs. One of them is Aichi Prefectural Agricultural Experiment Station in central Honshu. This station is famous among Japanese rice breeders for its unique method of breeding and its excellent varieties. The point of the breeding method is that promising lines even in early generations, i.e. F_3 to F_5, are frequently used as parents for further steps of breeding program (Aichi Prefectural Government, 1969). This method is not popular in Japan.

Mutation breeding

Mutation breeding has been used in Japan as a supplement to cross breeding. Reimei, released in 1966, is the first rice variety developed from Fujiminori through treatment of dry seeds with gamma-rays. Futsuhara, Toriyama, and Tsunoda (1967) reported that Reimei is similar to Fujiminori except that its culm length is reduced by 15 cm which gives it higher lodging resistance and higher yield than the original variety. Reimei made up 5.4 percent of the total harvested rice area of Japan in 1970. In spite of such a successful achievement, mutation breeding has not become popular in Japan.

Size of breeding populations

Each rice breeding station has about 3 hectares of experimental fields and about 140 sq m of greenhouses. Breeders feel 3 hectares is not sufficient, particularly for raising progeny lines which sometimes number more than 10,000. To contain as many progeny lines as possible in the breeding program, some breeders are using the panicle-to-row method in middle generations, especially in the generation following bulk selection. Each row or line has only five to eight plants. This technique allows breeders to handle many progeny lines in a limited experimental field. The details have been mentioned earlier in this paper.

Breeders' criteria in selection

The procedures mentioned are meant both for producing a high-yielding variety and for reaching general breeding objectives. All rice breeders in Japan have always placed the greatest importance on yield increases, however. If any line under testing shows lower yielding ability than existing check varieties, it would never be released as a recommended variety, even if it is superior in other agronomic characters. It will be, at most, used as a parent in the next breeding program.

In breeding programs for high yielding varieties, Kushibuchi (1966) pointed out that rice breeders, in choosing parents for crosses, place emphasis on lodging resistance, panicle type and panicle weight, performance in farmers' fields, high panicle fertility, and larger grains. Table 3 shows the answers of breeders to questionnaires on characters of parents in breeding for high yields (Kushibuchi, 1966). More than six breeders out of 10 place importance on lodging resistance and panicle type and weight, which were recognized as being directly related to high yielding ability.

Evaluation of rice hybrids in early generations is usually based on the appearance of bulk populations, where breeders' interests are mainly concerned with blast disease damage, plant height, culm quality, plant color and withering of lower leaves at maturity, plant and leaf type, grain quality, growth duration, and low-temperature injury. Thus, yield itself is not their major concern at this stage.

Table 3. Traits on which rice breeders placed great importance in their breeding programs for high yielding ability (Kushibuchi, 1966).

Characteristic	Breeder										Total
	A	B	C	D	E	F	G	H	I	J	
Lodging resistance	—	—	√	√	√	√	√	√	—	√	7
Appearance of panicle type and weight	—	√	√	—	√	√	√		√		6
Data on actual achievement of high yield	√	√	—	√	√	√					5
Larger size of grains	—	√	√	—	√	—	√	√			5
Grain ripening features	√	—	√	—	—	—	√	√			4
Plant type	—	—	—	—	—	√	√	√	√		4
Panicle length	—	√	√	—	—		√		√		4
Short plant height	—	—	—	—	—	√	√	—	√	—	3
Disease resistance	—	—	—	—	—			√	√	√	3
Vigorous early, seedling growth	—	—	—	√	—	√					2
Total	2	4	5	3	4	6	7	5	5	2	

Selection of progeny lines in middle and later generations is usually based on: 1) Height, leaf erectness, and vigor of seedlings. 2) Heading date and its uniformity within plants. 3) Plant type including plant height, panicle length and number, and uniformity of panicle height within plants. 4) Lodging resistance. 5) Panicle type and grain-ripening features. 6) Awns. 7) Shattering. 8) Resistance to diseases and insects. 9) Tolerance to low temperatures. 10) Grain quality and its related characters such as foliage color at maturity, size, shape, and appearance of grains. 11) Grain dormancy and overall superiority.

Some of these data are measured, others are merely observed. Breeders evaluate the superiority or prospects of each line by these criteria. Appropriate check varieties provide the breeders with useful information and a basis for evaluation. The final selection, however, is made without reference to selection indexes. Therefore breeders must be well trained and experienced in selection techniques. The breeders must also be aware of and responsive to changes in agriculture. Fortunately rice breeders in Japan have always had close communication with agricultural extension workers and progressive farmers.

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Discussion: Breeding for high-yielding varieties in Japan

J. B. DAVIS: Do any stations or countries use computers to record information about breeding material which might prove useful in later breeding work?

S. Okabe: A computer that can automatically transfer, record, and process field plot data has already been installed at the National Institute of Agricultural Sciences, Hiratsuka, Kanagawa, Japan. This device is expected to be used for the purpose you have pointed out.

A. O. ABIFARIN: Since lodging is of great concern, what are the methods of observation and recording used in Japan for this trait?

S. Okabe: Observations in fields on lodging and its related characteristics, such as plant height, culm stiffness, and sheath senescence, are used for evaluating lodging resistance in the early and middle generations. The same type of observations are made in later generations under heavy applications of nitrogen.

S. YOSHIDA: What is the definition of plant type in Table 3? Does this refer to "panicle-number type" or "panicle-weight type?"

S. Okabe: It refers not only to panicle-number type or panicle-weight type, but also to the type of leaves, i.e. erectness or leafiness, and to the uniformity of panicle height within a plant or hill, which has been recognized by rice breeders in Japan to be associated with high stability in grain yield.

I. W. BUDDENHAGEN: I note the low priority of disease resistance in importance placed by breeders in Japan in their program for high yielding ability (your Table 3). Is this due to highly developed chemical disease-control practices in Japan or to other reasons? Is this low priority wise?

S. Okabe: Two factors are involved. First, diseases are generally not a limiting factor for achieving high yield in Japan, except in a few localities where disease attacks are frequent and severe. Second, as you have pointed out, chemical control practices are well developed in Japan. In some regions, however, disease resistant varieties have the first priority in the breeding program.

P. A. LIEUW-KIE-SONG: What is the difference in yield between direct sowing and transplanting of very early varieties in Japan?

S. Okabe: At low-yield levels, say 3.0 to 3.5 t/ha in brown rice, there is no difference between the two practices. But for achieving higher yield levels, the direct sowing method has many difficulties.

R. K. WALKER: You stated, "Longer panicles accompanied by fewer tillers are likely to ensure high yield, since this combination gives a large number of grains with better filling." In Japan, how many tillers and what panicle length is considered optimum?

S. Okabe: The situation depends upon cultural conditions. It may be said, however, that 22 to 25 tillers per hill (at two plants per hill) might be optimum under the spacing of 30 x 15 cm. An average of 85 to 95 filled grains per panicle is obtained in such cases.

D. J. MCDONALD: In Australia, "panicle-weight type" varieties have yielded more than the "panicle-number type" (up to 13.2 t/ha), but this has been accompanied by greatly increased variation within panicles for flowering time as well as in grain shape and size. Is this also evident in Japanese high yielding selections?

S. Okabe: In Japan we have no data on such high yielding level with "panicle-weight type" varieties. I suspect the situation might be the same as yours in Australia if varieties of this type are used.

S. K. SINHA: Do you think wide adaptability should be a criterion for choosing parents in breeding for higher yield levels?

S. Okabe: I would say, yes, in general. It might be particularly so in a short-term breeding program. But, in long-term programs, wide adaptability may not always be an essential criterion.

S. V. S. SHASTRY: A small population in the F_4 or F_5 generations would limit recombination. How much would this be a problem in the derived-line method?

S. Okabe: In the derived-line method used in Japan, a fairly large number of lines — more than 1,000 — are grown in the F_5 generation. Therefore, I would say, few significant problems exist in relation to recombination.

P. R. JENNINGS: Why have preliminary efforts to incorporate the IR8-type dwarfing gene into Japanese varieties failed?

S. Okabe: I don't think that efforts to incorporate dwarfing gene or genes into Japanese varieties have failed in Japan. The efforts are now under way and, we expect, will be successful in the near future. Breeding materials developed from hybrids of IR8 have had many undesirable characteristics however. It seems some of the general background of IR8 other than the dwarfing gene have given deleterious effects on its progeny. Actually, it is observed that breeding lines derived from IR8 hybrids have leaf discoloration at different growth stages and poor grain maturation.

The development of early maturing and nitrogen-responsive rice varieties in the United States

T. H. Johnston, N. E. Jodon, C. N. Bollich, J. N. Rutger

The coordinated rice improvement program in the United States was established by the U.S. Department of Agriculture and the agricultural experiment stations of the four major rice-producing states in 1931. Its continuing primary breeding objective is to develop varieties that will assure a maximum and stable production of rice types required by producers and consumers. Varieties developed in the cooperative program occupy almost the entire area planted to rice in the U.S. Yields of rough rice in the U.S. have doubled in recent years primarily because of new disease-resistant, stiff-strawed, nitrogen-responsive, high-yielding varieties; new chemicals for weed control; and the increased and more efficient application of nitrogen fertilizers. Breeding for early maturity has been quite successful. The development of the Bluebelle variety in Texas and of Starbonnet in Arkansas has greatly increased lodging resistance and grain yields. Advanced-generation selections from crosses with various sources of short stature and nitrogen responsiveness currently are being evaluated in the breeding programs of all four major rice-growing states.

INTRODUCTION

Cooperative rice breeding studies were started in the United States when the first major rice experiment station was established at Crowley, Louisiana, in 1909. Rice breeding research in the U.S. from 1909 to 1961 has been discussed by Jones (1936), Jones et al. (1941, 1953), and Adair et al. (1966).

COORDINATED PROGRAM OF RICE IMPROVEMENT

The present coordinated rice breeding programs of the Agricultural Research Service (ARS), U.S. Department of Agriculture and the state agricultural experiment stations in the four major rice-producing states were started in 1931. USDA rice breeders were employed to work with state personnel and other agencies to improve rice varieties and cultural practices. The work is centered at the Louisiana State University Rice Experiment Station at Crowley, Louisiana, the Rice Experiment Station at Biggs, California, the University of California at Davis, the Texas A&M University Agricultural Research and

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Extension Center at Beaumont, Texas, and the University of Arkansas Rice Branch Experiment Station at Stuttgart, Arkansas. In addition, rice research has been conducted for 20 years at the Delta Branch Experiment Station at Stoneville, Mississippi, and at two or three locations in Missouri.

The continuing primary objective of rice breeding in the U.S. is to develop varieties that will assure a maximum and stable production of the types of rice required by producers and consumers or exporters (Adair et al., 1966). The development of very short-season and short-season varieties (100-day to 130-day) of short-grain, medium-grain, and long-grain types is emphasized. Attention is given to developing varieties with a reasonably wide maturity range within each grain type, however.

ACHIEVEMENTS AND APPRAISAL OF PAST ACTIVITIES

Adair (1967) described the rice research conducted by the Crops Research Division (now the Plant Science Research Division), ARS, USDA. The investigations are carried out cooperatively with the agricultural experiment stations in Arkansas, California, Louisiana, Texas, and Mississippi; the California Cooperative Rice Research Foundation, Inc.; and the Texas Rice Improvement Association. Additional tests have been conducted cooperatively in countries in Central and South America.

Early cooperative investigations dealt mainly with research on cultural practices, breeding, and diseases. Adair (1967) stated that many of the cultural practices, most of the varieties grown, and most disease control methods used in the U.S. have resulted from this research and that the varieties developed in the cooperative rice breeding programs have been of immeasurable value to the U.S. rice industry. Nearly all rice land in the U.S. is planted to these varieties. Adair (1967) listed 32 principal varieties developed in the cooperative program. Since his report, four additional varieties have been released. All these varieties are listed in Table 1.

As an example of the potential value of a single variety, Johnston and Adair (1969) pointed out that the newest major variety, Starbonnet, averaged 8 percent more milled rice per unit area than Bluebonnet 50 in 35 major tests in Arkansas from 1964 to 1968. This advantage was in addition to the savings in harvest costs that resulted from Starbonnet's increased lodging resistance and ease of harvesting. Based on the 1970 acreage of Starbonnet in Arkansas (Rice Millers Association, 1970) this meant an increased value of over $5 million to the Arkansas rice industry in 1970 alone. Other major varieties which have had similar impact during the past 35 years include Zenith, Bluebonnet 50, Nato, Belle Patna, Saturn, and Bluebelle.

All new rice varieties developed in the program are named and released cooperatively by the Plant Science Research Division and the State agricultural experiment station involved. The experiment stations maintain breeder seed of each variety released.

Most of the research on culture is conducted by state experiment station personnel (Adair, 1967; Adair, Miller, and Beachell, 1962). Numerous

Table 1. Principal rice varieties developed in cooperative Federal state breeding programs in the United States.

Variety	C.I. no.[a]	Grain type	Year released	Station producing	Breeders involved	Parent varieties	Duration[b]
Colusa	1600	short	1917	La.	Chambliss & Jenkins	Chinese	Ey
Fortuna	1344	long	1918	La.	Chambliss & Jenkins	Pa Chiam	Ms
Caloro	1561-1	short	1921	Calif.	Adams, Chambliss & Jones	Early Wateribune	Ms
Rexoro	1779	long	1928	La.	Chambliss & Jenkins	Marong-Paroc	L
Nira	2702	long	1932	La.	Chambliss & Jenkins	Sel. fr. unnamed Philippine var.	L
Zenith	7787	medium	1936	Ark.	Adair	Blue Rose	Ey
Arkrose	8310	medium	1942	Ark.	Jones & Adair	Caloro × Blue Rose	Ms
Texas Patna	8321	long	1942	Tex.	Beachell	Rexoro × C.I. 5094	L
Bluebonnet	8322	long	1944	Tex.	Beachell	Rexoro × Fortuna	Ms
Cody	8642	short	1944	Mo.	Jones, Davis & King	Colusa × Lady Wright	Ey
Magnolia	8318	medium	1945	La.	Jones & Jodon	Imp. Blue Rose × Fortuna	Ey
Calrose	8988	medium	1948	Calif.	Jones & Davis	Caloro/2 × Calady	Ms
TP 49	8991	long	1948	Tex.	Beachell	Tex. Patna × Rexoro C.I. 7689	L
Lacrosse	8985	medium	1949	La.	Jodon	Colusa–BR × Shoemed Fortuna	Ey
Bluebonnet 50	8990	long	1951	Tex.	Beachell	Bluebonnet	Ms
Century Patna 231	8993	long	1951	Tex.	Beachell	Tex. Patna × Rexo.–Sup. Bl. Rose	Ey
Improved Bluebonnet	8992	long	1951	Tex.	Beachell	Rexoro × Nira	Ms
Sunbonnet	8989	long	1953	La.	Jodon	Bluebonnet	Ms
Toro	9013	long	1955	La.	Jodon	Bbt. × Rexoro/2 –Blue Rose	Ms
Nato	8998	medium	1956	La.	Jodon	Rexoro–Pr Leaf × Magnolia	Ey
Mo. R 500	9155	medium	1956	Mo.	Adair, Poehlman & Cavanah	Mesh. Zen. × Gin Bozu–Ey BR	V Ey
Gulfrose	9416	medium	1960	Tex.	Beachell, Bollich & Scott	Bruinmissie sel. × Zenith	Ey

Continued on next page.

Table 1. *Continued*

Variety	C.I. no.[a]	Grain type	Year released	Station producing	Breeders involved	Parent varieties	Duration[b]
Belle Patna	9433	long	1961	Tex.	Beachell, Bollich & Scott	Rexoro × Hill sel. Bluebonnet	V Ey
Northrose	9407	medium	1962	Ark.	Johnston & Adair	Lacrosse × Arkrose	Ey
Nova	9459	medium	1963	Ark.	Johnston & Adair	Lacrosse × Zenith Nira	Ey
Palmyra	9463	medium	1963	Mo.	Poehlman	Caloro × Blue Rose	Ey
Vegold	9386	long	1963	Ark.	Adair & Johnston	Hill sel. × (T. Patna × Rex-SBR)	V Ey
Saturn	9540	medium	1964	La.	Jodon & Atkins	Lacrosse × Magnolia	Ey
Bluebelle	9544	long	1965	Tex.	Bollich, Beachell & Webb	C.I. 9214 × CP 231 C.I. 9122	V Ey
Dawn	9534	long	1966	Tex.	Bollich & Atkins	CP 231 × TP49 C.I. 9515	Ey
Nova 66	9481	medium	1966	Ark.	Johnston & Templeton	Nova	Ey
Starbonnet	9584	long	1967	Ark.	Johnston & Webb	CP 231 × Bluebonnet	Ms
CS-M3	9675	medium	1968	Calif.	Mastenbroek & Adair	Smooth No. 4 Calady 40 × Calrose	Ms
Della	9483	long	1970	La.	Jodon, Sonnier & McIlrath	R-D × (Century × Rexoro Zenith)	Ey
Vista	9628	medium	1970	La.	Jodon, Sonnier & McIlrath	Rexoro-Zenith × Lac. Magnolia	V Ey
CS-S4	9835	short	1971	Calif.	Adair & Mastenbroek	Sm 487-1 × Caloro	Ms

[a]Cereal Investigation no. [b]Relative maturity: V Ey very early, Ey early, Ms midseason, L late.

cooperative experiments have been conducted in Arkansas to determine the optimum rate and timing of applications of nitrogen fertilizer for individual rice varieties (Hall, Sims, and Johnston, 1968; Sims, Hall, and Johnston, 1967; Sims, Hall, Johnston, and Blackmon, 1967; Sims, Johnston, and Henry, 1965; Wells and Johnston, 1970; Wells et al., 1970). Three developments are largely responsible for the doubling of rice grain yields in recent years: the increased and more efficient use of nitrogen fertilizers and, in Arkansas, the development of the "internode method" of timing midseason applications; new disease-resistant, stiff-strawed, nitrogen-responsive, high-yielding varieties; and new chemical methods of controlling weeds, especially grassy weeds (Smith and Shaw, 1966; Smith, 1968, 1970). Second cropping or stubble-cropping also contributed greatly to doubling the annual rice yields in Texas (Evatt and Beachell, 1962).

BREEDING FOR EARLY MATURITY

Jenkins (1936) reported on an experiment that was started in 1917 to determine the best seeding dates for rice varieties then available. Since then, numerous date-of-seeding experiments have been conducted, especially in Louisiana (Jodon, 1953, 1966; Jodon and McIlrath, 1971) and Arkansas (Adair, 1940; Adair and Cralley, 1950; Johnston, 1970). These tests emphasized the need for and provided a means of differentiating between true earliness and responsiveness to daylength. Adair (1940) examined the effect of seeding time on grain yield and milling quality and stressed that for high yields of good milling quality, early (short-season) varieties should not be seeded so early that they mature during hot summer weather. In Louisiana, varieties that mature in 115 to 130 days tend to be the most productive, but when they are seeded early in the spring and ripen in midsummer, their grain quality may suffer.

Time of maturity (length of growing season) is an important consideration (Adair et al., 1966). Although short-season and very-short-season types have gained favor in recent years, midseason types also are being developed to fill a need to spread out the harvest season.

Pure-line selections from the then existing varieties may have provided the major sources of earliness 40 to 50 years ago. For example, Zenith was selected in 1930 from the later maturing variety, Blue Rose (Jones et al., 1953).

Transgressive segregation for earliness has provided material from which several commercial and experimental varieties have been selected. Northrose, for example, was several days earlier in maturity than its parents (Johnston et al., 1962*a*, 1962*b*).

Improved varieties of shorter duration have been developed by crossing adapted varieties with available sources of earliness. One source of extreme earliness was an unnamed long-grain type designated Hill Selection (B45-2253). It was crossed with another unnamed selection, Texas Patna x Rexoro—Supreme Blue Rose (4033A4-30-2), in 1945. Seed from an F_1 plant was sent to Stuttgart and an F_6 line from this material eventually became Vegold (Johnston and Adair, 1965).

The extreme earliness of Belle Patna also was derived from Hill Selection. C.I. 9122 (a selection from the cross Hill Sel. x Bluebonnet) was crossed with Rexoro, giving rise to Belle Patna (Beachell et al., 1961; Bollich, Scott, and Beachell, 1965*a*), the first variety released primarily for "doubling cropping" or production of a stubble crop. The extreme importance of a high degree of weed control was emphasized in the first commercial production of Belle Patna and Vegold. Belle Patna constituted 64 percent of the Texas rice acreage in 1965 (Rice Millers Association, 1965).

Bluebelle, the next major very-short-season variety, also derived its earliness from C.I. 9122. Bluebelle originated from a cross between the unnamed selection, C.I. 9214, and a selection from Century Patna 231 x C.I. 9122 (Bollich et al., 1966, 1968). In 1970, Bluebelle and Belle Patna composed 75 percent of the Texas acreage (Rice Millers Association, 1970).

Early segregates from a cross between Rexoro and a strain of red rice were a source of earliness used in crosses at Crowley. Vista is the earliest medium-grain variety available for the southern rice area (Jodon, Sonnier, and McIlrath, 1971). Starbonnet, the leading variety in the U.S., is classed midseason in maturity but it is 7 to 10 days earlier than Bluebonnet 50, the variety it replaced.

The very-short-season varieties currently being tested in the Uniform Performance Nursery groups in the southern rice area are primarily early segregates from crosses involving the long-grain varieties, Vegold, Belle Patna, and Bluebelle, and the medium-grain varieties, Gulfrose, (Bollich, Scott, and Beachell, 1965*b*) and Palmyra (Poehlman, 1965).

Several sources of extremely early maturity were included in the California breeding program in 1967 (J. R. Erickson, *unpublished*). One of these lines, Kitaminori (P.I. 291650) from Japan, matures 3 weeks sooner than Colusa and Earlirose, the two earliest California varieties. In 1970, F_4 populations from crosses between Kitaminori and three California varieties were evaluated at Davis and Biggs. Many lines were 2 weeks earlier than Colusa but yield data were inconclusive. Other breeding lines selected at Biggs in 1970 were 10 days earlier than Colusa and 6 percent higher in yield.

Considerable progress is being made in the development of early, long-grain varieties adapted to California conditions. One experimental line produced 8.97 t/ha of rough rice at Biggs in 1970, but it appears to have a narrow range of adaptation.

BREEDING FOR LODGING RESISTANCE

Plant height and lodging resistance are closely related. Short straw, however, does not guarantee a high degree of lodging resistance. For example, Taichung Native 1 produces short-strawed plants but they are rather susceptible to lodging in the southern U.S. The development of medium-grain varieties with increased lodging resistance has been a gradual process. Zenith (Jones et al., 1941) showed more lodging resistance than Early Prolific and earlier varieties. Nato had shorter straw than Zenith and lodged less (Jodon, 1957). Northrose had shorter straw and resisted lodging more than did either of its parents (Johnston et al., 1962*a*, 1962*b*) or other medium-grain varieties then available. Nova 66 showed considerably more lodging resistance than Nato and Nova (Johnston et al., 1966). Also, under conditions of severe lodging, Nato usually falls flat on the ground while the stems of Nova 66 characteristically bend over about 25 cm above the ground permitting almost normal combine harvesting. Vista shows a similar advantage compared with Saturn in Louisiana (Jodon et al., 1971).

In the mid-1950's, especially in Arkansas, the rate and timing of N-fertilizer applications profoundly affected plant height and subsequently lodging, particularly in medium-grain varieties which showed a rather heavy vegetative response. The importance of nitrogen fertilization in rice varietal improvement was emphasized in 1962 (Johnston, 1963). In a cooperative experiment at Stuttgart (Johnston et al., 1966), nitrogen was applied in split doses of 45 kg/ha N about 15 days after seedling emergence and varying amounts near midseason. Maximum grain yields were obtained from the 90 kg/ha rate of nitrogen. The timing of the second increment had a marked effect on plant height, lodging, and grain yield, however. Delaying its application for 67 days from the earliest time used (43 days after seedling emergence during the active tillering stage) until 24 days later (during the reproductive growth phase), increased rough rice yield from 5.68 to 7.91 t/ha, decreased plant height from 137 to 119 cm, and drastically reduced lodging at maturity from 69 percent to 2 percent. This clearly indicates the importance, especially under Arkansas conditions, of adopting fertilization practices that bring out the optimum performance from breeding material and potential new varieties. In some varietal tests, a moderate rate of nitrogen fertilization is used on two replications and a higher rate on the other two to get more information on lodging resistance.

Considerable lodging resistance has been observed in long-grain varieties since the release of Bluebonnet in 1944 (Beachell, 1946). Bluebonnet 50 was more uniform and averaged a few inches shorter in plant height. Century Patna 231 also was fairly resistant to lodging. Belle Patna, the first very-short-season variety to be released (Beachell et al., 1961), had only moderate lodging resistance which was noticeably influenced by fertilization practices. With the release of Bluebelle in 1965 (Bollich et al., 1966), a variety highly resistant to lodging became available to Texas and Louisiana growers of very-short-season (double crop) rice. Starbonnet, released in Arkansas in 1967 (Johnston et al., 1967), provided growers in Arkansas and Mississippi with a midseason variety that had more lodging resistance and 15 percent shorter straw than Bluebonnet 50, which it rapidly replaced.

Sources of germ plasm used in the past 15 years to develop varieties with shorter straw and increased lodging resistance include: (a) shorter-strawed mutants from seeds treated with X-ray and thermal neutrons (Beachell, 1957); (b) dwarf mutants from C.I. 9187 and Nova from Stuttgart; (c) transgressive segregates such as Northrose (Johnston et al., 1962*a*, 1962*b*) and Starbonnet (Johnston et al., 1967), with shorter and stiffer straw than their parent varieties; (d) occasional shorter strawed segregates, such as those found in large blocks of breeder-seed head rows of Starbonnet (short-strawed Starbonnet, C.I. 9722) and Dawn (short-strawed Dawn, C.I. 9649); (e) short-strawed selection, 13d, used extensively in crosses at Crowley; (f) short-strawed introductions such as the japonica-type variety Tainan-iku 487 (P.I. 215936) and Taichung Native 1 from Taiwan, and, more recently, IR8 and other semi-dwarf introductions from IRRI which carry germ plasm for short straw.

Short-strawed selections have been obtained from crosses with sources (a) and (b), above, but none of these have been as productive as segregates from normal parents. Both Northrose and Starbonnet have been used extensively in the crossing program.

Short-strawed Starbonnet (SSS) has 15 percent shorter straw than Starbonnet and preliminary evaluation of unpublished data on large populations of F_2 and parent plants grown at Stuttgart in 1970 indicates that the two selections differ in height by only one major recessive gene. SSS is quite similar to Starbonnet in yielding ability and in cooking and processing characteristics. The latter characteristic makes SSS a potentially important contributor of shorter straw for long-grain crosses in the U.S. due to complex inheritance of quality characteristics. SSS has 30 percent shorter straw than Bluebonnet 50. All of the hundreds of F_2 plants grown at Stuttgart in 1970 from a cross between them were intermediate in plant height. Nearly all were shorter than the mean height of 100 plants grown of the Bluebonnet 50 parent. Many were nearly as short as SSS.

The short-statured selection, 13d, characterized by shorter lower internodes which are quantitatively inherited, has been used extensively as a parent in the Louisiana program. Consequently, the average height of advanced selections has been reduced considerably in recent years. Over half of the advanced early to midseason breeding lines grown at Crowley in 1970 have 13d parentage. The selections tend to be leafy and low tillering, however. None have been released.

One dwarf of diminutive plant type used as a parent at Crowley has given rise to selections of practical stature and fairly desirable long-grain type, though none appear sufficiently productive. A stocky, intermediate-stature, single-gene dwarf was obtained from an F_2 population. Unfortunately, an undesirable grain shape appeared to be completely linked with the dwarfness.

The Taiwan semidwarf character became available only a few years ago. Progress in developing acceptable varieties of this type is slow. Taichung Native 1 is susceptible to lodging and to blast, but is highly productive. It was crossed with H4 at Crowley, and highly blast-resistant, upright dwarf types were obtained before IR8 was available. Increased susceptibility to *Helminthosporium oryzae* Breda de Haan and straighthead has appeared in semidwarf segregates as have undersized, ill-shaped, and chalky grains. A selection of note is one with large, clear, cylindrical long grain, which matures at the same time as Dawn. Unfortunately, quality tests show that the milled kernels of this selection are typical of medium-grain rather than long-grain varieties. These results further emphasize the desirability of having germ plasm for short stature in a parent variety already possessing the desired milling, cooking, and processing characteristics. Such a variety greatly reduces the number of crosses and backcrosses and the amount of selecting and testing needed to develop improved types with short straw and lodging resistance and acceptable grain quality.

Although treated separately here, breeding for shorter straw and lodging resistance is not divorced from breeding for responsiveness to higher rates of nitrogen fertilizer.

BREEDING FOR IMPROVED PLANT TYPE AND RESPONSIVENESS TO NITROGEN FERTILIZER

The unnamed Stuttgart selection, C.I. 9187, is one of the most outstanding parents used to date in breeding for desirable plant type and responsiveness to nitrogen-fertilizer (Adair et al., 1966). It came from the cross, R-7689 x

(TP x R-SBR), made at Beaumont in 1945. Seed from an F_1 plant was sent to Stuttgart where succeeding generations were grown. C.I. 9187 showed outstanding response to high rates of nitrogen fertilizer at Beaumont in 1957 and 1958 (Evatt, Johnston, and Beachell, 1960) and even greater response in tests at Stuttgart in 1957, 1958, and 1959 (Sims et al., 1965).

C.I. 9187 is in the parentage of 12 of the 48 long-grain varieties included in the Uniform Performance Nursery groups grown in the southern U.S. in 1971. One of these, C.I. 9654, a selection from the cross C.I. 9453 – Bluebonnet 50 x C.I. 9187 – has established an outstanding performance record. In 1968, it ranked first among the 18 entries in the seven major replicated performance tests grown in Arkansas with an average of 6.72 t/ha of rough rice compared to 6.71 t/ha for the consistently high-yielding Nova 66. This was the first time a long-grain variety ranked above all medium-grain entries in Arkansas tests (Johnston, 1969*b*).

C.I. 9654 has slightly less resistance to lodging than the popular Starbonnet. But, it has averaged over 670 kg/ha more grain and about 225 kg/ha more head rice than Starbonnet in 32 replicated tests in Arkansas over the past several years (Johnston, 1971).

Beachell and Evatt (1961) reported that P.I. 215936 produced 6.17 t/ha from 180 kg/ha N in a Texas fertilizer test while Bluebonnet 50 produced its highest yield of 4.50 t/ha from 90 kg/ha N. P.I. 215936 produced somewhat higher yields than Bluebonnet 50 even without nitrogen-fertilizer. Although Beachell and Evatt (1961) pointed out that certain characteristics of P.I. 215936 precluded its acceptance as a commercial variety in Texas, they suggested that its desirable features might be of value in developing high-yielding varieties for the southern U.S. rice area. Three medium-grain selections and one long-grain selection from Beaumont and Crowley, that are entries in the Uniform Performance Nursery groups in 1971, have P.I. 215936 as a parent. In addition, an unnamed short-grain Stuttgart selection from the cross Northrose x P.I. 215936, designated as C.I. 9836, appears very promising in Arkansas (Johnston, 1971). Besides having smooth hulls, it has other distinct advantages over Caloro: much shorter straw, much less lodging, less chalky milled kernels, greater resistance to blast, and greater response to nitrogen fertilizer.

Bollich et al. (1969) report that Taichung Native 1 has been used as a parent in the cooperative breeding program in Texas since 1962. Numerous high-yielding lines have been selected from the crosses but their grain quality has failed to meet the rigid standards required for U.S. varieties. IR8 has been used as a parent in the breeding programs in the U.S. since it became available in 1966.

Breeding for improved plant types that are responsive to high rates of nitrogen has been increasingly emphasized for the past several years. At Beaumont, Taichung Native 1, IR8, IR20, IR22, IR160 lines, P.I. 331581, and P.I. 331582 were used as sources of improved plant types. The latter two selections are from the IRRI cross, Bluebelle/6 x Taichung Native 1. Although Taichung Native 1 and IR8 appear to have much higher yielding ability than the other semidwarf lines, the latter seem to offer the best potential as parents because they have better grain quality. Although the two selections from the cross, Bluebelle/6 x

Taichung Native 1, have only average yield potential, they have excellent long-grain size, shape, and clearness, and typical U.S. long-grain quality. In Texas, where the primary interest is in long-grain varieties, these two selections should prove very valuable as parents.

The semidwarf types were crossed with various U.S. medium- and long-grain varieties and selections and many dwarf lines have been selected. A number of advanced-generation, semidwarf lines from the cross, Taichung Native 1 x C.I. 9545, have produced grain yields nearly as high as those of Taichung Native 1 and IR8 in Texas tests. But all produce kernels that are very chalky and all have an amylose content that is atypical of U.S. medium-grain or short-grain varieties. Although unacceptable as varieties in the U.S., some of these selections are being tested in other states to determine their yield potential over a wider environmental range. Since they are glabrous, earlier than IR8, and have acceptable grain size and shape, these selections are being used as parents.

IR8 and Taichung Native 1 also have been used in crosses at Crowley and Stuttgart. At Stuttgart, however, they have been crossed only with short-grain and medium-grain varieties. Many advanced-generation lines from crosses between IR8 and Nova 66 and other, smooth-hulled, medium-grain varieties are being grown at Stuttgart in 1971. A recent round-seeded mutation from Starbonnet (C.I. 9834) that appears to have short-grain quality characteristics and the Starbonnet plant type is being crossed with adapted short-grain varieties at Stuttgart.

Existing California varieties are likely to lodge at high fertility levels. Several sources of short stature, including Taichung Native 1 and IR8, were introduced by Erickson and Mastenbroek into the breeding program in 1967 and 1968 (Carnahan, Mastenbroek, and Morse, 1970). Many of the first short-statured segregates were rather late maturing for California; however, short-statured lines of suitable maturity have been selected for further testing and for back-crossing to the California parents. Several hundred lines introduced from IRRI in 1969 provided additional short-statured sources (Lehman et al., 1970). Some are now being used in the California breeding program.

Semidwarf parents have been used extensively in recent crosses, but significant improvements in plant type also are being achieved by using parents that have normal, i.e. non-dwarf, plant type. The parent most widely used for this purpose at Beaumont has been C.I. 9545, a selection from the cross, P.I. 215936 x C.I. 9214. Numerous medium-grain lines from crosses of C.I. 9545 with Nova, Northrose, Dawn, and experimental lines have shown excellent plant type, straw almost as short as that of IR8, high resistance to lodging, and excellent clear grains with acceptable size, shape, and quality. These selections have tended to produce yields well above those of present commercial varieties in Texas. But the maximum rough rice yield at Beaumont, according to available records, is 8.97 t/ha, produced by Taichung Native 1 in 1967. The highest yield achieved thus far in Texas from IR8 is 8.60 t/ha, produced in 1970.

The rice varieties that have produced the highest yields in Arkansas tests over the past 30 years vary widely in plant type. Nira, a very tall but fairly stiff-strawed, leafy, late-maturing, long-grain variety, produced over 6.5 t/ha of rough rice in a replicated test on newly cleared woodland in 1941 (C. Roy Adair, *unpublished*). This yield apparently was not exceeded until 1954 when Caloro, a japonica-type variety, produced slightly more. In 1958, C.I. 9187, the narrow-leaved, nitrogen-responsive, experimental variety mentioned previously, produced about 7.8 t/ha. More recently, improved long-grain experimental varieties have produced 8.2 to 8.4 t/ha. Outstanding yields by commercial medium-grain varieties include 9.5 t/ha in 1966 produced by Arkrose, a tall weak-strawed variety, and about 9.0 t/ha by Nova 66. A Stuttgart selection from the cross Nova x Gulfrose produced nearly 9.4 t/ha in 1970. Outstanding yields produced by short-grain varieties include about 9.1 t/ha by P.I. 215936 and about 9.3 t/ha by Caloro, both in 1966. B. R. Wells (*unpublished*) reported that in nitrogen fertilizer tests at Stuttgart Nova 66 produced about 9.2 t/ha in 1967 and the experimental long-grain variety, C.I. 9654, produced over 9.4 t/ha in 1970. In a rate-of-seeding and row-width test in 1970, Wade F. Faw (*unpublished*) reported a yield of about 9.2 t/ha for C.I. 9654.

The highest yields obtained so far at Stuttgart from IR8 have been 9.75 t/ha in 1969 and from Taichung Native 1 about 10.1 t/ha in 1970. The latter averaged 58 percent lodging in this test. The promising long-grain variety, C.I. 9654, produced 9.18 t/ha in the same 1970 test, with an average of 29 percent lodging. The plant type of C.I. 9654 is fairly desirable and is similar to that of one of its parents, C.I. 9187.

The highest grain yield ever recorded in the southern U.S. was 10.49 t/ha, produced at Stuttgart in 1970 by a selection from IR84-82-3-43 (Peta x P.I. 215936). It averaged 109 cm in plant height (to the tip of the extended panicles) compared to 84 cm for Taichung Native 1 and 109 cm for C.I. 9654. This IRRI selection is designated P.I. 325893. In the test in which it received a high rate of nitrogen in a three-way split, the selection was not excessively tall but was rather leafy a few days before harvest. The panicles were fairly heavy and many of the plants lodged 10 days before harvest. Lodging at maturity averaged 60 percent. The milled kernels of this rough-hulled, medium-grain variety are quite chalky and unsuitable for the U.S. market. Also, the cooking characteristics are atypical of U.S. medium-grain rice.

Selections such as P.I. 325893 and others that show signs of high yield potential in preliminary tests are included in a "Special Yield Test" at Stuttgart. Sixteen entries in each of two maturity groups were grown in each of the last 3 years. The only criterion used for varieties in these two tests is an indication of high yield potential. The highest yielding varieties from a wide range of parentage and plant type are included without regard for lack of disease resistance or other undesirable characteristics.

The rice varieties that have produced the highest grain yields over the past 30 years have ranged in plant height from 80 to 150 cm; in leaf width from narrow to wide; in leaf length from medium to long; and, in leaf position from erect to drooping. For varieties that are somewhat tall and only moderately resistant to lodging, the rate and timing of nitrogen fertilization for optimum yields are much more critical than the rate and timing for shorter and stiffer strawed types.

As a result in Arkansas before potential varieties are released to growers they are tested at three rates of nitrogen fertilizer in two and three split doses and at five to seven timings for midseason applications (Johnston, 1963). Outstanding experimental varieties are compared with the leading commercial varieties of the same maturity and grain type. The primary purpose of this test is to develop the best possible fertilizer schedule for each variety so that it will give consistently high grain yields with a minimum of lodging and disease.

Results from this experiment also provide a reliable basis for deciding the appropriate fertilizer treatments for use in breeding and preliminary and replicated varietal performance tests. In general, relatively high rates of nitrogen fertilizer are used for varietal performance tests and, usually, in three-way split applications. About 40 to 50 percent of the total nitrogen rate is applied with the first flood, about 15 days after seedling emergence and about 1 to 3 days after herbicide application. The first midseason application is scheduled when the proper median internode length is reached in the standard check variety. The final application is made about 10 to 14 days later. The rates for the two midseason applications usually are equal.

Generally, all nitrogen fertilizer for the performance tests at Crowley, Louisiana, and Stoneville, Mississippi, is applied at seeding time. At Beaumont, Texas, about two-thirds of the nitrogen is applied at the time of the first flood and the remainder just after "jointing" has started. Practices for tests in California vary somewhat but split applications often are used.

Wells and Johnston (1970) reported on the differential response of three rice varieties to timing of midseason nitrogen applications in Arkansas. Two commercial long-grain varieties with short, stiff straw, Starbonnet and Bluebelle, were compared with the taller and somewhat more leafy medium-grain variety Nova 66. The timing of the midseason applications was measured from seedling emergence to bracket the recommended internode length for each variety, based on previous results from Sims, Hall, Johnston, and Blackmon (1967); Sims, Hall, and Johnston (1967); Hall, Sims, and Johnston (1968); and Wells et al. (1970). Maximum grain yields were associated with nitrogen applied at median internode lengths averaging 21.0 mm for the very-short-season Bluebelle, 58.5 mm for the short-season Nova 66, and 5.0 mm for the midseason maturing variety Starbonnet. Delaying midseason nitrogen applications until these stages of plant development resulted in shorter straw, less lodging, and increased grain weight and head-rice yields.

Wells and Johnston (1970) pointed out that the mean length of the first elongating internode in the main culms which is used to time nitrogen application for maximum grain yield and minimum plant height and lodging, is closely associated with plant type. Starbonnet and Bluebelle, which have short, stiff straw and fairly erect leaves, responded better to nitrogen applied at a shorter internode length than Nova 66, a taller, broader leaved variety. When nitrogen was applied too early, Nova 66 produced considerably more excess vegetation than did Bluebelle and Starbonnet. The latter two varieties have plant types which approach one currently favored by many plant breeders.

The relation of plant type to yield at Beaumont was studied for several years to determine the best plant type for Texas environmental conditions and cultural practices (Bollich and Scott, 1969, 1970; Scott and Bollich, 1970). Concern with this problem was prompted by the fact that the highest yields in uniform trials in southern U.S. were frequently produced by leafy types. Results to date indicate that the nitrogen level at which selections are tested is important, since leafy types may show a yield advantage at lower nitrogen levels but little response to higher nitrogen rates, while less leafy types tend to show a strong positive response to high rates; that both high yielding and low yielding lines can be found in all plant types from segregating populations, but the semidwarf types tend to produce the top yields; and that the 18- to 20-cm row spacing currently used in drill-seeded yield trials in the southern United States favors the less leafy types, since the leafy types respond markedly to high nitrogen levels at a wide row spacing. The superiority of the "excellent" (short-strawed, less leafy) plant types frequently vanishes if the yield of excellent types at 18-cm row spacing is compared with the yields of the leafy types at 27-cm row spacing and at high nitrogen levels.

Other experiments concerned with effects of test conditions on the results obtained from different varieties have been described by McIlrath (1969, 1970); Scott and Bollich (1969); Teng et al. (1970); Templeton, Wells, and Johnston (1970); Wells and Kanarengsa (1970); Johnston (1969*a*); and Johnston and Templeton (1970).

In Texas, selection of types with shorter height, less leafiness, and more upright leaf habit has been emphasized. On the average, these selections appear to be shorter and less leafy than the Arkansas selections included in regional trials. Although the selections with "improved plant type" tend to produce the top yields in the regional trial at Beaumont, the somewhat taller Arkansas selections tend to be superior in tests at Stuttgart, suggesting that there probably is no one superior plant type for all conditions and environments. Many of these somewhat leafy types show 10 to 20 percent shorter straw and higher grain yields at Stuttgart than at Beaumont and Crowley, under the fertilizer rates and other cultural practices currently being used. Splitting the nitrogen fertilizer into one early (15-day) and two midseason applications in Arkansas tests may have partly caused the differential responses in plant growth.

The fact that Taichung Native 1 has tended to produce the top yields at Beaumont and that IR8 also has produced excellent yields has encouraged use of semidwarf parents at Beaumont. Whether or not short, lodging resistant, upright-leaf types derived from normal parents can yield as much under Texas conditions and cultural practices as lines of similar plant types derived from semidwarf parents should be studied. For the present, breeders assume that semidwarf types will produce maximum yields in Texas as they have in the tropics.

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Discussion: The development of early maturing and nitrogen-responsive rice varieties in the United States

B. B. SHAHI: Although you have been trying to develop early maturing and nitrogen-responsive varieties, you at the same time stated that attention is given to developing a reasonably wide maturity range. What do you mean by wide maturity range?

T. H. Johnston: About 100 to 145 days from seeding to maturity.

E. C. CADA: In breeding for high response to nitrogen fertilizer, is the cost-benefit ratio given consideration in the process of selection?

T. H. Johnston: Breeding material is grown at levels of nitrogen slightly above those recommended and used by most advanced rice growers. Row spacing also corresponds to that recommended for high production according to results obtained by agronomists and physiologists in special field trials. Nitrogen rates used are at economically feasible levels. The most promising lines being increased and purified for possible commercial production are included in special cooperative tests under very high levels of nitrogen fertilization and seeding rate to study their reactions.

G. L. WILSON: Referring to the statement of timing the second nitrogen application, Matsushima has described this effect in both morphological and physiological terms. The reference might be added to your Literature Cited so that other workers might try in relation to critical developmental stages, rather than number of days shown in your paper.

T. H. Johnston: We used the number of days in experimental procedure to get a spread in morphological development; plant samples were taken at each time of application to determine actual stage of growth for each treatment. For reference, please see Hall, Sims, and Johnston, 1968.

H. M. BEACHELL: What is the row spacing used in growing the semidwarfs?

T. H. Johnston: Formerly we used 12-inch rows. Now we use $7\frac{1}{2}$-inch row spacing.

H. M. BEACHELL: Why not use a wider row spacing?

T. H. Johnston: Dr. Wells obtained high yields with narrow row spacings which stopped when the row spacing reached 8 inches.

The impact of the improved tropical plant type on rice yields in South and Southeast Asia

Robert F. Chandler, Jr.

The new plant type in tropical rice is characterized by short, sturdy stems; short, erect leaves; and heavy tillering capacity. Top yields on experimental fields in tropical Asia have doubled as a result of the drastic change that has been brought about in canopy structure and lodging resistance. Farmers on well-irrigated land in South and Southeast Asia who have changed to the new high-yielding varieties are getting from 1 to 2 metric tons more grain per hectare than are those who have continued to grow the traditional varieties. Approximately 10 million hectares of the new varieties of rice were grown during 1970.

INTRODUCTION

A substantial increase in the yield potential of the tropical rice plant has resulted from the development through plant breeding of rice varieties that have a drastically changed canopy structure. This statement is generally accepted and rather easy to prove. To many, it seems evident that this change in grain yield potential will decidedly influence the yields on farmers' fields and the total supply of rice in tropical countries where yields traditionally have been low. It is difficult however to obtain reliable data on the impact of the improved plant type on general farm yields and on total national production in the rice-growing countries of South and Southeast Asia.

In this paper I shall define briefly what I consider the new tropical plant type to be, and then cite a number of comparisons of the yield potential of the new and traditional varieties as shown by experimental trials on various rice experiment stations. Next, inadequate though it may be, I shall present the best evidence I am able to find on the actual yield increases being obtained by farmers who have changed to the new varieties. These examples will not include any data from supervised demonstrations or applied research trials where conditions are more nearly ideal than on the average farm. The paper will conclude with an estimate of the spread of the high-yielding varieties in South and Southeast Asia.

THE IMPROVED PLANT TYPE

Although much influences the grain yield of rice, no advance in recent years has had as great an impact on the yield potential of rice as that of plant type.

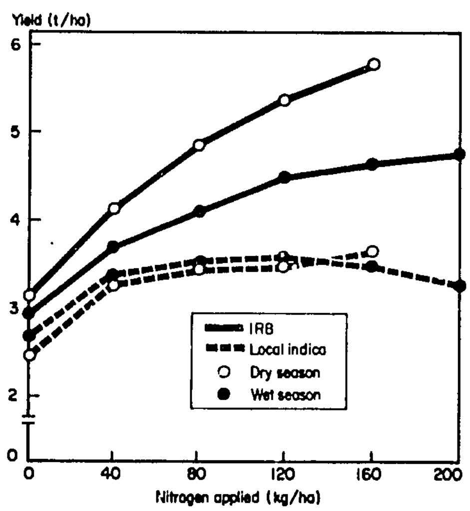
Robert R. Chandler, Jr. International Rice Research Institute.

The history of rice breeding in tropical Asia before 1960, and the development of better varieties in Taiwan and Japan make it clear that in the tropics too little attention was paid to plant type before 1960 and that the advances in Taiwan and Japan could not have been made without the development of lodging-resistant, fertilizer-responsive varieties.

For purposes of clarification I wish to define "improved tropical plant type." It is a plant of short stature that, under good growing conditions, has a total height of 90 to 110 cm. The culms are not only short but also relatively thick and sturdy so that they do not break or bend at high fertility levels or when heavy rains or moderately strong winds occur. Its leaves are erect, rather short, and not too wide. It has an inherent heavy tillering capacity. Each of these characters has a beneficial effect on grain yield (Tanaka, Kawano, and Yamaguchi, 1966; International Rice Research Institute, 1968, p. 17-45; Tanaka et al., 1969). The short, sturdy straw prevents lodging. The short, erect leaves permit greater penetration of sunlight and thus increase the efficiency of photosynthesis. The heavy tillering capacity aids in producing more panicles per unit area of land, allowing a stand of rice to compensate for missing hills or, in direct-seeded rice, for any thinly sown area.

COMPARISONS OF TRADITIONAL AND IMPROVED VARIETIES ON EXPERIMENTAL FIELDS

The All-India Coordinated Rice Improvement Project has conducted field trials of the high-yielding varieties throughout India, always growing a local traditional variety as a control. Patnaik (1969*a*) has presented data showing the yield response of IR8 to varying levels of nitrogen in the wet and dry seasons, as compared with local varieties receiving the same treatments. Figure 1 shows the average results obtained from eight to 10 different locations during each growing season from 1966 to 1968.



1. The grain yield of IR8, in the wet season and in the dry season, compared to that of local varieties grown under the same conditions in India.

Table 1. Grain yield of local and improved rice varieties grown at high fertility levels at the Central Rice Research Institute in India. 1965-66.

Variety	Yield (t/ha)		
	Dryseason	Wet season	Total
Ptb 10	2.02	2.87	4.89
MTU 15	3.36	2.45	5.81
Taichung Native 1	8.00	5.02	13.02
Tainan 3	6.40	4.21	10.61
Chianung 242	7.85	3.19	11.04

It is evident that IR8 substantially outyielded the local varieties at all nitrogen levels and in both seasons. Even without the addition of nitrogen, IR8 yields were about one-half ton higher than those of the traditional varieties.

Patnaik (1969*b*) reports a study conducted at the Central Rice Research Institute in Cuttack, India in 1965-66, just before IR8 was named, showing the yields obtained at high fertility levels for a dry-season and a wet-season crop of two local varieties, Ptb 10 and MTU 15, as compared with three Taiwanese varieties of improved plant type, Taichung Native 1, Tainan 3, and Chianung 242. The results are shown in Table 1. These data indicate that the yield potential of the local varieties is only about one-half that of the varieties with the improved plant type.

Another way of showing the increased yield potential of the new rice varieties is to examine the average grain yield at the Central Rice Research Institute in India before and after the new varieties were created and introduced. The information in Table 2 was furnished by Dr. S. Y. Padmanabhan (*personal communication*), the director of the institute. It is obvious that the productivity of the experimental farm more than doubled after the new varieties were introduced. Those of us who have been visiting the Central Rice Research Institute for the past decade have seen first-hand the great change that occurred as the new varieties were substituted for the old ones.

To cite another example of the productivity of the new varieties, the agronomy department of IRRI has been conducting nitrogen-variety interaction trials with a number of the new varieties developed both at IRRI and in other countries. The complete results have been reported elsewhere (International Rice Research Institute, 1971, p. 123-156) but selected data are reproduced in Table 3.

Table 3 shows that the new varieties when grown in the Philippines produced from 6 to over 8 t/ha in the dry season and from 4 to 6 t/ha in the wet season. The only traditional variety planted in the trial was Peta and its yields were from one-sixth to one-third those of the improved varieties. In fairness to the traditional varieties, however, it should be stated that the yield of Peta when no fertilizer was applied was 2.80 t/ha in the wet season and 4.6 t/ha in the dry season. This supports the often-made statement that the yield potential of the tropical rice plant essentially has been doubled by changing its plant type.

Table 2. Area production and yield of rice from 1960 to 1970 on the experimental farm[a] of the Central Rice Research Institute, Cuttack, India.

Year	Area cultivated (ha)	Yield (t/ha)
1960	57.5	0.93
1961	65.5	1.07
1962	63.0	0.58
1963	63.5	1.20
1964	64.5	1.20
1965	63.5	2.04
1966	70.7	2.15
1967	62.7	3.25
1968	72.0	2.35
1969	74.9	2.99
1970	77.2	2.89

[a]The data represent the combined totals for wet and dry seasons. From 53 to 57 hectares were grown during each wet season and from 10 to 20 hectares were cultivated during the dry season. The new varieties, such as Taichung Native 1, were first grown on the farm in 1965.

According to Jackson, Panichapat, and Awakul (1969), the new Thai dwarf variety, RD1, produced a yield of 6.48 t/ha on experimental fields in the dry season as compared to 3.5 t/ha for the tall local variety, Leuang Tawng. In the wet season the yields were 4.64 t/ha for RD1 and 2.94 t/ha for another local variety, Nahng Mon S-4. The yields of RD3, another selection from the same

Table 3. The grain yield of selected varieties in the wet and dry seasons of 1970 at the International Rice Research Institute.[a]

Variety	Origin	Yield (t/ha) Wet season	Yield (t/ha) Dry season
IR24	IRRI	—	8.3
IR8	IRRI	5.6	7.3
IR22	IRRI	4.6	7.8
RD1	Thailand	4.3	7.6
RD3	Thailand	4.9	7.0
Jaya	India	6.2	8.2
Padma	India	4.7	6.3
Taichung Native 1	Taiwan	4.9	6.9
C4-63	Philippines	3.8	6.6
Peta (check)	Indonesia	0.9	2.4

[a]The data used here were from plots receiving optimum levels of nitrogen, which were 90 kg/ha in the wet season, and 140 kg/ha in the dry season. Phosphorus and potassium were in adequate supply.

cross, were similar except that RD3 seemed to perform a little better than RD1 at lower fertility levels.

Although rice improvement has been under way for many years in the U.S., it is interesting that further improvement in yield potential appears to be possible by using the dwarf indica plant type, as exemplified by IR8 or Taichung Native 1. In a study conducted by Bollich et al. (1969) at Beaumont, Texas, Taichung Native 1 produced a yield of 7.9 t/ha and IR8 produced 6.7 t/ha. Under the same conditions, Bluebelle and Saturn produced 5.4 t/ha.

YIELD PERFORMANCE OF NEW VARIETIES ON FARMERS' FIELDS

Villegas and Feuer (1970) have presented data to show that in the Philippines the average yield in 1968 of 221,000 hectares of lowland rice planted to the high-yielding varieties was 3.3 t/ha, while the yield from 773,000 hectares of similar land planted to the traditional varieties was 1.5 t/ha. Thus even on farmers' fields the average yields appeared to have doubled when the improved varieties were grown.

Barker (International Rice Research Institute, 1971, p. 173-198) has studied 152 farms in Laguna, a province of the Philippines, before and after the adoption of the new varieties. His studies show that those who were full adopters (i.e. planted 100% of their rice land to the new varieties) in 1969 obtained an average yield of 3.8 t/ha while in 1966 (before the new varieties were being grown), the yield on the same farms was only 2.3 t/ha. The non-adopters, who obtained an average yield of 2.5 t/ha in 1966 were still getting only 2.8 t/ha in 1969. This increase of $1\frac{1}{2}$ t/ha by the adopters is not as large as one would expect after examining the results on experimental fields, but these yield data included those from farms with inadequate irrigation facilities. If the full adopters from the town of Cabuyao, where good irrigation facilities exist, are considered separately, the average grain yield from 1966 to 1969 increased from 2.1 t/ha to 4.6 t/ha, representing a yield increase of over 100 percent.

When the high-yielding varieties are planted in areas with adequate irrigation facilities and abundant sunshine, and if high rates of fertilizer are applied, yield increases are often substantial. A good example of such a situation is West Pakistan where rainfall is low but a good irrigation system exists in most of the rice-growing areas. West Pakistan planted essentially no semidwarf indicas in 1966, but 3 years later over 500,000 hectares of IR8 had been planted, representing about one-third of the rice-growing area (Athwal, 1971). Total rice production increased by 80 percent and per-hectare yields by 50 percent during this period.

In East Pakistan, where most of Pakistan's rice is grown, many production problems are associated with the wet, humid climate. IR8 did not prove satisfactory there, but in 1970 1,800 metric tons of IR20 seed were imported and planted. Only one preliminary study of the results in the 1970 wet season appears to have been made (R. I. Rochin, *unpublished*). The author of this study concludes that the accelerated program to introduce IR20 was a success. But, due to typhoons, inadequate guidance to innovating farmers, and certain other problems, the yield increases were not as great as expected. A survey of 228 farmers, including both adopters and non-adopters, revealed that the average yield of IR20 was 3.1 t/ha, while the yield of the traditional varieties was 2.3 t/ha. The yield data were separated by districts. In areas that had superior environmental conditions (water control, absence of severe typhoon damage, etc.) average yield increases ranged from 40 to 56 percent. One would judge from the data that the farmers sampled in the survey were not completely typical because the survey figures for the yield of the traditional varieties were about double the average yields for East Pakistan.

The East Godavari and West Godavari districts of Andhra Pradesh in India constitute an important rice-growing area of the country. G. Parthasarathy and D. S. Prasad (*unpublished*) made a rather thorough economic study of the adoption of, and economic returns from, the high-yielding varieties in these productive river delta districts.

Because there were no striking differences between the figures for the two districts, I have averaged them here. In the wet season, the average yield of IR8 was 6.02 t/ha. The corresponding figure for the local variety was 4.4 t/ha. An economic analysis of the costs and returns showed that there was no advantage in growing IR8 in the wet season because prices were lower than for the local varieties and the farmers tended to spend more money cultivating IR8 than they did when growing the local varieties. In the dry season the average yield of IR8 was 5.59 t/ha while that of the local varieties was 2.82 t/ha. The difference of 2.77 t/ha proved highly profitable to the farmer, giving him an advantage, on the average, of over 1,000 rupees per hectare by growing IR8. The authors of the article conclude that since the yield differential is greater in the dry season and since the price of rice is higher in that season (as compared with the wet season), the farmers should grow the high-yielding varieties in the dry season and the traditional ones in the wet season.

Considering results obtained from many other rice-growing areas in South and Southeast Asia, one cannot help but feel that the situation in the Godavari river delta needs closer examination. Usually yields of both traditional and high-yielding varieties are greater in the dry season than in the wet season. Furthermore, often there is a decided advantage in growing the lodging-resistant varieties in the wet season because the tall, traditional varieties lodge earlier and more severely then than in the dry season.

Another consideration in determining future policy is that several new varieties, developed both in India and at IRRI, have grain quality and disease and insect resistance that are far superior to those of IR8 and Jaya, two of the principal varieties now being grown in Andhra Pradesh. The new varieties should be tested on a broad scale. Not only should their yields be higher on farmer's fields, but the market price of the grain should be as good as that of the preferred local varieties.

Although the data presented here for yields on farmers' fields are scanty and can serve only as examples, they seem fairly consistent: under average farm conditions with reasonably good water supply and with the application of at

Table 4. Area planted to high-yielding rice varieties in the developing countries (estimates for 1970).

Country	Area (000 ha)
India	4,860
Philippines	1,200
Indonesia	1,000
Pakistan	1,000
South Vietnam	250
Burma	180
Ceylon	150
All others	1,500
World total	10,140

least moderate amounts of fertilizer, farmers are getting 1 to 2 t/ha more rice than they would have had they continued to use the traditional varieties.

These data seem more representative of actual farm conditions than those presented by various enthusiastic writers dealing with the green revolution. It is not uncommon to read statements to the effect that the new rice varieties have enabled farmers to grow from three to six times more rice than they were able to grow before. These conclusions were often reached by comparing the 10-ton yields which are occasionally obtained under ideal conditions with average national yields of 1 to 2 t/ha. Such statements, although true for selected comparisons, are not indicative of what is actually happening on average farms where such factors as unfavorable weather, insect and disease attack, and weed competition reduce yields.

THE SPREAD OF THE HIGH-YIELDING RICE VARIETIES

The most rapid spread of high-yielding rice varieties has occurred in the Philippines, Pakistan, and India. National rice production programs involving the new varieties are now progressing well in Indonesia, Thailand, Ceylon, Malaysia, Burma, and South Vietnam. Programs are starting in Latin America. For example, the Centro Internacional de Agricultura Tropical released two varieties for Latin America in 1971, and Cuba recently reported that over three-fourths of its rice land was planted to high-yielding varieties, mostly IR8. Athwal (1971) made an excellent review of the background and impact of the semidwarf rice and wheat varieties.

Table 4 shows the best possible estimates of the area planted to the new high-yielding rice varieties. The figures in Table 4 are undoubtedly low. There is a time lag between the actual use of the new varieties and the reporting of the data. Furthermore the situation is changing so rapidly that no figures are truly up to date. The best estimates appear to be those published by Dalrymple (1971).

Approximately 130 million hectares of land in the world are planted to rice. If we deduct the rice land in mainland China, about which we have no accurate information, and also subtract the area devoted to rice in the developed countries such as Japan, Taiwan, the U.S., and the European countries (which have improved their rice varieties and cultivation techniques gradually during the past several decades), we find that approximately 12 percent of the remaining area is planted to the high-yielding varieties. Although much remains to be achieved, this is a substantial gain when you consider that no high-yielding varieties were being planted in any of these countries 5 years ago.

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Discussion: The impact of the improved tropical plant type on rice yields in South and Southeast Asia

B. B. SHAHI: The IRRI-plant type definitely needs high doses of nitrogen for its full expression and yield. But in developing countries where farmers are poor, they cannot afford to apply even 20 kg/ha N. Or where shortage of nitrogen fertilizer exists, what would be your alternative for the years to come? Or do you think high yielding varieties without fertilization can give as high a yield as a local variety?

R. F. Chandler: Our evidence so far is that the improved varieties even at low nitrogen levels yield better than the local varieties. Nitrogen application pays handsomely, with 15 to 30 kg of grain for each kilogram of nitrogen. Yet about 3.5 kg of rice will buy 1 kg of nitrogen. So if he can find the money, the poor farmer can afford to apply nitrogen to his rice crop.

W. H. FREEMAN: What is the relative proportion of the area planted to the new varieties in wet season and dry season in the Philippines?

R. F. Chandler: The percentage is probably a little higher in the dry season because the irrigated farms are the most progressive. But some farmers plant high-quality local varieties in the dry season because there is less lodging and the prices of local varieties may be higher.

R. FEUER: A higher proportion of the high-yielding varieties are grown in the wet season. Twenty-five percent of the area in the wet season was planted to the high yielding varieties 3 years ago.

S. V. S. SHASTRY: Our West Godavari data indicate tall varieties grown in wet season have a higher yield potential than those grown in dry season.

R. F. Chandler: I believe Dr. Shastry's remark is only a comment and needs no response. But I believe the subject needs more investigation.

Current breeding programs

IRRI's international breeding program

Henry M. Beachell, Gurdev S. Khush, Rodolfo C. Aquino

Since it began in 1961, the IRRI rice breeding program has been international in scope. The major breeding objectives relate directly to increasing rice yields on Asian farms, to stabilizing of rice yields by breeding for disease and insect resistance and other factors, to developing varieties that possess the grain type and cooking and eating qualities preferred by consumers, and to high protein content. Special programs include breeding for cold resistance, adaptability to deep water conditions, and upland culture. Rapid screening techniques have been developed by cereal chemists, entomologists, pathologists, and others working with the breeders. Fifteen varieties have been named by IRRI and other agencies from IRRI breeding materials. They make up a major part of the 10 million hectares of improved varieties grown throughout the world. Seed purification and production in quantity of new varieties have led to the rapid spread of new varieties. IRRI cooperates closely with rice breeders in many countries and since 1961 nearly 58,000 packets of breeding lines have been sent to rice research workers in 80 countries. Over 70 individuals have received training in plant breeding at IRRI.

INTRODUCTION

In 1961, when the IRRI breeding program was started, one of the most important breeding objectives was to develop high-yielding, short, sturdy-strawed rice varieties that would resist lodging even at high rates of nitrogen fertilization. Today, varieties with improved plant type are planted on about 10 million of the world's approximately 130 million hectares planted to rice (Athwal, 1971). Most of the 10 million hectares is planted to varieties developed from IRRI breeding lines by IRRI and by other agencies. The five IRRI-named varieties and the 10 varieties named by other agencies appear in Table 1.

Today, the major objectives of the IRRI breeding program are to combine with the improved plant type other important traits. The traits include desired growth duration and photoperiod response; disease and insect resistance; tough leaves; grain dormancy; threshability; proper grain shape, appearance, and cooking behavior; increased protein content; and special features such as cold resistance, deep water tolerance, and adaptability to upland culture.

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PLANT TYPE

The major breakthrough in the IRRI breeding program was the dramatic success of the semidwarf tropical indica plant type represented by IR8. IR8 was selected from a cross of Peta and the semidwarf Taiwan variety Dee-geo-woo-gen. The use of the Taiwan semidwarf varieties in the IRRI breeding program was logical since Taichung Native 1, derived from Dee-geo-woo-gen, had been successfully grown in Taiwan (Chang, 1961). When the first IRRI crosses were made, it was not known that the short stature of the Taiwan semidwarfs was conditioned by a single recessive gene (Chang et al., 1965; Aquino and Jennings, 1966). The improved plant type objectives, as described by Tsunoda (1961), Jennings (1964), Beachell and Jennings (1965), Jennings and Beachell (1965), and Beachell (1966), were short, sturdy stems, moderate tillering, lodging resistance, erect leaves, and nitrogen responsiveness, which certain japonica and U.S. varieties possess. Based on the performance of IR8 at many locations its high tillering and vegetative vigor are other important attributes of semidwarf genotypes which are derived from tropical indica varieties.

Only when the tall, vigorous, tropical indica genotypes are dwarfed do they exhibit high yield potential. The severe lodging and mutual shading of the tall, tropical indicas preclude the use of large amounts of nitr gen fertilizer which are essential for high grain yields. When tropical indica varieties are dwarfed, lodging and mutual shading are reduced and they respond with high grain yield to nitrogen fertilizer even when leaf area index is excessively high. The tropical indica varieties have a distinct advantage over semidwarf japonica and U.S. varieties mainly because of their vegetative vigor, high tillering, and high leaf area index.

In the 1966 dry season at IRRI (IRRI, 1967*b*, p. 66) 25 of 30 lines yielding over 8 t/ha in a replicated variety test were semidwarf tropical indica lines.

Table 1. Varieties developed from IRRI lines by IRRI and by other agencies.

Name	IRRI line	Parents	Where named
IR8	IR8-288-3	Peta x Dee-geo-woo-gen	Philippines (IRRI)
IR5	IR5-47-2	Peta x Tangkai Rotan	Philippines (IRRI)
IR20	IR532E576	IR262-24 x TKM-6	Philippines (IRRI)
IR22	IR579-160-2	IR8 x Tadukan	Philippines (IRRI)
IR24	IR661-1-140-3	IR8 x [(CP 231 x SLO 17) x Sigadis]	Philippines (IRRI)
Pankaj	IR5-114-3	Peta x Tangkai Rotan	India
Bahagia	IR5-278	Peta x Tangkai Rotan	Malaysia
Chandina	IR532-1-176	IR262-24-3 x TKM-6	Pakistan (East)
Mehran 69	IR6-156-2	Siam 29 x Dee-geo-woo-gen	Pakistan (West)
CICA 4	IR930-31	IR8 x IR12-178	Columbia
Sinaloa A68	IR160-27-4	Nahng Mon S-4 x Taichung Native 1	Mexico
CS-1	IR262-7-1	Peta/3 x Taichung Native 1	Ivory Coast
CS-2	IR160-25-1	Nahng Mon S-4 x Taichung Native 1	Ivory Coast
CS-3	IR253-16-1	Gam Pai 15/2 x Taichung Native 1	Ivory Coast
RD2	IR253-4	Gam Pai 15/2 x Taichung Native 1	Thailand

Twenty-two of them originated from crosses between Peta and semidwarf varieties. Similar results have been obtained annually at IRRI and elsewhere.

Semidwarf japonica and U.S. genotypes were developed using Chianung 242 (japonica) and Bluebelle (U.S.) in backcross programs with Taichung Native 1 as the donor parent of short stature. These semidwarf lines seldom yielded as much as the taller Chianung 242 and Bluebelle and they usually yielded considerably less than semidwarf indica genotypes. Many of the segregates from crosses involving japonica and U.S. varieties tend to have an erect tiller arrangement compared with the open tiller arrangement of IR8. Our observations are that lines with erect tillers tend to yield less than those with open tillers like IR8. A slightly spreading tiller arrangement like that of IR9-60 is less desirable because such varieties are more apt to lodge.

Other sources of relatively short stature have been used with some success. C4-63 developed at the University of the Philippines, College of Agriculture (Escuro et al., 1969) and IR5 represent varieties of intermediate height in which the reduced plant height is conditioned by polygenes. In Indonesia, IR5 and C4-63 are preferred to IR8 partly because they are slightly taller. Semidwarf lines selected from crosses between IR8 and tall varieties of Thailand approach IR5 in height so a wide range in plant height is possible within the semidwarf genotypes, depending upon the genetic background of the tall parents involved.

IRRI Acc. 6993, a short-statured U.S. breeding line from the cross Century Patna 231 x SLO 17, has been used extensively in the IRRI breeding program for short stature and other traits (grain shape and appearance, glabrous plant parts, and tough leaves). Its reduced plant height appears to be controlled by a polygenic system (IRRI, 1967*a*).

In areas where low temperatures prevail throughout the growing season, the plant height of all varieties is reduced. The semidwarf genotype may not be as well suited to these conditions as slightly taller genotypes such as IR5, C4-63, and Acc. 6993.

GROWTH DURATION AND PHOTOPERIOD RESPONSE

The development of photoperiod-insensitive varieties was an early breeding objective. The insensitive varieties of shorter growth duration are important in areas where more intensive farming methods are used and adequate facilities are available for harvesting and drying the crop during unfavorable weather. But weakly photoperiod sensitive types are essential in many places in tropical Asia, such as in East Pakistan, parts of India, and other countries where sun-drying is used. In these areas, the rice crop should mature towards the end of the rainy season when favorable weather for sun-drying occurs. Photoperiod-sensitive varieties are essential because their maturity date is fixed by daylength and they ripen at approximately the same time of the year regardless of planting date. In these areas the planting date may vary by as much as 6 weeks depending on prevailing weather and soil moisture during the planting period. Since many genes affect photoperiod-sensitivity, lines with the desired photoperiod response can be developed. The use of IR20 in East Pakistan is an example of a variety meeting these requirements. In the deep-water areas of East Pakistan, India, and Thailand, where the fields remain flooded until late in the season, varieties that are strongly photoperiod-sensitive are essential.

Early-maturing varieties—ones that require 100 days from seeding to maturity—are being developed. They are suitable as boro and aus varieties in East Pakistan, rabi and kharif crops in India, and in multiple cropping systems. Breeding lines, such as IR579-48-1 from IR8 x Tadukan; IR747B2-6 from (Peta/3 x Taichung Native 1) x TKM-6/2, and Chandina, a variety developed in East Pakistan from IRRI cross IR532, (Peta/3 x Taichung Native 1) x TKM-6, are examples of promising early maturing lines suitable for use as parental sources of early maturity. Promising early maturing types are being selected from IR1561 lines (IR747B2-6 x IR579-48-1) that combine desirable features of both parent lines, which include seedling vigor and rather high levels of insect and disease resistance, all important traits in early maturing varieties.

DISEASE AND INSECT RESISTANCE

In close cooperation with pathologists and entomologists we have identified a series of varieties possessing high levels of resistance to diseases and insects. These strains are being used in the breeding program at IRRI and in other countries and are discussed in detail elsewhere in this book.

Pathologists and entomologists are searching for better sources of resistance to diseases and insects. Breeders are transferring disease and insect resistance to high yielding lines with improved plant type. The ultimate objective is to incorporate high levels of resistance to all diseases and insects into a series of early, midseason, and late-maturing varieties of varying grain shape and cooking behavior. Some of the more recent IRRI crosses combine good levels of resistance to all diseases and insects mentioned here. It should be possible to select lines that have improved-plant type and possess this combined resistance.

TOUGH LEAVES

Rice varieties that have thick or tough leaves which resist shredding and breaking by strong winds are needed in the typhoon-ravaged areas of the Philippines, Taiwan, and Japan. Tropical indica varieties have fragile leaves while japonica varieties tend to have tough leaves. Some U.S. varieties of japonica x indica origin have reasonably tough leaves. The program for developing tough-leaved varieties has had limited success but there do not appear to be any genetic barriers to combining this trait with improved plant type and other desirable characters.

GRAIN DORMANCY

The grain embryo of most tropical indica varieties is dormant from just before harvest to some time after harvest. The degree of dormancy in rice varieties varies from weak to strong and is related to the length of the dormant period, which varies from a few days to several months (B. S. Vergara, *unpublished*). Most japonica varieties and some indicas show essentially no dormancy. The IRRI varieties, IR5, IR8, IR20, IR22, and IR24 are all weakly dormant. It is possible that IR20 shows stronger dormancy than the other IRRI varieties. Strongly dormant varieties are desirable in areas where sun-drying is used and rainy or cloudy weather occurs during the harvest season. Weakly dormant varieties frequently show some sprouting under these conditions particularly if the crop is not harvested immediately upon maturity. In many parts of the tropics fields are not harvested until they become over-ripe. The strongly dormant grains resist sprouting even though the moisture content of the grain remains high for several days after harvest. On the other hand, strong dormancy is undesirable because of "dropped seed" or grains that shatter from the panicles during harvest. If the seed is strongly dormant it can remain viable in the soil for a long time. Weakly dormant grains buried in rice fields remain viable for 6 to 8 months (B. S. Vergara, *unpublished*) while strongly dormant grains may remain viable for several years (Goss and Brown, 1939). For these reasons, we feel that varieties with both weak and strong dormancy should be developed.

THRESHABILITY

IRRI varieties, like most tropical indica varieties, are relatively easy to thresh. As harvesting and threshing become mechanized, non-shattering may be desired in some areas. Lines with improved plant type that do not shatter have been selected from the IR4 cross (H 105 x Dee-geo-woo-gen), bulu crosses, and japonica x semidwarf indica crosses.

GRAIN SHAPE, APPEARANCE, AND COOKING QUALITY

Commercially grown rice varieties have a wide range of grain length and width. It is therefore essential that grain size and shape be considered in breeding programs. Grain appearance is also important. The white-belly characteristic of grains of IR8 (IRRI, 1966, p. 84-85), Dee-geo-woo-gen, and many tropical indica varieties is a genetic trait. Through rigid selection pressure in our breeding program, clear or translucent grain types have been evolved so that this undesirable trait can be eliminated. Precise information on mode of inheritance has not been worked out, but lines without white belly spots are readily identified in crosses between varieties and lines with white belly and those without white belly. Clear-grain varieties used as parents for elimination of white belly are the U.S. long-grain varieties, Tadukan, TKM-6, and Thailand long-grain varieties. IR20, IR22, and IR24 are essentially free from white belly.

The cooking characteristics of rice are important breeding objectives. The amylose content of the grain influences its cooking quality. High amylose rice, when cooked, is dry and fluffy; low amylose rice is sticky. In tropical Asia, rices with high (30%), intermediate (25%), and low (20%) amylose are grown. At IRRI, we are attempting to develop all three types. IR24, a low-amylose type, is popular with Filipino consumers. In Indonesia, intermediate and low amylose types are preferred, but in India high amylose varieties are popular. Germ plasm sources of high and low amylose content are readily available from tropical indica varieties. Lines with intermediate amylose content have been selected from crosses involving BPI-76, IR12-178 (which apparently inherited intermediate amylose content from the variety Mong Chim Vang A), U.S. varieties, and the Indonesian varieties, Intan, Bengawan, and Syntha. It is questionable whether lines with truly intermediate amylose content can be selected from crosses between high and low amylose strains. A recent improvement in the method of determining amylose content (B. O. Juliano, *unpublished*) will speed up this program since it is now possible to identify the three types accurately and rapidly.

The gelatinization temperatures of rice grains of different varieties range from about 55 to 79 C (B. O. Juliano, *unpublished*). Varieties with intermediate or low gelatinization temperatures occur among tropical indica varieties. At least one tropical indica variety, Khao Dawk Mali from Thailand, has high gelatinization temperature. We have selected many lines with high gelatinization temperature from japonica x dwarf tropical indica crosses and from U.S. varieties. High gelatinization temperature frequently appears in crosses between indica varieties that have intermediate gelatinization temperature and japonica varieties that have low gelatinization temperature. Gelatinization temperature is measured by an alkali digestion technique (Little, Hilder, and Dawson, 1958).

Amylose content and gelatinization temperature are not inherited independently. Several relationships exist between them that are not fully understood. All lines that have high gelatinization temperature show low amylose content; so far we have not found a line that has high gelatinization temperature and high or intermediate amylose content. BPI-76 and some hybrid lines derived from BPI-76 have intermediate amylose content and a relatively high gelatinization temperature, though not as high as that of a typical variety with high gelatinization temperature. Whether intermediate gelatinization temperature and low amylose content have been combined is not clear. More information on the genetic relationships between these two traits is needed. The importance of gelatinization temperature to the farmer and the consumer is not fully understood. Since the varieties and lines used as parents may differ in gelatinization temperature their progenies must be examined for this character at least until they are homozygous for a particular gelatinization temperature.

SPECIAL BREEDING PROBLEMS

Protein content

From the time it was founded IRRI recognized the importance of increasing the protein content of rice. Shortly thereafter it began screening varieties for protein content (IRRI, [1965]).

Breeding for increased protein content has been under way at IRRI since 1967 under a contract with National Institute of Health (IRRI, 1967*b*, p. 53-56). IR8 was crossed with six high-protein varieties screened by IRRI chemists from the world collection (IRRI, 1967*b*, p. 53-56). The goal of this program is to raise the average protein content of IR8 brown rice 2 percentage points from, say, 8 percent to 10 percent. Environmental variability has been a serious drawback (see the paper by H. M. Beachell, G. S. Khush, and B. O. Juliano, elsewhere in this book). At present several lines from the high protein crosses, along with other lines selected from the breeding program, appear to have higher protein content than IR8. Although grain yields of the high protein lines tend to be lower than the yield of IR8, genetic differences in protein content probably exist within the material tested. A new series of crosses combine divergent sources of high protein with improved plant type.

Cold resistance

The breeding program for cold resistance is an outgrowth of a cooperative breeding program started in 1965 with the Republic of Korea (IRRI, 1971, p. 205-206). In this breeding program, the semidwarf tropical indica plant type is being combined with cold resistance and other essential traits for Korean conditions. This program has led to the development of IR667-98, selected from the cross IR8 x (Yukara x Taichung Native 1). IR667-98 has a plant type similar to that of IR8. It was tested on 2,700 hectares in Korea in 1971. It is not highly tolerant of low temperatures, but a new series of crosses have been made which show promise for transferring cold resistance to it and to similar plant types. Cold-resistant varieties from many countries are being tested (see the paper by C. Kaneda and H. M. Beachell, elsewhere in this book). Cold resistance is complex and varieties resistant in the seedling stage may not be resistant in the vegetative or flowering stages.

Deep-water varieties

In 1965 two deep-water, floating varieties from Thailand were crossed with a semidwarf line, from Peta/2 x Taichung Native 1. Pedigree selections made at IRRI from the IR442 combination, (Peta/2 x Taichung Native 1) x Leb Muc Nahng, have been widely tested at IRRI and elsewhere. Selections were made in Thailand from a bulked hybrid population of this cross (Yantasast, Prechachat, and Jackson, 1970). Many of the IRRI and Thailand lines combine the semidwarf height and floating ability. Crosses between the better IR442 lines and deep-water varieties from East Pakistan such as Habiganj D. W. 8, have been made to obtain more photoperiod sensitivity. Actually, Habiganj D. W. 8, besides having superior ability to emerge through rising flood waters, is highly resistant to the tungro virus. Line selections from the backcross IR701 (Pingaew 56/2 x Tainan 3) and IR435 [(CP 231 x SLO 17) x Pingaew 56] have tougher leaves than Pingaew 56, the floating parent, so they may be useful as parental material.

Upland rice

Agronomists and breeders have been evaluating varieties and breeding lines for yielding ability under upland conditions (IRRI, 1970, 1971). Growth characteristics of varieties and their agronomic response to upland conditions were studied in detail by geneticists to assess their potential value in breeding programs (IRRI, 1971, p. 214). Single and three-way crosses are being made from upland and lowland varieties and lines that are promising under upland conditions (See Chang, Loresto, and Tagumpay, elsewhere in this book).

An effective breeding procedure might be to bulk several upland crosses and grow a bulk hybrid population for several seasons at many locations. Seeding at several dates at a given location would further increase the possibilities of subjecting populations to rigid selection pressure for drought, diseases, insects, and other factors peculiar to upland culture. Plant selections would be made from these plots to form new bulk populations. The intercrossing of promising plants from the populations would further combine desirable traits.

Disease and insect resistance are vital in upland culture so high levels of resistance should be given priority in an upland rice breeding program. Deep-water Asian indica varieties and *O. glaberrima* deep-water varieties grown in Africa should be investigated for drought resistance. These varieties are direct seeded and frequently are subjected to severe drought before the rainy season begins. They may possess some drought resistance not present in other varieties.

BREEDING PROCEDURES AND PROGRESS

The varieties and breeding lines used in the breeding program possess a wide range of genetic variability. We have used the tropical indica varieties for short stature, vegetative vigor, and high tillering. The japonica and U.S. varieties were used for specific traits not present in indica varieties such as glabrous plant parts, resistance to diseases, tolerance to low temperature, tough leaves, slow senescence, and good grain shape, appearance and cooking quality. Varieties used in the crossing program that have provided valuable traits to breeding lines are shown in Table 2.

Many of the varieties listed in Table 2 were selected early in the breeding program and as a group they possess most of the traits that breeders are incorporating into the improved plant type.

As soon as IR8 was identified, it and similar semidwarf lines were used extensively as parents. Many backcrosses were made using IR8 and similar semidwarf indica lines as recurrent parents. Usually the backcrosses were made on F_1 single cross plants and large numbers of crossed seeds were produced. The F_2 populations produced from each crossed seed were grown independently in populations of about 150 plants. In some seasons as many as 1,200 F_2 backcross populations were grown. Many of the populations were rejected in the F_2 generation. Table 3 shows the cross combinations from which promising lines have been selected. We have used three-way cross combinations and other complex combinations of promising breeding lines and varieties in an effort to combine desirable traits. The crosses that were assigned cross numbers from 1962 to 1970 are shown in Table 4. Many crosses made for genetic studies, by entomologists and pathologists, and by IRRI trainees for use in their breeding programs are not included in the 1,745 crosses listed.

The progress in combining many of the traits was slow because suitable testing techniques were not available or because resistant genotypes had not

Table 2. Varieties and lines used in IRRI crosses which have contributed toward the improvement of rice varieties.

IRRI acc. no.	Variety or line	Origin	Traits
		Indica varieties	
105	Taichung Native 1	Taiwan	Semidwarf
123	Dee-geo-woo-gen	Taiwan	Semidwarf
120	I-geo-tze	Taiwan	Semidwarf
39	BPI-76	Philippines	High protein, intermediate amylose
9804	Tadukan	Philippines	Bacterial leaf blight, blast resistance
57	FB-24	Philippines	Tungro resistance, grain appearance
5824	Wagwag	Philippines	Strong photoperiod sensitivity, grain quality
3634	Peta	Indonesia	Erect leaves, resistance to leafhopper, tungro
611	Sigadis	Indonesia	Resistance to leafhopper, tungro, blast, bacterial leaf blight
3612	Mas	Indonesia	Resistance to leafhopper, tungro
4230	Intan	Indonesia	Intermediate amylose
31	Tangkai Rotan	Malaysia	Grain appearance
27	Siam 29	Malaysia	Grain appearance
219	Mong Chim Vang A	Vietnam	Intermediate amylose
158	H 105	Ceylon	Resistance to blast, planthopper
831	Gam Pai	Thailand	Waxy endosperm, resistance to tungro
9438	Leuang Hawn	Thailand	Aroma, grain appearance
172	Nahng Mon S-4	Thailand	Aroma, grain appearance
850	Khao Dawk Mali	Thailand	High gel. temp., low amylose, grain appearance, aroma
862	Muey Nahng 62 M	Thailand	Waxy endosperm, resistance to gall midge
173	Puang Nahk 16	Thailand	Grain appearance, sturdy straw
7819	Leb Mue Nahng	Thailand	Deep water, grain appearance
7889	Pingaew 56	Thailand	Deep water, grain appearance
237	TKM-6	India	Resistance to tungro, leafhopper, stem borer
5999	Pankhari 203	India	Resistance to tungro, leafhopper
6663	Mudgo	India	Resistance to planthopper
6303	ASD 7	India	Resistance to leafhopper and planthopper
--	EK lines	India	Resistance to gall midge
64	T-141	India	Photosynthetic efficiency
11 751	Habiganj DW-8	Pakistan	Resistance to deep water, tungro
8343	Kataktara	Pakistan	Resistance to blast, sheath blight
6426	Basmati 370	Pakistan	Aroma and cooking quality
259	81B-25	Surinam	Grain appearance, plant type
		Indica x japonica varieties	
134	Century Patna 231	U.S.A.	High gel. temp., grain appearance, glabrousness
2026	Dawn	U.S.A.	Intermediate amylose, blast, glabrousness, grain appearance
6755	Bluebelle	U.S.A.	Intermediate amylose, earliness, grain appearance

Continued on next page.

Table 2. *Continued.*

IRRI acc. no.	Variety or line	Origin	Traits
6993	CP 231 x SLO 17	U.S.A.	Glabrousness, short height, grain appearance, high gel. temp., resistance to bacterial leaf blight
251	Belle Patna	U.S.A.	Earliness, glabrousness, grain appearance, intermediate amylose
9797	B589A4-18	U.S.A.	Grain appearance, resistance to bacterial leaf blight, blast
131	Zenith	U.S.A.	Earliness, grain appearance, resistance to bacterial leaf blight, blast
		Bulu varieties	
9241 13736	Sukanandi	Indonesia	Non-shattering
		Japonica varieties	
9740	Yukara	Japan	Cold resistance, tough leaf
523	Wase Aikoku 3	Japan	Tough leaves, resistance to bacterial leaf blight
410	Rikuto Norin 20	Japan	High protein
2251	Santo	Korea	High protein
2171	Chow-sung	Korea	High protein
3192	Crythoceros Korn	Portugal	High protein
2169	Chok-jye-bi-chal	Korea	High protein
11137	Jinheung	Korea	Cold resistance, tough leaves, slow senescence
3165	Omirt 39	Hungary	High protein
98	Kaohsiung 68	Taiwan	Tough leaves, grain appearance, resistance to bacterial leaf blight
102	Taichung 172	Taiwan	Tough leaves, grain appearance, blast resistance, bacterial leaf blight
90	Chianan 8	Taiwan	Tough leaves, grain appearance, resistance to blast, bacterial leaf blight
87	Chianung 242	Taiwan	Tough leaves, grain appearance, resistance to blast, bacterial leaf blight
146	PI 215936	Taiwan	Tough leaves, grain appearance, resistance to bacterial leaf blight
145	Calrose	U.S.A.	Cold resistance
10810	Earlirose	U.S.A.	Cold resistance
		Wild species	
101508	*Oryza nivara*	India	Grassy stunt resistance

been identified. For example, sources of leafhopper and planthopper resistance were not known until 1966 (IRRI, 1967*a*). Today testing techniques are available for screening most characters. But testing techniques must be improved further and the search for more and better sources of disease and insect resistance and other desirable traits must continue.

Table 3. IRRI crosses from which promising lines have been selected or which appear promising.

IRRI cross no.	Parents
IR4	H 105 x Dee-geo-woo-gen
IR5	Peta x Tangkai Rotan
IR6	Siam 29 x Dee-geo-woo-gen
IR8	Peta x Dee-geo-woo-gen
IR9	Peta x I-geo-tze
IR11	FB-24 x Dee-geo-woo-gen
IR12	Mong Chim Vang A x I-geo-tze
IR14	Kaohsiung 68 x BPI-76
IR39	Peta x Taichung Native 1
IR66	Century Patna 231 x Kaohsiung 68
IR68	Century Patna x PI 215936
IR76	BPI-76 x Taichung 176
IR84	Peta x PI 215936
IR95	Peta/2 x Taichung Native 1
IR127	(CP231 x SLO 17) x Sigadis
IR140	(CP231 x SLO 17) x Mas
IR154	(CP231 x SLO 17) x Taichung Native 1
IR159	Basmati 370 x Taichung Native 1
IR253	Gam Pai/2 x Taichung Native 1
IR262	Peta/3 x Taichung Native 1
IR272	(CP231 x SLO 17)/2 x Sigadis
IR305	Sigadis/2 x Taichung Native 1
IR400	Peta/4 x Taichung Native 1
IR407	Peta/3 x Dawn
IR424	Basmati 370/3 x Taichung Native 1
IR425	Sigadis/3 x Taichung Native 1
IR435	(CP231 x SLO 17) x Pingaew 56
IR438	Tainan 3 x Pingaew 56
IR441	(CP231 x SLO 17) x Leb Mue Nahng
IR442	(Peta/2 x Taichung Native 1) x Leb Mue Nahng
IR474	Sukanandi x Taichung Native 1
IR478	(CP 231 x SLO 17) x Sukanandi
IR480	Nahng Mon S-4/2 x Taichung Native 1
IR482	Peta/5 x Taichung Native 1
IR485	Peta/5 x Belle Patna
IR489	Bluebelle/4 x Taichung Native 1
IR498	[(CP231 x SLO 17)/2 x Taichung Native 1] x Zenith
IR506	IR8 x [B589A4-18/2 x Taichung Native 1]
IR509	Chianung 242/2 x (Tainan 3 x Taichung Native 1)
IR520	Basmati 370/2 x Taichung Native 1
IR532	(Peta/3 x Taichung Native 1) x TKM-6
IR533	[(CP231 x SLO 17)/2 x Sigadis] x (Peta/3 x Taichung Native 1)
IR564	Peta/6 x Taichung Native 1

Continued on next page.

Table 3. *Continued.*

IRRI cross no.	Parents
IR568	Yukara x Taichung Native 1
IR577	IR8 x Sigadis
IR578	IR8 x (Sigadis x Taichung Native 1)
IR579	IR8 x Tadukan
IR596	IR8 x Pankhari 203
IR609	Taichung Native 1 x Kalijiira Aman
IR626	IR8 x (Peta/5 x Belle Patna)
IR627	IR8 x Wagwag
IR630	IR8 x IR5
IR665	IR8 x (Peta/5 x Belle Patna)
IR666	IR8 x Yukara
IR667	IR8 x (Yukara x Taichung Native 1)
IR743	Peta/7 x Belle Patna
IR747	TKM-6/2 x Taichung Native 1
IR751	IR8/2 x (Peta/5 x Belle Patna)
IR758	IR8/2 x Dawn
IR759	IR8 x (Peta/3 x Dawn)
IR781	IR8/2 x (Yukara x Taichung Native 1)
IR789	IR8 x Muey Nahng 62 M
IR790	(Peta/4 x Taichung Native 1) x {IR8 x [(H 105 x Taichung Native 1) x (B589A4-18/2 x Taichung Native 1)]}
IR810	IR8 x Khao Dawk Mali
IR822	IR8/2 x Pankhari 203
IR825	(IR8 x Pankhari 203) x (Peta/6 x Taichung Native 1)
IR828	IR8/2 x Basmati 370
IR829	IR8 x [(CP231 x SLO 17) x Gam Pai]
IR833	(Peta/3 x Taichung Native 1) x Gam Pai
IR835	Peta/3 x Taichung Native 1 x Leuang Hawn
IR841	Peta/3 x Taichung Native 1 x Khao Dawk Mali
IR844	Peta/3 x Taichung Native 1 x Puang Nahk 16
IR848	Peta/3 x Taichung Native 1 x [(CP 231 x SLO 17) x Gam Pai]
IR874	IR8/2 x [(CP 231 x SLO 17)/2 x Nahng Mon S-4)]
IR878	IR8/2 x [(CP 231 x SLO 17) x Nahng Mon S-4]
IR879	IR8/2 x (Peta/3 x Dawn)
IR880	IR8/3 x (81B-25 x Dawn)
IR881	IR8/3 x Wagwag
IR887	IR8/2 x Muey Nahng 62 M
IR930	IR8 x IR12-178
IR932	IR8/3 x Pankhari 203
IR934	IR8/3 x (Yukara x Taichung Native 1)
IR946	IR4-93-2 x H 4

Continued on next page.

Table 3. *Continued.*

IRRI cross no.	Parents
IR951	IR12-178 x BPI-76
IR968	IR8 x IR12-178
IR1001	IR8 x T-3 (Basmati)
IR1006	IR8 x BPI-76
IR1008	IR8 x IR154-61-1
IR1093	IR8 x Intan
IR1100	IR8 x Rikuto Norin 20
IR1101	IR8 x Omirt 39
IR1102	IR8 x Santo
IR1103	IR8 x Chow-sung
IR1104	IR8 x Crythoceros Korn.
IR1105	IR8 x Chok-jye-bi-chal
IR1108	(Peta/3 x Taichung Native 1)/2 x Puang Nahk-16
IR1154	IR8/2 x Zenith
IR1201	IR11-288-3 x Intan
IR1253	IR8 x T-141
IR1302	Intan/2 x IR8
IR1317	Jinheung x (Peta/3 x Taichung Native 1)/2
IR1325	[Jinheung x (Peta/3 x Taichung Native 1)] x IR781-495
IR1409	IR8/2 x T-141
IR1414	Mudgo x IR8/2
IR1529	(Sigadis/3 x Taichung Native 1) x IR24
IR1544	IR24 x Tetep
IR1561	(IR8 x Tadukan) x (TKM-6/2 x Taichung Native 1)
IR1587	[IR8 x (Yukara x Taichung Native 1)] x [Jinheung x (Peta/3 x Taichung Native 1)]
IR1614	IR22 x (Mudgo x IR8)
IR1641	IR24 x *O. nivara*
IR1668	Calrose x [IR8/3 x (Yukara x Taichung Native 1)]
IR1703	IR24/2 x Tetep
IR1707	IR22/2 x (Mudgo x IR8)
IR1737	IR24/4 x *O. nivara*
Pathology	IR8/4 x Wase Aikoku 3
Pathology	IR8/4 x *O. nivara*
Pathology	IR8/5 x (Dawn x Kataktara)
Entomology	IR841 x (Mudgo x IR8)
Entomology	TKM-6 x IR20

So far no variety with improved plant type has all of the desired traits. Rapid progress is being made and many of the new crosses combine essentially all the desirable traits.

The pedigree method has been the main breeding procedure used at IRRI. Some modified bulk-hybrid populations have been grown but since our effort tends to be a crash program, we considered the pedigree method, supported

Table 4. Number of crosses made at IRRI since 1962.

Year	Total crosses (no.)	IRRI cross numbers
1962	38	IR1 to IR38
1963	48	IR39 to IR86
1964	215	IR87 to IR301
1965	282	IR302 to IR583
1966	345	IR584 to IR928
1967	359	IR929 to IR1287
1968	171	IR1288 to IR1458
1969	170	IR1459 to IR1628
1970	117	IR1629 to IR1745

by the rapid screening techniques, to be the fastest way to achieve progress. The first pedigree rows were grown in 1964 and through the 1971 wet season crop, over 218,000 pedigree rows have been grown at the IRRI farm.

Plant breeders must work continuously to build up a widely divergent genetic background for varieties to avoid crop failures due to outbreaks of diseases and insects, or other factors. Since we depend heavily upon the semidwarf indicas as a source of short stature and nitrogen responsiveness, a wide range of varieties must be used in developing varieties that have improved plant type. We have attempted to do this. It is encouraging that rice breeders in many countries are using local varieties in crosses with IRRI lines to develop varieties that have improved plant type. This leads to greater divergency of germ plasm and only if complete or near-complete linkage of some undesirable trait, such as disease susceptibility, existed would the semidwarf genotype be endangered by epidemics which, so far, have not appeared but which might develop in the future.

COOPERATION WITH OTHER COUNTRIES

IRRI cooperates closely with rice breeders in many countries and rapidly disseminates all new information concerning rice. Since the breeding program was started in 1961, nearly 58,000 packets of IRRI breeding lines have been sent to scientists in 80 countries. Over 1,200 individual requests for seeds of breeding lines have been filled. In addition 24,000 packets of seed from the world collection have been distributed.

In 1966, a collection of 303 varieties and breeding lines was sent to India, Malaysia, Pakistan, Taiwan, Thailand, Colombia, Costa Rica, Dominican Republic, Mexico, and USA. Parts of the collection were sent to 30 other countries. The collection was made up of 92 lines from Taiwan japonica (ponlai) x tall tropical indica varieties, 160 lines from semidwarf indica x tall tropical indica, and 51 varieties, many of which were parent varieties or have since become parent varieties.

In 1 year, the collection established the superiority of the semidwarf indica x tropical indica lines over japonica x indica and other breeding lines. Included among the semidwarf indica x tropical indica lines were IR8, IR5, IR9-60, IR4-93-2, IR5-114-3 (Pankj), and IR6 lines similar to Mehran 69. Breeding lines that have been used frequently at IRRI and in other countries as parent lines or which show promise as varieties are shown in Table 5. There were 26 different parent varieties used in developing the 24 lines shown in Table 5. Two lines have plant height genes from Acc. 6993 and the others have Taiwan semidwarf height genes. Peta occurs in the pedigree of 17 of the lines and IR8 in 11 of them.

Obviously, the IRRI breeding program is not intended to develop varieties for all of Asia. The objectives are to combine improved plant type with disease and insect resistance, cold resistance, different growth durations and photosensitivity, and different grain shapes and cooking properties, and to make these varieties or breeding lines available to other countries. Sometimes the varieties

Table 5. IRRI breeding lines which show promise for use in breeding programs at IRRI and elsewhere.

Line	Parents
IR4-93-2	H-105 x Dee-geo-woo-gen
IR127-80-1	(CP-231 x SLO 17) x Sigadis
IR140-136	(CP-231 x SLO 17) x Mas
IR253-16-1	Gam Pai/2 x Taichung Native 1
IR262-43-8	Peta/3 x Taichung Native 1
IR272-4-1	(CP231 x SLO 17)/2 x Sigadis
IR532-1-218	(Peta/3 x Taichung Native 1) x TKM-6
IR579-48-1	IR8 x Tadukan
IR667-98	IR8 x (Yukara x Taichung Native 1)
IR747B2-6	TKM-6/2 x Taichung Native 1
IR751-595	IR8/2 x (Peta/5 x Belle Patna)
IR756-88-2	IR8/3 x [(Bluebonnet 50/2 x Gulfrose/2 x Taichung Native 1)]
IR828-28-1	IR8/2 x Basmati 370
IR833-6-2	(Peta/3 x Taichung Native 1) x Gam Pai
IR841-67-1	(Peta/3 x Taichung Native 1) x Khao Dawk Mali
IR878B4-220-3	IR8/2 x [(CP-231 x SLO 17) x Nahng Mon S-4]
IR879-183-2	IR8/2 x (Peta/3 x Dawn)
IR944-102-2	(Taichung Native 1 x Malagkit Sungsong) x IR8
IR1093-104-2	IR8 x Intan
IR1108-3-5	(Peta/3 x Taichung Native 1)/2 x Puang Nahk 16
IR1112-28-1	(Peta/3 x Taichung Native 1)/2 x Khao Dawk Mali
IR1154-681-2	IR8/2 x Zenith
IR1168-58-2	IR8/2 x [(CP231 x SLO 17) x Taichung Native 1)]
IR1201-1-1	(FB24 x Dee-geo-woo-gen) x Intan

may be suitable for commercial use but frequently their value as parent material is more important.

IRRI and the Government of Korea designed a special program for developing varieties specifically for Korea with most of the work being done there by Koreans. IRRI filled in the gaps by making crosses and growing breeding lines in the Philippines during the winter months so that hybrid material would be advanced by two generations a year. IRRI also trained Korean rice breeders and did some of the evaluation for disease and insect resistance and grain quality.

Another means of cooperation with other breeding programs is through the IRRI training program. Over 70 individuals have been trained in the varietal improvement department and most received practical training in plant breeding. In the course of such training, they study the IRRI breeding lines and make crosses between their own country's varieties and IRRI material. When they return to their home country they take with them the newly crossed material and other breeding material as well as the knowledge they have accumulated.

SEED PROGRAM

It is essential that pure seed be widely distributed as soon as new varieties are named and released for commercial production. At IRRI a special effort is made to have up to 70 tons of pure seed of each new variety available at the time it is named. We also assist official seed producing agencies in the Philippines and elsewhere by providing them with breeder seed of IRRI varieties for use in certified seed programs. More attention must be given to this important work so that the farmer and consumer will benefit fully from improved varieties.

At IRRI, many promising lines are grown in seed-increase plots. This seed is used for wide-scale testing in the Philippines and in other countries. In addition it provides a source of plant material for seed purification. During the past several seasons this program has been given considerable attention. During 1971, 122 advanced-generation lines were grown in head-row blocks to determine homozygosity. Seed lots of the lines that are judged to be homozygous for the characters identified are then set aside for use in yield trials and for use in growing breeder seed. Usually 150 to 300 plant selections, each grown in a separate four-row plot, 5 m long, are planted for the production of breeder seed. In the preliminary purification stage, from 30 to 40 plant selections from each line are grown in four-row plots.

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Discussion: IRRI's international breeding program

B. H. CHEW: In your early maturity lines, such as the IR1561 line, which I understand will mature in less than 100 days, do you have any difficulty in getting enough tillers to boost its yielding potential?

H. M. Beachell: The IR1561 lines require slightly more than 100 days from seeding in the seedbed to maturity. Under intense management practices an adequate number of tillers is produced. In the U.S., following good management practices, early maturing varieties of about 100 days yield as well as varieties maturing in 134 to 170 days.

T. H. JOHNSTON: How many generations of breeding were required to get the clear-kernel types with IR8 plant type?

H. M. Beachell: Grains free of genetic white belly were identified in F_3 lines and possibly in grains of F_2 plants. Clear-grain lines have been obtained from backcross combinations of IR8/2 x clear-grained U.S. varieties which would indicate a few genes controlling white belly.

Y. L. TENG: Do you think we should develop direct-seeding and transplanting rice varieties separately, or should we develop rice varieties adapted to both direct-seeding and transplanting?

H. M. Beachell: IR8, a variety developed for transplanted culture, has produced higher yields under broadcast direct-seeding than under transplanted culture at Los Baños. Likewise, IR5 grown under direct-seeded upland conditions has produced a higher yield than any upland variety in tests conducted by IRRI. This indicates that a variety adapted to transplanted conditions would, likewise, be adapted to direct-seeded conditions. Low tillering varieties adapted to direct seeded conditions would not be adapted to transplanted conditions.

N. PARTHASARATHY: Under the same temperature conditions, have you found any variation in the grain ripening period from heading?

H. M. Beachell: Japonica varieties usually take longer from heading to maturity than indica varieties. This is true in the U.S. as well as in the tropics.

S. OKABE: You have showed several early maturing lines in your slides. Do they have the same photoperiod-sensitivity as IR8? And are they all tolerant to low temperature during the vegetative growth stage?

H. M. Beachell: The early maturing varieties are possibly less photoperiod sensitive than IR8. Some of them mature 20 or more days earlier than IR8 and they are not tolerant to low temperatures.

R. K. WALKER: In addition to problems of drying grain, another important reason for photoperiod sensitivity in the monsoon season is flowering and maturation under good climatic conditions.

T. H. JOHNSTON: As breeders, should we be concerned with concentrations of large expanses of individual varieties within a country?

H. M. Beachell: We should be concerned with a reasonable number of high yielding varieties of the grain type and maturity variation to meet the needs of farmers and consumers within the country. In addition, the varieties should represent considerable genetic diversity to provide insurance against a major disease epidemic.

Rice breeding in Colombia

Manuel J. Rosero M.

A new variety, CICA 4, was jointly named by Centro Internacional de Agricultura Tropical and the Instituto Colombiano Agropecuario in 1971. This variety combines good plant type with other desirable traits, such as grain quality and insect and disease resistance. It is recommended for irrigated and upland areas up to 1,000 meters above sea level. Along with CICA 4, the variety IR22 has been extensively tested in Colombia and is recommended for irrigated areas up to 700 meters above sea level. Lines of IR822, T319 (Colombia 1), and T507C along with the varieties Tetep, Dissi Hatif, Mamoriaka, and C46-15 have been crossed and backcrossed as sources of blast resistance with several promising high-quality dwarfs. F_2 and F_3 selections from these crosses are being evaluated. Selection of resistant progeny is directed toward horizontal (general) resistance. Several crosses involving CICA 4 and related IR930 selections are being studied in F_5 generation to identify lines 15 days earlier than CICA 4, that have slow leaf senescence and slightly less amylose in the endosperm. Lines that combine these traits will be developed as eventual replacements for IR22 and CICA 4.

INTRODUCTION

In Latin America, rice is an important crop. It is a staple of the daily diets of the people. In countries like Colombia, Ecuador, Brazil, and Panama, most families on the coasts and in valley rivers below 500 meters above sea level depend on rice for their survival.

In 1969 about 6.6 million hectares was planted to rice in Latin America. The total production was 10.7 million tons of rough rice, giving an average yield of 1.6 t/ha. This average yield is low mainly because 60 percent of the rice area is upland, because there is lack of high yielding varieties with acceptable milling and cooking quality and disease and insect resistance, and because cultural practices are inadequate.

In Colombia, rice makes up 9 percent of the total agriculture production. While the total agriculture production from 1958 to 1968 increased 30 percent, rice production for the same period increased 70 percent. Since 1962, rice production has been large enough not only to satisfy the national consumption but also to accumulate a surplus which is being stored to cover production deficiencies in some years and occasionally to export to countries of the Andean

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Region. In 1969, Colombia exported 25,000 tons of brown and milled rice to Peru, Ecuador, and Curaçao.

In Colombia, rice is direct seeded and grown under both irrigated and upland conditions. The irrigated area is highly mechanized from seeding to harvest; most of the nonirrigated area is under a primitive cropping system. About 300,000 hectares are planted to rice each year although variations occur from one year to another. Between 1965 and 1969 the area of production decreased continuously with the greatest reduction in the nonirrigated area. By 1969 the area planted to rice was only one-third of the area planted in 1965. But an increase in the productivity of irrigated land during these years compensated for the reduction in area. The yield on irrigated land in 1969, 4.1 t/ha, was 55 percent greater than the yield in 1965. Despite this increase, the overall average yield including upland rice was only 2.7 t/ha.

PROBLEMS OF RICE IN COLOMBIA

The main problems affecting yield are lack of high yielding varieties with good milling and cooking quality and disease resistance, and cultural practices.

Varieties

In the irrigated area the varieties grown are Bluebonnet 50, Tapuripa, IR8, Starbonnet, and Bluebelle, while in the upland area Bluebonnet 50 and several native varieties are predominant. Bluebonnet 50 is a low yielding variety that is susceptible to diseases and insects. But it ranks first in the commercial market in Colombia because of its good milling and cooking qualities.

Tapuripa (SML 140/5) was introduced from Surinam in 1965. This variety has higher yielding ability than Bluebonnet 50, but it is late in maturity and poor in milling and cooking quality. Because of its high yields it was extensively grown in 1967 and 1968. In 1969, however, this variety was severely affected by sheath blight which reduced its yield 20 to 30 percent. Consequently, Tapuripa is being replaced with varieties like IR8, Starbonnet, and Bluebelle.

IR8 has had high yields in irrigated areas located below 500 meters above sea level. Average yields of 6 to 7 t/ha have been obtained on large farms. But IR8's milling and cooking quality have impeded its widespread adoption by the farmers; nevertheless, in 1970, 20,000 hectares were planted to IR8 and its production saved Colombia from importing milled rice to satisfy the national consumption needs. The future of IR8 in Colombia probably will be short. The farmers will quickly change from IR8 to the first variety that has similar yield with acceptable grain quality.

Starbonnet and Bluebelle have been introduced recently. These varieties have the same disadvantage of Bluebonnet 50: low yield and susceptibility to diseases and insects. Thus, only a few farmers in a small area can use them.

Diseases

Blast, hoja blanca, and sheath blight are the most destructive diseases of rice in Colombia. Blast is serious especially in the eastern upland area where it is favored by a high relative humidity and moderate temperature. All varieties grown in Colombia are susceptible to blast. The hoja blanca virus has been a critical problem in both irrigated and upland areas planted with U.S. varieties. During the last 3 years sheath blight has been an important problem especially on the Atlantic coast and in the departments of Meta and Tolima, affecting the Tapuripa variety severely.

Insects

Sogatodes orizicola (Muir) limits Colombian rice production. This insect not only is vector of the hoja blanca virus but it does direct damage to rice. During the last 5 years the direct feeding damage has been more important than the virus. All commercial varieties grown in Colombia, except IR8, are susceptible to the insect damage.

RICE BREEDING PROGRAM

During the 1950's, rice production in Colombia was low and the government imported milled rice. In 1957 the rice industry was seriously affected by a new disease, now known as hoja blanca, that caused losses greater than 50 percent, especially in the Cauca Valley.

Thus in 1957, the Agricultural Department of Investigation, a branch of the Ministry of Agriculture, now known as Instituto Colombiano Agropecuario (ICA), with the cooperation of The Rockefeller Foundation, began a rice breeding program. This program was located first at the Palmira station and in 1959 it was expanded to Nataima station in the Tolima, a main rice producing state. By 1960, the rice area had increased greatly along the Atlantic coast and in the eastern part of Colombia. To serve these zones the rice breeding programs of the La Libertad and Turipaná stations began operations in 1962.

From the start, the rice breeding program was aimed at developing high-yielding varieties with resistance to hoja blanca and with acceptable grain quality. To accomplish this objective an international nursery of 3,000 rice varieties was introduced from the U.S. Department of Agriculture. The nursery was planted at the Palmira station and a group of varieties with resistance to hoja blanca was selected to start a breeding program.

From 1958 to 1966 over 800 crosses were made at both Palmira and Nataima stations. The crosses resulted in several lines that yielded better than the commercial Bluebonnet 50 variety and had resistance to hoja blanca. Two varieties were developed from these materials. One was named Napal and released to farmers in 1963. In 1964 Napal became highly susceptible to blast and was rejected by the farmers. The second variety, ICA-10, was released in 1967 and recommended for the Cauca Valley region. ICA-10 is highly resistant to hoja blanca and higher in yield capacity than Bluebonnet 50 but inferior in cooking quality and blast resistance. Its cooking quality has limited its adoption by farmers.

By mid-1967 the rice breeding program was completely reorganized. With the cooperation of the Inter-American Rice Program of Centro Internacional de

Agricultura Tropical (CIAT) good facilities were provided for testing quality, and techniques to evaluate blast and insect resistance were developed.

The goal of the cooperative work of CIAT and ICA is to develop superior high yielding varieties with:

—Improved plant type, emphasizing strong seedling vigor, moderately heavy tillering, semidwarf stature, and erect leaves.

—Early maturity, a range of 90 to 120 days.

—Resistance to blast and sheath blight.

—Resistance to hoja blanca virus and *Sogatodes orizicola.*

—Good milling and cooking quality. Colombian people prefer long, slender, and translucent grain, intermediate in both amylose content and gelatinization temperature.

BREEDING RESULTS

Breeding populations

To accomplish the principal breeding objectives, several advanced IRRI lines, some with IR8 parentage having good plant type and insect resistance, were crossed with sources of good grain characteristics, earliness, and resistance to the hoja blanca virus and blast disease. Since 1967 a total of 550 crosses have been made. In the second crop of 1969 and first crop of 1970, 11,188 segregates in F_2 to F_7 generations were studied at the Palmira station. From these segregates 6,600 plants were selected and studied in the following generations during the second crop of 1970. From the F_3 to F_5 segregating rows, 2,346 individual plants were selected which are under study in later generations. The selection of this material was made on the basis of good plant type, long grain with clear endosperm, intermediate or low gelatinization temperature, and resistance to hoja blanca virus, insect damage, and the blast disease.

All plant selections from F_3 to F_7 and fixed lines in observation plots and yield trials are tested for insect resistance. Fifteen-day-old seedlings selected from individual plants of segregating lines are exposed to large numbers of virus-free insects. Reactions were recorded after 8 days. The test clearly distinguishes among resistant, segregating, and susceptible plants. Seedling reaction is highly related to the reaction of adult plants. Seedlings or adult plants of resistant varieties, like IR8 and Mudgo, show little or no reaction, while susceptible ones, like Bluebonnet 50, are killed by the insect. Resistance to the insect appears to be highly heritable and is easily combined with all other desired traits.

In 1970, 99 crosses were made with the primary purpose of combining blast resistance with other desired traits already present in several promising IRRI lines. As sources of blast resistance, lines of IR822, T319 (Colombia 1), and T507C were used along with Tetep, Dissi Hatif, Mamoriaka, and C46-15. These materials have shown a broad resistance for several seasons under the blast bed conditions at La Libertad station. From these crosses 1,000 F_2 and 3,400 F_3 plants are being studied at present on the Palmira station. Normally, a single backcross to the semidwarf parent is made for all blast crosses. Selection of resistant progeny is directed toward horizontal (general) resistance.

Variety multiplication

From the segregating lines introduced from IRRI by CIAT in 1967 and evaluated in 1968 at the Palmira station, 191 lines were purified in the first crop of 1969. In the second crop of 1969, these lines were evaluated in observation plots and yield trials at the rice research stations at Palmira, Nataima, La Libertad, and Turipaná and also at a farm in Codazzi, Cesar. Fifteen promising lines were selected that combined excellent plant type with superior grain quality and resistance to insect damage. These lines were multiplied in the first crop of 1970 at the CIAT farm and at the same time were tested in regional trials under farm conditions in different areas of Colombia. Based on yields, grain characteristics, and resistance to insect damage and certain diseases, the five best lines were selected for further multiplication and production of foundation seed.

In the multiplication plots of CIAT, over 1 ton of seed of each selection was obtained by mid-1970. Ten hectares of each selection were planted in September 1970 at the Nataima station. Over 50 tons of seed of each line were harvested in February 1971. A multiplication program at CIAT produced about 10 tons of each line by early 1971.

Table 1 lists the five promising lines including disease reaction, maturity, height, and yields obtained in Colombia in several regional tests in comparison with some commercial varieties. These data represent an average of 22 plantings made in 17 locations during 1970. The five lines showed less hoja blanca infection than all commercial varieties except ICA-10. Although these lines are susceptible

Table 1. Some plant characteristics of five promising lines and commercial varieties observed in regional trials in 1970.

Line number	Name and pedigree	Hoja blanca[a]	Leaf[b] blast	Neck blast (%)	Maturity range[c] (days) 0 to 700 m	Maturity range[c] (days) 700 to 1000 m	Mean plant height (cm)	Grain yield (t/ha)
4	IR930-31-1-1B (IR8 x IR12)	0.6	1.7	10	124	137	81	6.25
10	IR579-160-2 (IR8 x Tadukan)	1.1	1.6	10	123	134	79	5.40
13	IR665-23-3-1-1B (IR8 x [Peta[5] x Belle Patna])	0.7	2.4	24	117	131	84	6.28
14	IR665-33-5-8-1B (IR8 x [Peta[5] x Belle Patna])	0.8	2.2	24	114	131	73	5.19
15	IR665-33-1-3-1B (IR8 x [Peta[5] x Belle Patna])	0.5	2.0	15	115	131	75	4.88
	IR8	1.4	2.0	14	129	143	71	5.37
	Bluebonnet 50	4.1	2.8	17	123	137	123	3.53
	Tapuripa	2.0	1.6	8	148	152	117	4.41
	Starbonnet	3.1	2.3	3	122	147	107	3.89
	Bluebelle	2.1	2.6	18	100	—	99	2.93
	ICA-10	0.0	2.0	46	125	136	100	3.79

[a]1-2 = resistant; 2-3 = moderately resistant; 3-4 = moderately susceptible; 4-9 = susceptible.
[b]1-2 = resistant; 2-3 = moderately resistant; 3-4 = moderately susceptible; 4-7 = susceptible.
[c]Seeding to harvest at 0 to 700 m above sea level and 700 to 1,000 m above sea level.

to blast in the blast nurseries they showed a moderate reaction under field conditions. Lines 4 and 10 were less affected by both leaf and neck infections. The other lines were similar in leaf blast infection to commercial varieties but showed a higher incidence of neck rot.

The lines ranged in maturity (seeding to harvest) from 114 to 124 days for areas up to 700 meters above sea level and from 131 to 137 days for areas 700 to 1,000 meters above sea level. Lines 4 and 10 were similar in maturity to Bluebonnet 50 and were earlier than IR8 and Tapuripa. In plant height, lines 14 and 15 were similar to IR8 and the others were 8 or 10 cm taller. All were short compared with Bluebonnet 50, Tapuripa, Starbonnet, Bluebelle, and ICA-10. Lines 4 and 13 averaged approximately 1 t/ha more than the other lines and IR8. Yields of lines 10, 14, 15, and IR8 were similar but 1 to 2 tons higher than yields of the other commercial varieties.

For semi-commercial evaluation of the milling quality of these five selections, 4 tons of each were processed in a commercial mill. The milling results plus gelatinization temperature and amylose content are shown in Table 2. All selections, except line 13, gave excellent milling yields. Line 4 was the highest in both head rice and total rice. Line 13 was lowest in head rice percentage. These results confirmed those of several tests made in the laboratory at Palmira.

Seed of the five promising selections provided by CIAT was planted in other Latin American countries in 1970 (Table 3). In Honduras, lines 10, 13, and 14 were not included. Line 4 gave the highest yield. It yielded 1 to 2 t/ha more than IR8 in all these upland areas. In a test at Tumaco, Colombia, the same line yielded 4.9 t/ha. This was 2.2 t/ha higher than that of any other entry. These upland results and those reported on irrigated areas indicate that line 4 has a wide range of adaptability.

Release of new varieties

Since two of the five promising selections, were superior to the others as reported in Tables 1, 2, and 3, CIAT and ICA rice technicians released lines 4 and 10 in 1971. Line 4, IR930-31-1-1B, was named CICA 4. "CICA" combines the initials of CIAT and ICA. The number "4" was retained because the line was known by this number in all regional tests in Colombia. The other line

Table 2. Milling quality, gelatinization temperature, and amylose content of the five promising selections.

Line	Head rice (%)	Total milled rice (%)	Gelatinization temperature	Amylose (%)
4	64.7	69.7	Intermediate	27
10	63.1	69.4	Low	29
13	51.8	67.5	Intermediate	27
14	60.0	64.8	Intermediate	28
15	61.0	67.5	Intermediate	30

Table 3. Grain yields of the five promising lines obtained in several Latin American countries in 1970.

Line number or variety	Yield (t/ha)			
	Honduras[a]	Panama[b]	Ecuador[c]	Costa Rica[d]
Line 4	6.80	5.66	5.76	5.04
Line 10	—	5.05	5.87	4.18
Line 13	—	2.66	8.96	4.88
Line 14	—	2.77	5.34	4.93
Line 15	5.60	2.46	6.08	4.66
IR8	5.60	4.09	7.05	3.39

[a]Ministry of Agriculture: one test, upland, moderate rainfall.
[b]National University: one test, upland, moderate rainfall.
[c]INIAP: average of five tests, irrigated, four transplanted.
[d]Ministry of Agriculture: average of three tests, upland, heavy rainfall.

selected was the number 10, IR579-160-2. This corresponded to IR22, released by IRRI in 1969.

CICA 4 was obtained by three cycles of selection of segregating material introduced from IRRI in 1968. It is being recommended for all irrigated and upland rice areas of Colombia up to 1,000 meters above sea level. CICA 4 has excellent seedling vigor and thick, sturdy culms. The grain is long and vitreous and has excellent milling and cooking qualities. The leaves are light green throughout the growth period. At maturity the leaves dry quickly. The flag leaves extend above the panicles. This trait apparently protects the variety against species of blackbirds, doves, and sparrows that damage tall varieties that have prominent panicles. CICA 4 is resistant to hoja blanca and highly resistant to *Sogatodes*. It has shown, under field conditions, a moderate resistance to sheath blight. It is susceptible to blast.

IR22 is recommended in Colombia for irrigated areas up to 700 meters above sea level. It is not well adapted at higher altitudes, such as Cauca Valley and the high plains of Ibague. It is sensitive to low temperatures. IR22 is resistant to *Sogatodes*, moderately resistant to hoja blanca, and susceptible to blast.

The ICA rice program distributed 44 tons of foundation seed of CICA 4 and 31 tons of IR22 to registered seed producers in Colombia. In 1971 seed producers planted about 350 hectares of CICA 4 and 243 hectares of IR22 under irrigated conditions. These plantings are being supervised by the ICA seed certification program to produce registered or certified seed.

The quality, insect resistance, and yield potential of CICA 4 should allow it to replace commercial varieties presently grown in Colombia. Its wide range of adaptability to both irrigated and upland conditions is important, too. All these advantages might cause CICA 4 to initiate a "green revolution" that is badly needed not only in Colombia but also in other Latin American countries.

To influence its adoption, ICA distributed about 5 tons of CICA 4 seed among several small, marginal upland rice farmers. Concurrently, CIAT distributed about 4 tons of CICA 4 seed outside Colombia, and about 3 tons for regional trials of 1 hectare each among several Colombian farmers.

CIAT and ICA scientists are studying several crosses involving CICA 4 and related IR930 selections to identify lines 15 days earlier than CICA 4, with blast resistance, green leaves functioning until harvest, and slightly less amylose in the endosperm. In the F_5 generation a large number of lines appear to combine these traits. This material should allow rapid development of a variety to replace IR22 and CICA 4.

Discussion: Rice breeding in Colombia

P. A. LIEUW-KIE-SONG: What is the grain size of your lines with more than 60 percent head rice?

M. J. Rosero: All five selections have long grains, that is, the rough rice is 7.5 to 9.0 mm long. Lines 4 and 10 which correspond to CICA 4 and IR22, respectively, have this range of grain length and gave more than 60 percent head rice.

A. O. ABIFARIN: You mentioned that CICA 4 has been recommended for both upland and lowland cultivation. What is its relative performance under the two cultural conditions?

M. J. Rosero: Under irrigated conditions the yield of CICA 4 has been between 3.0 to 9.0 t/ha, with an average of 6.2 t/ha. Under upland conditions in several locations in Colombia and Central American countries, the yield of CICA 4 has been between 3 to 7 t/ha, with an average of 5.6 t/ha. These data were obtained from regional tests under farm conditions and from small plots.

B. H. SIWI: You mention that CICA 4 is quite adapted to altitudes from 0 to 1,000 meters above sea level and it can be grown under irrigated as well as under upland conditions. Do you have information on the latitudes to which this variety is adapted?

M. J. Rosero: CICA 4 has been tested on regional trials in the main irrigated and upland rice areas of Colombia which are located from 3°N to 12°N. It has also been tested in Central American countries like Costa Rica, Panama, and Honduras. These countries are located at about 15°N. In Ecuador, CICA 4 is well adapted to rice areas between 4°S and 5°S.

H. L. CARNAHAN: Is the insect resistance of CICA 4 effective in minimizing virus loss across the entire area where CICA 4 is adapted?

P. R. JENNINGS: Yes.

Rice improvement in India—the coordinated approach

Wayne H. Freeman, S. V. S. Shastry

The All-India Coordinated Rice Improvement Project (AICRIP), whose primary objective has been the evolution of a common multi-discipline program encompassing over 100 experiment stations in the country, has rapidly progressed in various aspects of rice improvement. AICRIP's immediate objective is the identification of consumer-preferred, pest and disease-resistant, high yielding semidwarf varieties that mature within 100 to 160 days. The program has released three IRRI varieties, IR8, Pankaj, and IR20, following countrywide testing, and has identified and released 11 varieties developed within the country. The locally developed varieties include Jaya for high yields; Cauvery and Bala for early maturity; Vijaya, Ratna, and Krishna for good grain type; and Jagannath for late maturity. In 1970 semidwarf rices covered 11 percent of the total rice area and 30 percent of the total irrigated rice area in India. The analyses of factors that determine high yields—nitrogen management, and pest and disease control—are prominent features of the program and are well integrated with varietal improvement. Screening nurseries for insect and disease reaction in specific localities reveal the merits and weaknesses of the experimental lines being tested for yield and guide the decisions on release. Extensive programs to identify new donors for resistance to bacterial leaf blight, gall midge, and tungro virus are under way to incorporate yield-stabilizing factors resulting from host-plant resistance.

INTRODUCTION

Science today is so complex that no individual working in isolation is able either to master all the facets of a single discipline or to contribute to substantial advances in that field. Common objectives are more rapidly achieved when a major effort is channeled through a team approach, each member pursuing a common objective, but undertaking only a particular facet of that objective as his assignment or responsibility. Where time and resources are limited, the team approach to a common objective is particularly appropriate.

The exchange of ideas and material which usually leads to the modification or clarification of an idea or to the evolution of a new variety or hybrid has frequently resulted in scientific advances. One good example in plant breeding is the evolution of dwarf wheats which triggered the well-known "green

Wayne H. Freeman, S. V. S. Shastry. All-India Coordinated Rice Improvement Project. Rajendranagar, Hyderabad, India.

revolution." This involved the isolation of Norin dwarf wheats, their introduction into the United States, the incorporation of the Norin genes into winter wheats, and the further crossing with Mexican wheats (Athwal, 1971).

RICE IMPROVEMENT THROUGH A COORDINATED APPROACH

The slow rate of increase in rice production in India has been the object of major concern for the last two decades. The marginal gains that could be obtained through such superior management of the existing varieties as the Japanese method of rice culture illustrated the futility of improved cultural management and emphasized that the potential of existing varieties had been almost fully exploited.

The earlier success of coordination in other cereal crop improvement programs led the Scientists' Panel to recommend to the Minister of Agriculture a coordinated program for rice. Research on rice had been pursued in India since the establishment of rice stations in Tamil Nadu and West Bengal about 1910. Early rice improvement work evolved tall indica varieties that suited farm conditions of a more or less low-investment and low-reward rice culture that involved minimal levels of fertilizer use, plant protection, water management, and weed control. Attempts to improve production through indica x japonica breeding programs produced a few varieties that, at best, were marginally better than those that previously existed. Plant type, the key to the problem, had at the time not been recognized.

The use of semidwarf indicas from Taiwan led to the recognition of a plant type that could provide the basis for significant increases in rice production in tropical countries. Varieties that could respond to fertilization and that could remain erect until harvest used sunlight more efficiently. They offered the plant breeder a potential that had not been identified before. Scientists at the International Rice Research Institute used these semidwarf indicas in crosses with tropical indicas and by 1965 made available a sizeable collection of breeding material to several countries, including India. From early evaluations of these breeding materials the infant program in India identified IR8 as a variety with high yield potential. The primary objective was a coordinated program that could quickly pool information from trials for comparison.

The same dwarf progenies not only produced a selection which became a released variety, they also were used in crossing programs throughout the country. The coordinated program had provided a common ground for evaluating introduced material and germ plasm of dwarf indicas for crossing with locally adapted tall indicas. The coordinated program also undertook the exchange of new breeding lines evolved from various crossing programs and evaluated them in a common testing program. As a result, local varieties from one area had progeny doing well in other areas; for example, progeny of TKM-6 from Tamil Nadu did well in Uttar Pradesh.

Timely progress reports covering one season's trials have provided research workers with access to all the data available. These reports contain a comprehensive account of the performance of many selections in a single season.

ORGANIZING AND IMPLEMENTING THE COORDINATED PROGRAM

The All-India Coordinated Rice Improvement Project (AICRIP), consisting of a coordinating center at Hyderabad and other centers throughout India, was expected to provide a multi-disciplinary approach to the problems of rice production. Principal among these disciplines were agronomy-physiology, breeding, entomology, and pathology.

The national center at Hyderabad is headed by a project coordinator. The Rockefeller Foundation designated a senior scientist as joint coordinator and provided a junior staff on a training basis and equipment not readily available in India. Five senior foreign scientists are assigned by IRRI under a contract between the U.S. Agency for International Development, IRRI, and the Indian Council for Agricultural Research (ICAR).

The rice-growing area of the country was divided into seven agro-climatic zones. The major research center in each zone, the zonal center, is headed by a senior scientist, the zonal coordinator, who is in charge of AICRIP's program in the zone, but who is responsible to a local administration—either the agricultural university or the state department of agriculture. In addition, each of the 12 major rice growing states has a regional research center. Uttar Pradesh, Orissa, Andhra Pradesh, and Tamil Nadu have both zonal and regional centers. Three testing centers are at Upper Shillong (Meghalaya), at Kalimpong (West Bengal), and at Imphal (Manipur).

National resources were used to support, in addition to a national coordinated program, research on inter-state problems. Two approaches have been employed within the coordinated program. The first is to support the existing research programs in the states by supplementing research already underway or to be undertaken in an accelerated program. Since crop improvement involves a multi-disciplinary approach, ICAR provided all zonal and regional centers with a senior and junior scientist in each of the disciplines of breeding, agronomy, pathology, and entomology. The only difference in assistance between zonal and regional centers was the identification of a zonal coordinator in the former. The testing centers were provided with a junior staff in the most important discipline in each location.

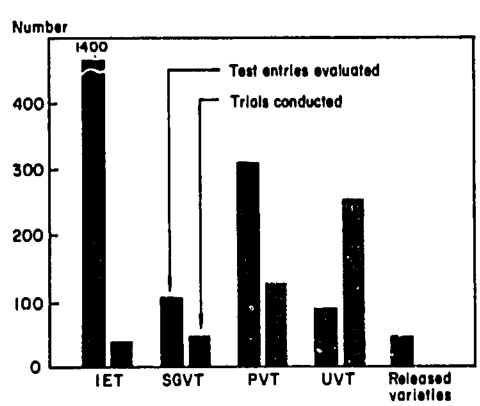
The second approach was to identify the centers that could help in solving national problems. Special staffs in bacteriology and virology have been provided at the Indian Agricultural Research Institute (IARI) to strengthen research in these fields. Warangal in Andhra Pradesh, which is consistently exposed to heavy depredation by rice gall midge, was designated as the national center for studies of the insect. It has been provided with a senior entomologist and a junior ecologist. Blast disease, deep water, or salinity in coastal areas are similar types of national problems. Support of an existing state center to enable it to concentrate on a specific problem should be seriously considered in the future.

Provisions have also been made for greenhouses, field equipment, seed storage buildings, and limited operational funds over and above those existing at the zonal, regional, and testing centers.

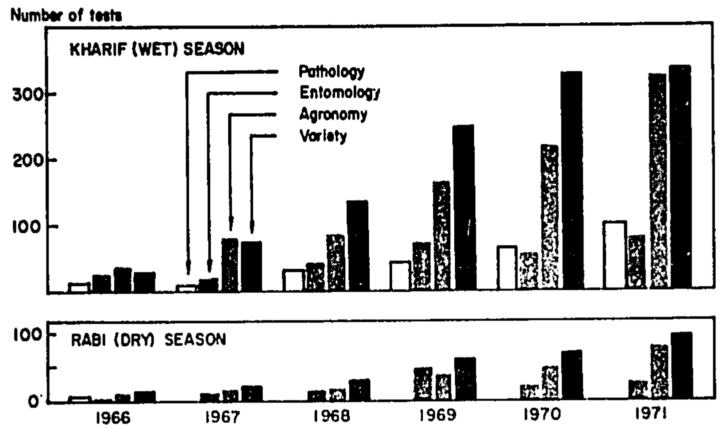
Table 1. Rice research centers involved in the AICRIP testing program, kharif (monsoon season), 1971.

AICRIP zone no.	Research centers (no.)				Trials programmed (no.)			
	Zonal	Regional	Others	Total	Breeding	Agronomy	Pathology	Entomology
I (Northern & northeastern hills)	1	2	7	10	21	24	1	2
II (Northeastern valleys)	1	-	4	5	19	32	3	6
III (Northwest plains)	1	1	16	18	51	67	15	10
IV (Northeast plains)	1	1	17	13	45	41	6	10
V (Central plains)	1	2	9	12	49	43	13	17
VI (Northern peninsula)	1	5	40	46	94	74	30	40
VII (Southern peninsula)	1	2	5	8	35	24	12	17
Total	7	13	98	112	314	305	80	102

Funding by ICAR began in 1968, nearly 2 years after an active coordinated program had begun. Although not planned, this sequence of events proved fortuitous because with or without funding the success of the program ultimately rested on the spirit of cooperation among the various workers in the program. Cooperators recognized that the benefits of cooperation largely depend on what the cooperator puts into a program and they enthusiastically carried out the program. As staffs grew with ICAR assistance, the program expanded in the centers.



1. Entries and locations involved in the stages of testing in initial evaluation trials (IET), slender grain variety trials (SGVT), preliminary variety trials (PVT), and uniform variety trials (UVT).



2. Coordinated trials, planned or conducted, 1966-71.

A functional coordinated program was developed from research plans drawn up by rice workers at semi-annual meetings. Previously, research staffs worked in isolation to quite an extent. Now the best genetic materials that breeding stations can provide to the testing program are systematically sent to them. Although a common testing program is evolved, specific locational advantages are exploited.

The underlying objective of the AICRIP is to promote among all rice scientists in the country a spirit of involvement in a common program. This objective has been achieved to a considerable extent through the active cooperation of the personnel involved. The testing program of AICRIP is not limited to 24 research centers receiving ICAR assistance, but is conducted at over 100 research stations all over the country (Table 1). IARI and the Central Rice Research Institute, nine agricultural universities, and several state departments of agriculture are involved.

The earliest stage of variety testing is the initial evaluation trial which involves breeding lines developed anywhere in the country together with the introductions from IRRI. The next stage is the preliminary variety trial undergone by superior performers in the initial evaluation trial. The final stage of testing is the uniform variety trial in which a variety's performance is judged not only on yield but also on nitrogen responsiveness. Varieties in all these trials are divided into three groups based on growth duration, 100 to 120 days, 120 to 140 days, and 140 to 160 days. The trials include progressively fewer test entries and are progressively more intensive (fig. 1). Because of increasing emphasis on breeding materials with high grain quality, a separate trial equivalent to a preliminary variety trial for varieties with slender grain was started in 1968.

In rabi (dry season), tests are made at fewer locations than in kharif because of seasonal conditions and lack of irrigation facilities. Testing locations are chosen to represent known variations in climate and soil. The number of locations has increased steadily from 1966 to 1971 (fig. 2).

The magnitude of the variety testing program is evident from the materials that were in multi-location tests which provided a sound basis for release of varieties. From 1966 to 1970, at different locations nearly 1,500 new materials from throughout the country were tested in the initial evaluation trials, 300 were tested in the slender grain variety trials, and 100 in the uniform variety trials. As a result of this program, 14 varieties (including three introductions) were released for cultivation.

More recently, adaptive testing of released varieties has been undertaken on state seed farms and on farmers' fields. The extension agencies are more closely involved in the conduct of these trials. These district-level trials have confirmed the superior performance of Jaya over IR8 in Punjab and Haryana states, and have led to the identification of an early maturing variety, Karuna, as being suitable for the Tanjavur delta of Tamil Nadu.

The coordinated testing program has seven key features. First, the program has a system of testing that involves planning by the group conducting the trials and those interested in the performance of entries in the trials they helped organize during annual workshop sessions, centralized pooling of seed for trials and dispatch by the coordinating center, well-defined trial plans from layout to data collection forms, assembly of data from various centers for compilation and calculation of national and zonal yields, and presentation of data in timely progress reports issued semi-annually.

Second, a working memorandum of understanding between the state centers and the coordinating center has been developed. Basic to the effectiveness of a written memorandum is the "intent" of the parties involved and the spirit of cooperation that exists among them. Fortunately, the cooperation had been achieved to a great extent before a memorandum of understanding was evolved. The problem of intent is of less concern since both state and center agencies that enter an agreement usually have one common objective.

Third, the research programs at the coordinating center and other national and state centers are designed to solve problems of rice production that will provide early pay-off in farmers' yields and national production.

Fourth, the program emphasizes flexibility of action. More flexibility than normally exists in governmental agencies is required for a coordinated program to function effectively. In the existing rice project, much of this added flexibility has been provided by assistance agencies. Since foreign assistance is not a permanent part of the program, the development of these additional degrees of flexibility by the government agencies will be important to the continuance of flexibility, since the need for flexibility will continue to exist in all action programs.

Fifth, team spirit among rice workers has developed from the exchange of seed materials, sharing of ideas in workshops, and information in progress reports.

Sixth, a multi-disciplinary approach to the study of the rice crop is used. Some rice problems such as insects and diseases must be attacked from several directions, so workers in different disciplines at different locations focus on the same problem. The efforts of these workers are coordinated. Without the cooperation of breeders on the one hand and of pathologists and entomologists on the other, a considerable range of host-plant resistance would not have been developed.

Furthermore, while inter-disciplinary cooperation is most needed in breeding for resistance to various diseases and pests, intradisciplinary coordination is required in studies of the disease organism or of the insect concerned. While more coordination is required to realize benefits more quickly in both phases, the progress made in these two aspects of coordination are exemplary. Coordination only needs to be pursued more vigorously to attain rapid progress in solving national problems in rice.

Seventh, the merit of the multi-location approach is self-evident. The limited resources of local experiment stations meant that previously no one station had enough funds to be able to quickly evaluate materials or to create populations large enough to permit the identification of the best strain for a locality. Now, crossing done at many locations creates enough progeny for effective selection, and evaluation at several locations allows potential varieties to be identified regardless of their origin. The more kinds of environment under which a variety has been proven, the more stable its performance is likely to be when grown by farmers in many different environments.

BREEDING METHODOLOGY

Breeding methods developed in the program accelerated the evaluation of new selections.

Large F_2 populations

The use of a large F_2 population was not a common plant breeding technique and still is not widely used. Initial crossing programs involved tall indica varieties whose stability "genes" were a result of many years of conscious or unconscious selection. The tall indicas were crossed with semidwarf indicas and an attempt was made to isolate semidwarf counterparts of the tall parent. This task required rigorous selection within large populations of a given cross. The general lack of success in this regard may be attributable in part to the small populations used. Table 2 illustrates the populations used in some crosses.

Pre-planting selection of semidwarfs

Seedlings can be sorted in a well-fertilized, thinly sown seedbed. In an F_2 population of the cross between tall and semidwarf varieties, the short-statured plants can easily be identified. Sorting the seedlings before transplanting allows the short plants to grow competitively with semidwarfs; selection among the semidwarfs can thus be done more effectively at harvest. Semidwarf plants cannot express their potential where tall segregates cause excessive shading. Where space is a limiting factor, eliminating the tall segregates permits a considerable saving in land and more intensive concentration on the important semidwarf segregates of the population is possible. Figure 3 shows the effectiveness of selecting under different environments by sorting and non-sorting.

Table 2. Populations involved in breeding for slender grain types, kharif (monsoon season), 1969.

Cross	F_2 dwarf plants (no.)	Population (no.) advanced to			Bulks (no.) during rabi 1970	
		F_3	F_4	F_5	IET[a]	Four-row
T 90 x TN1	5700	314	120	71	1	86
T 90 x IR8	13200	419	104	70	7	139
GEB 24 x TN1	8000	400	185	87	3	394
GEB 24 x TN1/2	2300	63	12	23	7	25
IR8 x GEB 24	6400	152	21	7	-	7
Dgwg x T 141	7300	187	33	-	-	-
Dgwg/2 x T 141	5000	177	102	-	-	102
IR8 x T 812	8800	250	-	-	-	-
IR 400 x T 141	1400	27	36	-	-	-
SK 20 x IR262	5700	92	15	2	-	-
SK 20 x IR8	5500	126	37	7	-	-
SLO 16 x IR262	6400	87	4	-	-	-
IR8 x SLO 16	4800	65	3	-	-	-
IR8 x Basmati 370	7500	74	8	-	-	-
IR8 x (GEB 24 x TN1)	4200	61	15	5	-	-

[a]Initial evaluation trial.

Use of optimum agronomic practices

Improved cultural management enables the plant breeder to select effectively within and between populations. The ideal situation, not achievable in practice, is for phenotypic expression to equal genotypic potential for yield. The closer the growing crop is to the genetic potential the more reliable the selection is. In the meantime, effective selection of individuals and uniform culture permit the identification of genetically uniform progeny for early testing.

Early testing

Early testing is a technique that has long been used in crop breeding. In rice, it has proven to be an effective means of identifying a variety. In the early years of the AICRIP testing program many varieties were in the F_4 to F_6 generation. This has been extended as more characteristics were included in the selection program or as the inheritance of a character became more complex. Uniformity within semidwarf segregates of a cross was often identifiable in the F_3 stage, provided the standards mentioned above were maintained to enable phenotypic performance to approach the genetic potential. As soon as breeders have access to resistant materials, the early testing concept will include screening for resistance to insects and diseases.

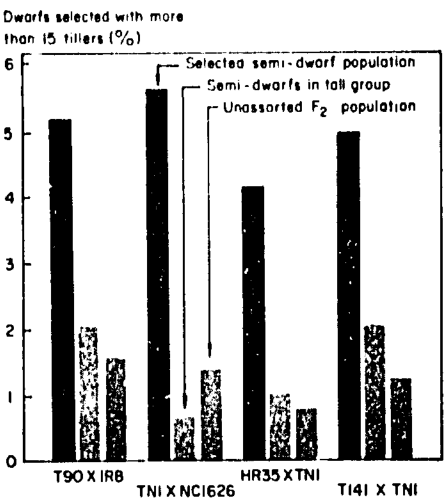
The merits of early testing for identifying better performance was demonstrated with data from the preliminary variety trials of the 1969 rabi season. The trial included 48 selections that had been in coordinated trials before and 32 selections that had been nominated to this level of testing by breeders. The 48 entries averaged 4.6 t/ha while the new entries averaged only 4.0 t/ha. More significantly, 20 out of the best 25 entries in the trial were in the second stage of testing.

VARIETY TESTING

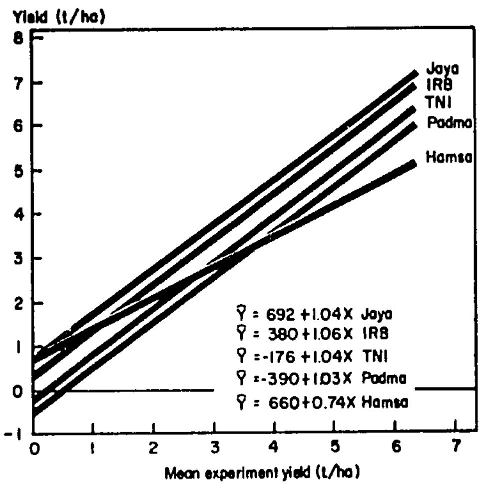
Breeding programs have created a wealth of new material. Approximately 2,000 different selections from at least 20 different centers in 11 states in the country have entered the testing program between 1966 and 1970. The selections supplied by each center appear in Table 3. Since the testing program identifies a variety, the cooperators involved are as important as those originally making the selection.

The entire community of rice researchers in over 100 rice experimental stations all over the country deserves the credit for identifying varieties as a result of evaluation in 400 comparative yield trials. Table 4 shows the varieties released under the coordinated program, the institution responsible for selection, and data on the varieties' duration, grain characteristics, and reactions to diseases and pests.

All fourteen semidwarf rices released by the Central Varietal Release Committee share some common features. All possess good plant type. They are all short-statured (81 to 100 cm), except the slightly taller Pankaj; profusely tillering, except Bala; photoperiod-insensitive, except Jagannath; and nitrogen responsive. They do not lodge under fair to good levels of nitrogen fertilization except Cauvery, Jagannath, and Pankaj. All except the photoperiod-sensitive variety, Jagannath, are suitable for sowing the year around in the plains of India, but not all are recommended for cultivation throughout the year because of restrictions in growing season, climate, water supply, etc. In the absence of other interfering factors, these varieties are suitable for all systems of rice culture: transplanting with normal or "dapog" seedlings, direct seeding, and dibbling in dry or puddled soil. All have good, stable yield under a wide range of management conditions. The regression of grain yields of five varieties grown in the uniform variety trials of 1968 indicates the general stability of their yields at various levels of production and their relative merits at different levels of trial performance (fig. 4). The realization of yields close to the potential depends on many factors, several of which are under the farmers' control. High yield



3. Influence of pre-planting selection for dwarf plants on the effectiveness of selection for desirable plants at harvest.



4. Regression of variety yields on experiment mean yields at relative locations in the Uniform Variety Trial-2, kharif 1968.

potential itself ensures good performance of these varieties under many conditions.

None of the varieties named are recommended for hilly regions or abnormally cool seasons that retard growth, prolong the growth duration, and reduce seed setting. None are resistant to rice gall midge and therefore they should not be

Table 3. Selections provided by different international, national, and state breeding programs to the coordinated testing program, 1966 kharif (wet season) to 1971 rabi (dry season).

Location	Selections (no.)				Released varieties (no.)	
	IET[a]	PVT[a]	SGVT[a]	UVT[a]	CVRC[b]	State
AICRIP[c]	470	30[d]	33[d]	13	2	-
Andhra Pradesh	453	76	25	8	-	1
CRRI	346	92	53	28	5	-
Tamil Nadu	286	29	11	10	1	1
IARI	68	4	8	5	2	-
Maharashtra	58	3	3	-	-	2
Kerala	39	1	-	2	-	4
Gujarat	22	-	3	-	-	-
Punjab	18	-	-	-	-	-
IRRI	14	132	14	29	3	-
Madhya Pradesh	12	-	-	-	-	-
Orissa	5	16	3	5	1	-
BARC	5	-	4	-	-	-
Mysore	4	3	1	-	-	2
Assam	2	-	-	-	-	-
Kashmir	-	108	-	4	-	-

[a]IET = initial evaluation trial, PVT = preliminary variety trial (or equivalent trial of varieties resistant to stem borers, gall midge, or drought), SGVT = slender grain variety trials, UVT = uniform variety trials. [b]Central variety release committee. [c]Includes some selections from crosses made initially at IRRI, Coimbatore, and Warangal. [d]Some entries in PVT and SGVT were direct nominations to the trials and were not advances from IET.

Table 4. Characteristics of varieties released by the Central Variety Release Committee and their relative yields.

				Grain yield (% of check)					Reaction[c]						
				Jaya[a]		Padma[b]			Pests[d]			Diseases[e]			
Variety	Parents	Origin	Year of release	K.69	R.70	K.69	R.70	Grain quality	SB	GM	LH	RTV	Blast	BLB	Hel.
				90 to 100 days duration											
Bala	TN1 × N 22	CRRI	1970	—	—	92	76	Coarse	S	S	S	S	S	S	MR
Cauvery	TN1 × TKM 6	AICRIP	1970	—	—	99	104	Fine	S	S	S	S	S	S	MR
				110 to 130 days duration											
Padma	T 141 × TN1	CRRI	1968	—	—	100	100	Coarse	S	S	HS	HS	S	HS	MR
Kanchi	TN1 × Co 29	Coimbatore	1970	—	—	108	101	Coarse	S	S	S	S	S	HS	MR
Ratna	TKM 6 × IR8	CRRI	1970	87	95	—	—	Fine	MR	S	S	S	MR	S	S
Krishna	GEB24 × TN1	CRRI	1970	—	—	107	102	Fine	S	S	S	S	—	S	MR
Sabarmati	TN1 × Bas 370/5	IARI	1970	72	63	—	—	Fine	S	S	S	S	MR	S	S
Jamuna	TN1 × Bas 370/5	IARI	1970	66	77	—	—	Fine	S	S	S	S	—	S	S
				130 to 150 days duration											
Jaya	TN1 × T 141	AICRIP	1968	100	100	—	—	Coarse	S	S	MR	MS	R	MS	S
IR8	Dgwg × Peta	IRRI	1966	94	95	—	—	Coarse	S	S	MR	MS	R	MS	S
IR 20	IR 262 × TKM 6	IRRI	1970	86	93	—	—	Fine	MR	S	MR	MR	R	MR	S
Vijaya	T 90 × IR8	CRRI	1970	94	92	—	—	Fine	S	S	R	MR	R	MR	S
				150 to 170 days duration											
Pankaj	Peta × T. Rotan	IRRI	1969	(113)[f]	—	—	—	Coarse	S	S	S	S	S	S	S
Jagannath	Mutant from T141	OUAT	1969	(115)[f]	—	—	—	Fine	S	S	S	S	HS	S	S

[a]Jaya – Yields: Kharif 1969, 4.7 to 4.9 t/ha; Rabi 1970, 5.5 to 6.0 t/ha. [b]Padma – Yields: Kharif 1969, 13.7 t/ha; Rabi 1970, 4.1 t/ha. [c]R = Resistant; MR = Moderately resistant; S = Susceptible; MS = Moderately susceptible; HS = Highly susceptible. [d]SB = Stem borer; GM = Gall midge; LH = Leafhoppers. [e]RTV = Rice tungro virus; BLB = Bacterial leaf blight; Hel. = Helminthosporium. [f]Compared with IR5, 3.45 t/ha.

planted in seasons and locations where the pest is a problem unless planting time is adjusted to escape the insect, or effective insect control measures are undertaken.

AGRONOMIC PRACTICES

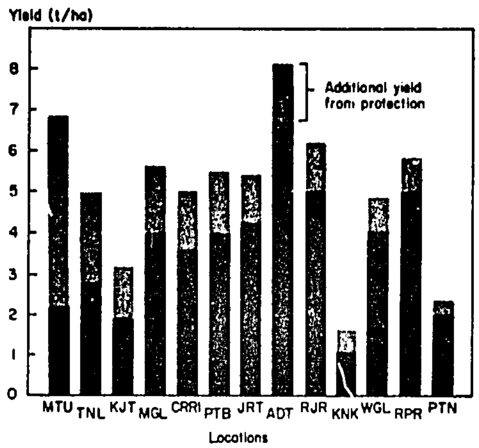
Extensive coordinated trials were initially designed to study nitrogen management. They included rates and times of nitrogen application combined with spacing and varieties as variables, and were aimed at determining the inherent yield potential of the varieties as well as their response to nitrogen. Timings of application were used to determine the most efficient way to exploit added nitrogen profitably. Split applications (Have, 1971) were a major factor in reducing losses when other factors of management were below optimum. The trials have led to a formulation of management practices that vary according to yield potential, season, and maturity period of the variety.

The expression of the potential yield of a variety is a product of the interaction between its genetic potential and the environment. The efficiency of nitrogen use as an indication of varietal response and nitrogen management is normally expressed as grain yield per kilogram of nitrogen applied. The Uniform Variety Trials seek to determine broadly the performance of varieties at two levels of nitrogen fertilization, 50 and 100 kg/ha. Data in Table 5 were taken from two different sets of trials. They illustrate how management can repress the variety's genetic potential and how the crop's response to nitrogen can be misleading as a measure of varietal efficiency. The three early varieties, Kanchi, Cauvery, and Bala, showed a grain yield increase of about 650 kg/ha with additional 50 kg N. Yet Kanchi yielded 550 kg/ha more than Bala at the higher nitrogen level. On the other hand, the three midseason varieties, Jaya, Vijaya, and IR8, demonstrate the fallacy of nitrogen response as a criterion of evaluation. Vijaya had an increased yield of 940 kg/ha with a nitrogen efficiency ratio of 18.8 kg. But there was essentially no difference in the yield between Jaya and Vijaya at 100 kg N. Vijaya showed more efficient nitrogen use through a lower base yield at 50 kg N.

The limitations management imposes on yield potential is reflected in both the absolute yields of 4 to 5 t/ha for the 100-kg nitrogen level and a general level of efficiency of about 13 to 14 kg grain/kg N.

Table 5. Response to nitrogen and other management factors of selected varieties in kharif 1969.

Variety	Grain yield (t/ha) 50 kg/ha N	100 kg/ha N	Difference	Grain: nitrogen ratio
Kanchi	3.63	4.27	0.64	12.8
Cauvery	3.36	4.01	0.65	13.0
Bala	3.07	3.72	0.65	13.0
Jaya	4.28	4.96	0.68	13.6
Vijaya	4.00	4.94	0.94	18.8
IR8	4.07	4.77	0.70	14.0



5. Effect of insect protection on grain yields of IR8 grown at 13 locations, kharif 1968.

Other types of agronomic practices are included in the trials. Because these trials are uniform and countrywide they have helped to quickly identify regions where certain agronomic practices are important and where they are not.

PLANT PROTECTION

Coordinated testing in entomology and pathology has had two objectives: pest control and identification of the varietal reaction to diseases and insects. The development of research activity in specific locations depends on the level of incidence of the disease or insect.

Coordinated tests for insect control have showed dramatic results, for example in 1968 when trials conducted at 13 locations showed an average yield increase of about 35 percent with a range of 13 to 200 percent (fig. 5). More recently this same trial has included insect-resistant material in an attempt to integrate pesticides with resistance for a rational plant protection program.

Insecticidal trials have demonstrated the merits of granular materials but more recent trials have included combinations of granules and sprays which promise more economical protection and a broader spectrum of protection.

In disease control experiments we have attempted to find effective measures against bacterial leaf blight and blast disease. It has become obvious that existing fungicides, antibiotics, etc., are ineffective in providing the desired levels of disease control. The extension of such materials for use in the farms appears remote until really effective chemicals are available.

The most valuable part of the coordinated program in both entomology and pathology has been the screening trials. These have been conducted in well-chosen locations where sufficient incidence of the disease or insect provides meaningful differential readings. One objective of the screening trials is to get reliable information on selections entering variety trials. A selection that has been tested sufficiently to qualify for release as a variety is understood to have merit in its reaction to major diseases and insects. If its reaction had been poor it would have been eliminated from the testing program. Another objective is to identify sources of resistance for use in breeding programs. A third objective

Table 6. Semidwarf lines selected for various characteristics for use in crossing programs, 1971.

Designation	Parents	Reaction[a]	Grain characteristics
	Resistance to bacterial leaf blight		
RP 291-7	IR8 x BJ 1	MR	Bold
RP 291-20	IR8 x BJ 1	MR	Bold
	IR8/3 x Zenith	MR	Bold
	IR8/3 x Wase Aikoku	MR	Bold
IR618 lines	TN1 x Malagkit Sungsung	MR	—
IR305-3-1 (RP 2)	Sigadis/2 x TN1	MR	Bold
	Resistance to blast		
CR 10-4181-1	T 90 x IR8	MR	Fine
IR577-24-1	IR8 x Sigadis	MR	Short, bold
IR578-76-1	IR8 x (Sigadis x TN1)	MR	Short, bold
IR579-97-2	IR8 x Tadukan	MR	Medium slender
IR589-87-2	IR8 x F_6(H105 x Dgwg)	MR	Medium slender
IR662-1-2	(IR8 x IR4-253-3) x (B589A4-18-1 x TN1)	MR	Medium slender
	Resistance to tungro virus		
IR20	IR 262 x TKM 6	MR	Medium slender
RP 260-822-9	IR8 x Latisail	R	
RP 260-818-4	IR8 x Latisail	R	
RP 260-98-13-1	IR8 x Latisail	R	
RP 271-43-7-3	IET 728 x Kataribhog	R	Slender
	Resistance to gall midge		
W 12708	IR8 x W 1263	R	
W 12787	IR8 x W 1263	R	
RP 6-13	IR8 x Siam 29	R	
CR 57-29	IR8 x Ptb 21	R	
CR 57-49	IR8 x Ptb 21	R	
	Resistance to leafhoppers		
Vijaya	T 90 x IR8	R	Medium slender
RP 4-11	T 90 x IR8	R	Fine
RP 4-10	T 90 x IR8	R	Fine
RP 4-12	T 90 x IR8	R	Fine
RP 4-13	T 90 x IR8	R	Fine
W 12787	IR8 x W 1263	R	Course
RP 5-12	GEB 24 x TN1	R	Fine
	Resistance to stem borer		
RP 6-508-2-3	TKM 6 x IR8	MR	
RP 6-590-14-1	TKM 6 x IR8	MR	
RP 6-590-17-1	TKM 6 x IR8	MR	
RP 6-1899-14-1-2	TKM 6 x IR8	MR	
RP 6-1899-17-9	TKM 6 x IR8	MR	
RP 6-1899-25-4	TKM 6 x IR8	MR	
CR 52-3	(TKM 6 x CB1) x IR8	MR	
W 12708	IR8 x W 1263	MR	

Continued on next page.

Table 6. *Continued.*

Designation	Parents	Reaction[a]	Grain characteristics
	Dormancy		
RP 79-2[b]	IR8 x N 22		
RP 79-3[b]	IR8 x N 22		
RP 79-4[b]	IR8 x N 22		
RP 79-5[b]	IR8 x N 22		
RP 79-6[b]	IR8 x N 22		

[a]To characteristic for which selected; R = resistant, MR = moderately resistant. [b]Highly dormant and early maturing.

is to identify the resistant progeny of crosses made to incorporate sources of resistance into agronomically desirable types.

LONG-RANGE OBJECTIVES

The choice of breeding methods, the identification of varieties and agronomic practices, and the rationalization of plant protection measures are all of immediate value and can be applied at the farm level through extension activity to increase production. To stabilize increases in yields on farmers' fields, breeding material must be produced continuously to meet the needs caused by changes in rice culture. These needs are largely related to insect and disease problems which often reach epidemic proportions in many parts of the country.

The coordinated research program is geared to provide breeding material ahead of shifts in insect population or changes in a disease organism or shifts in kinds of diseases or insects. Breeding for host-plant resistance to diseases and insects has become an important aspect of the breeding at the coordinating center, commensurate with the importance of these factors in rice production. As a result of these activities, research stations throughout the country were provided with breeding lines with resistance to one or more of the diseases and insects. These semidwarf selections (Table 6) are only donor sources of resistance that can be used in crosses with the local varieties. In addition, these selections carry the improved plant type and some selections themselves could be of value in some areas.

The use of the new photoperiod-insensitive semidwarf varieties in areas or seasons in which previously only photoperiod-sensitive varieties had been grown has offered new opportunities in rice production or multiple cropping. Occasionally the new varieties have not done well in some seasons because of weather damage or disease susceptibility. Other reasons have been advanced for their poor performance, but the rapid spread of the new varieties in seasons where these problems were minimized indicates that opportunities for increased production are the primary considerations that farmers have regarding the semidwarf varieties presently being grown on an extensive scale.

Two new approaches are being evaluated. One is to develop photoperiod-sensitive semidwarf varieties which would carry the advantages of dwarf type but which would fit the present pattern of rice culture. Some of these new selections are being evaluated in the monsoon season of 1971. The technique of identifying these selections involves three sowings in the dry, short-day season. Sowings made by December 15 or earlier at 17°N received the proper day length to induce flowering in the photoperiod-sensitive selections. Two sowings made later at 2-week intervals caused the mother tiller to flower in the photoperiod-sensitive selections when sown 2 weeks later and not to flower when sown 4 weeks later. This was done with 100 selections from three crosses identified as late or possibly photoperiod-sensitive in the previous monsoon season, and the uniform, truly photosensitive types were identified.

Since photoperiod-insensitive selections offer much greater cropping flexibility in areas that have traditionally grown photoperiod-sensitive varieties, strains that overcome the disadvantages of the present photoperiod-insensitive types must be developed. Resistance to weather damage is a main reason for adapting the dwarf, photoperiod-insensitive varieties to these conditions. This was achieved by crossing IR8 with an early variety, N 22, which carries grain dormancy. Subsequent germination tests in F_2 selections from the cross were classified on the basis of dormancy for 0, 1, 2, 3, and 4 weeks after harvest. These five classes were germinated for 4 consecutive weeks. Of 650 progeny, 188 had less than 30 percent germination at the fourth week while all others had 50 percent or higher. In succeeding generations over 600 progeny were identified that had a dormancy of 4 weeks or as long as that of the dormant parent. These selections have a range of maturity between that of the N 22 parent and that of the IR8 parent and many carry the plant type of IR8.

FUTURE PROGRAM

The features of a coordinated program have been linked with an impact program that, through accelerated effort, could create or adapt the necessary technology, such as new varieties, improved agronomy, and better plant protection, and that would have an early and visible effect on rice production.

To achieve its objectives, the impact program must effectively use the virtues of coordination. Can the same principles of coordination be applied to a sustained program of research directed toward a crop improvement program? The accomplishments during the impact period would show whether the program should continue to operate along the same pattern.

An impact program itself could become a sustained program if the level of research activity it has adopted will produce results of value to the farmer, and new areas of activity are made an adjunct of the program, e.g., surveillance, seed multiplication, etc.

Considering the future rice production targets and problems, there is no question that the need will continue for a program that will enable researchers to foresee future problems and have answers ready before these problems begin to seriously threaten national production. The need for accelerated activity cannot be avoided but that acceleration must be more efficient in the future.

The coordination of research and testing will involve additional improvements in agronomy to increase the reliability of results at various locations. The individual center is in a coordinated program to serve a particular set of conditions. Unless the research program at a station serves the set of conditions existing among farmers that station is failing to discharge its duties. Poor conduct of trials is a greater loss to the relative areas than it is to an overall program of evaluation.

Screening trials in the past have been aimed largely at characterizing the selections entering the yield evaluation program and at identifying sources of resistance. With the introduction of sources of resistance into the breeding programs (Table 6), screening would become the first aspect of coordinated testing. This would provide comparable data from more than one location on reactions to different diseases and insects. This procedure would eliminate the need to test material for yield until *after* it has been evaluated for resistance to pests and diseases. Breeders would nominate new progenies for coordinated screening after an initial screening has been done by a pathologist or entomologist at the breeding center.

The released varieties illustrate the need for this type of evaluation. The introduction of Taichung Native 1 was deplored because the variety was quite susceptible to bacterial leaf blight. Since its release, semidwarf selections in the national and state programs that are equally or more susceptible to disease have been released not because disease no longer was a problem but partly because the selections were not evaluated thoroughly or were evaluated too late in the testing program. The order of testing procedures needs to be reversed so that selections that carry such severe susceptibility never reach the stage of testing for agronomic value.

Surveillance programs now being developed in India will play an important role in coordinated programs in the future. Surveillance itself will be a speedy, concentrated effort patterned after the coordinated approach to other problems. These programs will necessarily be a primary responsibility of other agencies but their relationship to the coordinated program will provide feedback information on the farm-level performance of new varieties.

District-level testing, a part of the coordinated program already under way, will undoubtedly expand as the merits of these trials become known to extension workers and farmers. Here again, although these trials may not be the primary responsibility of the existing coordinated program they would be closely related to it so that new selections can move rapidly into such testing programs and become more quickly familar to the extension workers and farmers.

Seed multiplication programs must be tied more closely to coordinated programs. With approximately 85 percent of the rice area still to be covered by new varieties, seed multiplication programs must be able to move rapidly.

The coordination process has been quick at creating new information and new varieties, but communication of this information has been deficient. Future activity then will require a closer liaison with the media to provide farmers with the up-to-date information on rice production.

These several activities—communications, surveillance, seed multiplication, and district level testing—are not exclusively an integral part of the coordinated program now. In the future these activities should coordinate closely with the present program so that the final product is a closely knit coordinated effort that can deal effectively with rice improvement in India.

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Discussion: Rice improvement in India— the coordinated approach

S. K. SINHA: How early do the initial evaluation trials begin?

W. H. Freeman: F_6 or F_7 testing at six to eight sites.

B. B. SHAHI: Did you find much evidence on variety x nitrogen interaction?

S. V. S. Shastry: The management of nitrogen fertilization interacts with varieties much more than nitrogen itself. Locations with high mean yields for the experiments generally do not show this interaction.

S. K. SINHA: How do you relate regional adaptability to levels of grain yield?

S. V. S. Shastry: Varieties with high yield potentials are widely adaptable. It is the fair yielding varieties that do relatively better at specific locations.

Progress of rice breeding in Burma

Hla Myo Than

Until 1968, breeding work in Burma was coordinated by the Department of Agriculture and conducted at the Agricultural Research Institute, Gyogon, and at six central experiment stations. Recently, the work has been centralized under the Agricultural Research Institute. Early rice improvement involved making selections fron indigenous strains to improve grain quality and responsiveness to low rates of fertilizer. When IRRI varieties were introduced into Burma, IR5 became more popular than IR8 because the tallness and longer growth duration of IR5 fit Burmese conditions better. Since 1967, large numbers of nitrogen-responsive semidwarf lines have been introduced into Burma and tested and used in crosses with indigenous varieties that have superior grain type. Systematic screening for resistance to diseases and insects began in 1970.

Until 1968, rice breeding in Burma was carried out at the Agricultural Research Institute, Gyogon, and at six central agricultural experiment stations. Each station had its own breeding program but the work was coordinated by the Department of Agriculture. More than 70 improved varieties were evolved, mainly through selections from existing indigenous strains. Some of these varieties had excellent rice quality and were exported. Some were also highly responsive to low rates of added nitrogen.

Burma actively participated in the japonica-indica hybridization and selection program of the International Rice Commission in attempts to evolve new rice varieties with high grain quality and good response to high nitrogen levels. Outstanding rice varieties from Burma were sent to the Central Rice Research Institute, Cuttack, India, for crossing with japonica types. F_1 plants were vigorous but they showed high sterility. F_2 seed material was sent back to Burma and grown under high fertility levels. A moderately high percentage of F_2 plants were fertile and completely fertile plants were easily obtained in the later generations. Selections were made for the characters governed by the major genes during the early generations and selections for high yield were carried out from the F_5 or F_6 generations onwards. Of hundreds of lines from Cuttack crosses and subsequent crosses made in Burma, only a few possessed high grain quality, and their yields were no higher than those of the local parents. In spite of further selections, high responsiveness to added fertilizer was not achieved until 1961.

Hla Myo Than. Directorate of Agriculture, Rangoon.

A program involving the introduction and testing of rice varieties from abroad begun decades ago has been intensified recently. Well-known commercial varieties belonging to either the indica or the japonica type from many foreign countries were tested for their adaptability in Burma. No japonica rice varieties were adaptable to Burmese conditions. Most indica varieties from other tropical countries, though adaptable to Burmese conditions, were not appreciably better in grain quality and yielding capacity than the selected local varieties. Nor did any indica varieties introduced from abroad show high response to added nitrogen. Until 1965, the achievements of our rice breeding program were mainly the improvement in grain quality and response to low rates of fertilizer.

In 1966, IR8, developed by the International Rice Research Institute, was introduced into Burma. This variety was grown under a wide range of soil and climatic conditions. Farmers appreciated its plant type, its high responsiveness to fertilizer, and its photoperiod-insensitivity. But its early maturity and short plant stature were not suitable for most of the country's rice-growing areas, especially the low-lying delta and coastal regions where the high annual rainfall, 40 to 75 cm, occurs mostly from June to November.

IR5, which was introduced into Burma in 1968, was more popular than IR8 because of its longer growth duration and taller plant stature. C4-63, from the Philippines, also gained popularity among the farmers in some parts of the country for its superior grain and eating quality. IR20, IR22, IR24, C4-113, and C4-63(G) are being tested extensively in Burma.

The Agricultural Research Institute's experiences with IR8 and other introduced rice varieties led it to concentrate on obtaining rice varieties with a plant height of 120 to 140 cm and with a growth duration of 140 to 150 days in addition to efficient plant type, high fertilizer responsiveness, and superior grain quality. With these new breeding objectives, some organizational changes and new working procedures were adopted recently. All rice breeding programs are now centralized under the Agricultural Research Institute, Gyogon, which plans and distributes the work to make the best use of the facilities at the institute and the experiment stations. The Agricultural Research Institute is responsible for introducing exotic varieties and undertaking the hybridization program. With irrigation facilities available at Hmawbi Experiment Station during the dry months, breeders are growing two rice crops a year, thereby expediting the rice breeding and selection program.

More than 1,000 hybrid lines have been introduced from IRRI since 1967. These were tested at various localities and some were quite promising. In the 1970 wet season, Burma received 55 strains for the international yield trial. These were tested at Gyogon and Mandalay. Forty-five strains, notably those of IRRI hybrids, performed well and were included in the 1971 wet season trials. The more promising strains from this lot will be tested in the coming years under a wide range of conditions. Hybrid strains from some 20 crosses from IRRI almost fulfilled the breeding objectives of Burma.

The present hybridization program emphasizes the crossing of local varieties with introduced ones to incorporate high fertilizer responsiveness, improved plant type, and suitably short maturity into our indigenous commercial varieties that have superior grain quality. All the hybridization work, selection of early generations up to the F_3 or F_4 generation, together with screening for resistance to diseases and insect pests, were carried out at the Agricultural Research Institute. The F_4 or F_5 seeds were sent to various agricultural experiment stations for selection of later generations and testing in different regions. The parental strains of exotic origin used in our hybridization program were mostly from foreign varieties and hybrids.

Screening for resistance to diseases and insect pests was only started systematically in 1970 with the return to Burma of a trainee in this field from IRRI. Screening for resistance to rice blast and bacterial leaf blight has begun at the Agricultural Research Institute following IRRI methods and procedures. About 350 lines have been included in the screening for resistance to blast and bacterial leaf blight. Preparations also are in progress for screening for resistance to green leafhoppers and brown planthoppers. Surveys during the last rice growing season revealed some yellowing symptoms which may involve viruses or other causes. Facilities for rice quality testing now available at the Agricultural Research Institute enable it to assist rice breeders in selecting for grain quality. In addition, some experiments on the quality differences of rice grown under different soil and climatic conditions are being started.

Burma has many areas with diverse soil and climatic conditions. For this reason rice breeding has many different requirements. For instance, we need high yielding varieties that are early maturing and resistant to cold for the highlands as well as varieties for areas where rice can be sown only in September or October because of very deep water during the normal growing season.

Progress of rice breeding in Ceylon since 1960

Hector Weeraratne

The undesirable plant type of the traditional varieties has been the main barrier to increased grain yields of rice in Ceylon. Since 1960, three main breeding objectives high nitrogen responsiveness, resistance to lodging, and resistance to blast have been vigorously pursued. Breeding for short stature was attempted as a means of achieving the first two objectives. H-4 continues to dominate the medium-duration class, but severe lodging at high levels of added nitrogen has prevented it from expressing its full yield potential. IR8 was released as a quick remedy and in spite of its convincing superiority in yield trials, it failed to gain much popularity. Dwarfing of H-4 was attempted and the result was an H-4 dwarf with a yield potential comparable to that of IR8. Five new varieties were recently released to replace the traditional unproductive plant types in three major maturity classes.

INTRODUCTION

Heavy fertilizer applications were considered a quick solution to the low yields of rice in Ceylon before 1960. Attempts made to increase yields with high levels of fertilizer were unsuccessful because of poor yield response to added nitrogen, severe lodging, tallness and leafiness of plants, and susceptibility to blast.

Introductions were tested as a possible remedy to the problem. The Indonesian introduction Tjereh Mas gained popularity after its release but with high levels of nitrogen it succumbed to blast. H-4 resulted from initial attempts at hybridization among traditional varieties (Fernando, 1961), and it continues to dominate the medium-duration class of varieties that occupy 70 percent of the entire rice area. H-4 was also mainly responsible for raising the national average yield from 1.7 to 2.7 t/ha. Its tendency to lodge at high levels of nitrogen turned out to be a major drawback, however.

BREEDING OBJECTIVES

The major breeding objectives were increased nitrogen responsiveness and resistance to lodging and to blast. The relationship between nitrogen responsiveness and the morphological features of the plant clearly suggested that the most important varietal improvement objective in the tropics was the modification of the undesirable plant type of the traditional varieties. Breeding for short stature, a trait readily identifiable in early segregating generations, was

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undoubtedly a reliable step toward achieving nitrogen responsiveness and lodging resistance.

Even though medium maturity (120 to 130 days duration) and high yield are associated (International Rice Research Institute, [1964]), specific climatic conditions and restricted irrigation facilities preclude the cultivation of a given maturity group. Doubtless, it may be desirable to eliminate photoperiod sensitivity, but such sensitivity itself may have its own advantages under some environmental conditions. The following maturity groups are needed to suit the varying climatic conditions of Ceylon: $5\frac{1}{2}$ to 6 months duration (photoperiod-sensitive types), 38,000 hectares; 4 to $4\frac{1}{2}$ months duration, 509,000 hectares; $3\frac{1}{2}$ months duration, 65,000 hectares; 3 months duration, 75,000 hectares.

PARENTAL SOURCES FOR IMPROVED PLANT TYPE

IR8 proved to be a good combiner; it was one of the parents of two recently released improved varieties. Engkatek was exploited for intermediate height. A natural mutant isolated from a local strain, K8, was a good source of bacterial leaf blight resistance in addition to having profuse tillering. IR262-43-8 was also a promising parent. Recently, a few other IRRI lines, IR127-80-1, IR665-7-2, and IR577-24-1, have been used as parents. IR127-80-1 is one of the few IRRI lines that have a desirable culm length, 75 to 80 cm, under our climatic conditions.

PERFORMANCE OF IR8

IR8 outyielded H-4 in all areas of the island. It was released for wide-scale cultivation, but its susceptibility to bacterial leaf blight prevented it from becoming popular. I believe, however, that the main reason for the unpopularity of IR8 was the failure of farmers to use proper management practices for IR8, since in coordinated rice varietal trials, bacterial leaf blight did not depress yields as much as it did in farmers' fields.

IR8 is too short. Its culm length rarely reaches 60 cm under local conditions. Ceylon's ill-drained soils may contribute to restricting the height of IR8, thereby preventing the full expression of the variety's yield potential. Under such conditions the yield increase from extra inputs is unlikely to be sufficiently rewarding.

For these reasons, dwarfing of H-4 was considered a desirable approach, and irradiation, a quick solution. M.I.273, an induced H-4 mutant, did not exhibit any grain deformity or excessive sterility. Yield tests reveal that the mutant was far superior to H-4. The mere dwarfing of the variety resulted in spectacular yield increases. In all the agro-climatic zones of the island, the yield potential of the mutant was almost the same as that of IR8 (Table 1). Since the mutant has most of the desirable traits of H-4, the lodging resistance that resulted from dwarfing can be considered the major attribute of the mutant's vastly enhanced yield potential.

Table 1. Grain yield of M.I. 273 (induced H-4 mutant), H-4, and IR8.

Variety	Yield (t/ha)		
	Overall	Dry-zone	Wet-zone
H-4	3.59	3.67	3.51
M.I. 273	5.37	6.20	4.49
IR8	5.47	6.30	4.64

NEW VARIETIES

Five varieties were released in 1971 to replace the traditional types under cultivation in three major maturity classes. The new varieties satisfy almost all the major breeding objectives.

Bg 11-11, with an improved plant type of intermediate height, was recommended to replace H-4. The variety was rigorously tested under the best possible management in coordinated varietal trials at eight locations. Field trials were conducted with Bg 11-11 at varying management levels at 450 test sites throughout the island. In the coordinated trials, Bg 11-11 outyielded IR8 by a narrow margin when transplanted, but it yielded less than IR8 in broadcast seedings. Nevertheless, in field trials under moderate management levels (80 kg/ha N), Bg 11-11 had a higher yield potential. Thus until the farmer adopts vastly improved management practices, the intermediate height of Bg 11-11 appears better suited to the prevailing conditions than semidwarf plant type.

Bg 11-11 also disproves the popular conviction among rice breeders that varieties with small grains are poor yielders. The 1,000-grain weight of Bg 11-11 is about 18 g, which is two-thirds that of IR8, yet it yields as well as IR8 (Table 2).

Table 2. Grain yields of 10 varieties or lines.

Variety or line	Yield (t/ha)		
	Transplanted	Broadcast	
	Yala 1969	Maha 1969/70	Yala 1970
Bg 11-11	6.30	4.18	4.39
Bg 34-6	–	4.88	4.85
Bg 34-8		3.80	5.32
Bg 34-11	–	3.79	4.98
Ld 66	5.47	4.45	—
IR8	6.08	4.78	5.35
IR262-43-8	—	4.66	5.15
H-4	4.80	3.18	2.68
H-7	—	2.72	2.92
Patchaiperumal 2462/11	—	1.77	2.94

Ld 66, an improved plant-type line was recommended for problem soils of the low-country wet zone, mainly because of its resistance to bronzing. H-7 dominated the $3\frac{1}{2}$ months maturity class for over 7 years. Then IR262-43-8 was released to replace H-7. However, IR262-43-8 seldom is more than 46 cm in culm length, which is a drawback. Bg-34-6, recently recommended as a replacement for H-7, has a yield potential almost comparable to that of IR262-43-8 and a culm length of approximately 70 cm (Table 2).

Perhaps the greatest improvement has been achieved in the 90-day-maturity class. Patchaiperumal has been the standard variety of this duration for over 30 years. The new varieties, Bg 34-8 and Bg 34-11, were recently released to replace Patchaiperumal. Bg 34-8 has demonstrated a maximum yield potential of 7.25 t/ha. This represents a daily yield recovery of 81 kg/ha in the field compared with IR8's 71 kg/ha.

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Discussion: Progress of rice breeding in Ceylon since 1960

A. O. ABIFARIN: What are the conditions of your "ill-drained" soils that caused reduction of plant height?

H. Weeraratne: Dr. Ponnamperuma should comment.

F. N. PONNAMPERUMA: Strong acidity; deficiency of phosphorus, potassium, silica and bases; and perhaps iron toxicity.

P. B. ESCURO: What plant characteristics do you think contribute to the high yield of Bg 34-8, a 90-day variety?

H. Weeraratne: Non-lodging; high nitrogen response; heavy panicles; and moderately heavy tillering.

Breeding rice varieties for Indonesia

Z. Harahap, H. Siregar, B. H. Siwi

Indonesia began its varietal improvement program in the early 1900's to develop varieties adapted to a wide range of growing conditions. It was realized later, however, that it was not possible to develop a variety suitable for all environmental conditions in Indonesia and that varieties with good cooking quality were more important. In the 1960's breeding and selection techniques were modified to emphasize good grain quality, high yield, short straw, and disease resistance. Among the recently introduced varieties, IR5 is the most widely grown. Pelita I/1 and Pelita I/2, two new varieties from a cross between IR5 and Syntha were released recently. These two varieties have better cooking and milling qualities than IR5 and IR8. Advanced progenies of crosses between IRRI selections and Indonesian varieties are being tested for yield, disease, and insect resistance, early maturity, tolerance to cool temperature and adverse growing conditions, and cooking quality. Local germ plasm is being collected for future breeding work.

START OF THE RICE BREEDING PROGRAM

Rice in Indonesia is grown up to 1,800 meters above sea level during both the rainy and the dry seasons. It is grown by many methods. From 1900 to the mid-1960's breeders strived to develop rice varieties that were adapted to a wide range of Indonesian growing conditions.

Over 1,800 local varieties have been listed in the accession records. These varieties belong to two major types: indica, known in Indonesia as *tjere*; and sub-japonica, known in Indonesia as *bulu*. The differences between these types have been described by Wagenaar, Schouwenburg, and Siregar (1952).

Rice selection work started in Indonesia about 1900 at the country's only agricultural research station. The early work was aimed chiefly at screening local material by mass selection and purifying strains of local, well-adapted varieties. But the results in this program were not consistent with those in farmers' fields because of the great variability in soil type, climate, and cultural practices. Six regional stations were established between 1926 and 1945 to improve the evaluation of varieties.

The screening of local material and purifying of adapted varieties was not highly successful so many indica types were introduced from other countries. These introductions were a valuable gene-reservoir for the hybridization program

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Table 1. Improved varieties released from 1940 to 1965 and their parentage.

Varieties, year released	Parents
Mas (1940), Intan (1940), Tjahaja (1941), Fadjar (1941), Pelopor (1941), Bengawan (1941), Peta, (1941), Salak (1941)	Tjina x Latisail
Sigadis (1954)	Bluebonnet x Benong
Remadja (1954), Djelita (1955)	(Baiang x Tjina) x (Tjina x Latisail)
Dara (1960)	(Bengawan/3 x Sigadis)
Syntha (1963), Dewi Tara (1964), Arimbi (1965), Bathara (1965)	(Bengawan/4 x Sigadis)

that developed later, but none of them were released as varieties because they were photoperiod sensitive or lacked desirable agronomic features.

Rice hybridization started in Indonesia about 1920. Table 1 shows the varieties from the hybridization program that were released between 1940 and 1965.

PRESENT BREEDING PROGRAM

Introduced varieties

Before 1965, improved varieties in Indonesia were developed for cultivation on soils with moderate to low levels of fertility. These varieties were generally tall and leafy and they lodged under high nitrogen levels. The IRRI varieties and selections introduced into Indonesia in 1966 offered excellent potential for improving nitrogen responsiveness and yields.

IR8 and IR5 were among the early selections. At several locations they yielded more than 5 t/ha compared with less than 4 t/ha by local improved varieties. These two IRRI varieties were released to farmers and given Indonesian names, Peta Baru 8 and Peta Baru 5. At present about 1 million hectares are planted to high yielding varieties.

IR8 has, by Indonesian standards, poor cooking quality. In addition it is susceptible to bacterial blight. So it has never been widely accepted. IR5 however, has spread rapidly because it is more resistant to bacterial blight, has better grain quality, and is taller which makes it more suitable for traditional harvesting practices.

Indonesian farmers' acceptance of a new variety is more strongly influenced by its cooking and grain quality than by yield. For example, C4-63 introduced from the Philippines in 1968, rapidly became popular in West Java because of its cooking and grain quality although its yield is lower than that of IR5 and it shatters easily when mature. Two lines have been selected from this variety,

Table 2. Grain yield and other characteristics of seven varieties at different locations.

Variety	Yield[a] (t/ha) Wet season 1968/69 (12)	Dry season 1969 (17)	Wet season 1969/70 (35)	Dry season 1970 (18)	Wet season 1970/71 (13)	Avg	Maturity (days)	Plant ht (cm)	Eating quality[b]	Disease reaction[c] Bacterial leaf blight	Sheath blight
IR5	4.73	5.56	5.14	6.81	6.53	5.75	135	113	2.1	MR	S
IR8	4.39	5.35	4.96	–	–	4.90	129	92	1.8	HS	S
C4-63 (green)	–	5.53	4.81	6.31	5.54	5.55	125	100	4.1	MR	S
C4-63 (purple)	–	5.25	4.66	6.10	5.36	5.34	124	101	4.2	MR	S
IR20	–	5.19	4.77	6.33	6.04	5.58	126	98	2.4	R	MS
IR22	–	–	–	5.28	4.92	5.10	120	89	2.2	R	MS
Dewi Ratih	4.17	4.85	4.70	6.63	6.66	5.40	141	134	3.7	MR	MS

[a]The figures in parentheses denote number of locations. [b]1 = very poor, 2 = poor, 3 = medium, 4 = good, 5 = very good. [c]S = susceptible, R = resistant, MR = moderately resistant, HS = highly susceptible.

one with green basal leaf sheath and the other with purple leaf sheath. The former has outyielded the latter consistently.

Since 1968 several introduced varieties and lines have been tested at the substations of the Central Research Institute for Agriculture (CRIA) and on fields at the main rice producing centers. The plots were fertilized with 120 kg/ha nitrogen and with 60 kg/ha P_2O_5. Results of these tests from five successive seasons at 95 locations are shown in Table 2.

Hybridization

In 1962, the progeny of a backcross between Bengawan and Sigadis (with Bengawan as the recurrent parent) was crossed with Randa Tjupak by the pedigree breeding method. Dewi Ratih, the first Indonesian short-strawed variety, came from this cross. It was released in 1969.

Some IRRI breeding lines have proved to be excellent sources of germ plasm for the breeding program. IR5, IR8, IR305 selections, IR400 selections, and IR20 are some of the parents used in recent crosses. Also chosen as parents for their resistance to bacterial blight, bacterial leaf streak, and blast, their good grain and cooking quality, and their nonshattering grains are the Indonesian varieties, Bengawan, Syntha, Sukanandi, Seratus Malam, Gendjah Lampung, and Gendjah Beton. Table 3 lists some of the crosses being tested in the advanced generations and the characteristics for selection.

Current methods

Seeds from the F_1 generation are grown at the Central Station at Bogor, and F_2 populations are grown at the five main substations in West and East Java as well as at Bogor. At Bogor the pedigree method of selection is employed. Short culms, stiff straw, erect leaf habit, and early maturity are characteristics sought for in

Table 3. Promising crosses in advanced generation and their characteristics.

Cross no.	Parentage	Desirable characteristics[a]
440	IR5 x Syntha	1,2,3,5,6
446	IR8 x Syntha	1,2,3,5,6
529	Seratus Malam x IR5	1,2,3,5,6
531	Syntha x (IR5 x Syntha)	1,2,3,5,6
B58	Short Sigadis x (IR5 x Syntha)	1,2,3,5,6
B60	Short Sigadis x (TN1 x Bengawan)	1,2,3,5,6
B149	Sukanandi x IR400	1,2,3,4,5,6
B173	446b/33 x Gendjah Lampung	1,2,3,5,6,9
B295	B58b/Tk/95 x Gendjah Lampung	1,2,3,5,6,9
B412	IR127 x B63b/Tk/16	1,2,3,5,6
B450	C4-63 x 531b/Tk/51	1,2,3,5,6
B459	C4-63 x (IR127 x B63b/Tk/16)	1,2,3,5,6
B508	IR22 x 7977/1 (No. 531)	1,2,3,5,6
B531	IR1108 x 7947/20 (No. 531)	1,2,3,5,6,8
B540	440b/52/8 x IR474-38-3	1,2,3,5,6,8
B541	440b/52/1 x IR1108-2	1,2,3,5,6,8
B542	440b/52/1 x IR20/4	1,2,3,5,6,10

[a]1, high yielding; 2, of good eating quality; 3, of good plant type; 4, non-shattering; 5, early maturing; 6 resistant to bacterial leaf blight; 7, resistant to sheath blight; 8, resistant to leaf streak; 9, resistant to blast; 10, tolerant to stem borers.

the early generations, while grain quality is sought for in later generations. Selections are screened for resistance to major diseases and insects throughout the breeding program. At the substations the modified bulk method of selection is used. Tall and late-maturing plants are removed and seeds from one or two panicles of the remaining plants are bulked and saved for growing 5,000 to 10,000 plants in each generation. After several generations individual plant selections are made.

Uniform promising selections are screened for cooking quality in the F_6 and F_7 generations. Cooking quality is determined by two methods, amylose and organoleptic analyses. The organoleptic test is carried out by a 20-member panel. Samples of 500 g of milled rice are cooked and then cooled for 1 or 2 hours before being tested by the panel. Each sample is rated by each panel member for stickiness of cold cooked rice and for flavor. The results are used in determining the acceptability of a promising selection. In the future, amylose determination will be made on early generation lines.

After the F_7 generation, promising lines are tested for yield at 20 CRIA substations. Eight or ten of the best lines are then entered in advanced yield tests at 50 to 100 locations in the main rice producing areas. One or two outstanding lines are selected for inclusion in demonstration plots on farmers' fields. These trials are conducted by selected farmers and are closely supervised by the local extension agents.

Results

A number of promising selections derived from the crosses IR5 x Syntha, IR8 x Syntha, and IR5 x Syntha/2 were entered in the advanced yield trials described above. Two lines from the cross IR5 x Syntha, designated as 440b/52/1 and 440b/52/8, are similar to IR5 but have lower amylose content. These two lines were released in 1971; 440b/52/1 was given the name Pelita I/1 and 440b/52/8 was called Pelita I/2. Their reaction to bacterial blight and sheath blight is no better than that of IR5. But their cooking quality is more acceptable because of the lower amylose content (Table 4).

PROSPECTS FOR THE FUTURE

With the release of Pelita I/1 and Pelita I/2, the breeding program is being focused on developing varieties that are resistant to the major diseases and insects, and mature earlier (within 110 to 120 days).

Bacterial blight and sheath blight are the most important diseases of lowland rice in Indonesia. In preliminary yield trials, IR1317-369-2, IR661-98-2-2, IR667-98-2, and IR580E420-1-1 have shown moderate resistance to bacterial blight and bacterial leaf streak.

A disease known in Indonesia as "penjakit habang" has been reported in South Kalimantan and South Sumatra. This disease is very similar to tungro and is believed to be caused by virus. The local varieties, Benih Kuning, Pangamban, Rendah Polos, Katumping, Pirukat, Dewi Ratih, Syntha, Dara,

Table 4. Grain yield and other characteristics of 12 varieties and lines at 14 locations, wet season 1970-1971.

Variety or selection	Yield (t/ha) Range	Yield (t/ha) Average	Maturity (days)	Plant height (cm)	Eating quality[a]
IR5/84	3.33 to 9.18	6.53	135	113	2.1
C4-63gb/63	3.14 to 8.46	5.54	125	100	4.1
C4-63pb/42	2.69 to 8.57	5.36	125	101	4.2
IR20/2	3.81 to 8.25	6.04	124	98	2.4
IR22	1.86[b] to 7.08	4.92	121	89	2.2
IR661-1-139-1/3	3.03 to 6.98	5.23	129	89	4.6
Pelita I/1	3.81 to 10.87	7.06	137	126	4.0
Pelita I/2	3.75 to 10.59	7.05	138	114	4.0
446b/14/7	2.43 to 9.51	6.18	140	105	3.9
446b/34/1	3.82 to 9.11	6.39	139	110	2.2
529b/118/2	2.43 to 10.13	5.49	142	184	4.1
Dewi Ratih	4.23 to 10.30	6.66	142	134	3.7

[a]On a scale of 1 (very poor) to 5 (excellent). [b]Crop suffered bird damage.

Gembira, and the introduced varieties, IR5 and C4-63, were observed to be resistant to this disease.

Blast disease is quite serious on upland rice. Field screening tests for resistance to blast are conducted at four locations.

Varietal resistance to stem borers, gall midge, green leafhoppers and brown planthoppers occurs in other Asian countries. Efforts are being made to incorporate these types of resistance into Indonesian varieties. Some varieties introduced from India that are resistant to gall midge are now being used as parents in the hybridization program.

Other areas requiring the breeders' attention are testing of native varieties for resistance to disease and insects, improvement of the bulus, varieties tolerant to cool temperatures at high elevations (500 meters or above), and varieties adapted to problem soils.

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Discussion: Breeding rice varieties for Indonesia

B. R. JACKSON: Dewi Ratih is taller than IR5. Do you consider this an advantage from the standpoint of farmers' preference?

Z. Harahap: Yes, to some extent.

Progress of rice varietal improvement in West Malaysia

B. H. Chew, M. Sivanaser

The rice varietal improvement program in West Malaysia during the postwar period was limited to pure-line selections among the indigenous varieties. This was terminated in 1963 with the release of several strains for single cropping. The local hybridization program involving crosses between local indicas had failed to develop varieties suitable for double cropping. The Japanese in 1942 had introduced several varieties from Taiwan for double cropping. Breeding for double-cropping varieties was started in 1951 when West Malaysia participated in the International Hybridization Scheme of the International Rice Commission. Crosses were made in the Central Rice Research Institute, India, and the F_2 seeds were sent to West Malaysia for selection. This work culminated in the release of Malinja in 1964 and of Mahsuri in 1965. Cooperative work with the International Rice Research Institute, and the establishment of the Rice Research Unit under the Department of Agriculture of West Malaysia, led to the release of Ria (IR8) in 1966 and of Bahagia (sister strain of IR5) in 1968. Since then many local hybrids with good plant type have shown highly promising performance in the field. Varieties like C4-63, IR20, and IR22 are also being tested in major rice areas of the country.

INTRODUCTION

From World War II until 1960 several rice varieties were developed and released in West Malaysia. Several independent selection programs designed to improve popular indigenous varieties by pure-line selection and synthesis of new varieties through hybridization were started (Brown, 1955; Van, 1960).

From the pure-line selection programs came such varieties as Anak Naga 21, Radin Ebos 33, Seraup 50, and Siam 48. These programs were terminated in 1963. The hybrid selections from the hybridization programs involving local parents (indica x indica crosses), though possessing better plant traits and higher yield potential than their parents, were unsuitable because of poor grain characteristics and eating quality. All the varieties from both the pure-line selection and hybridization programs were photoperiod sensitive and therefore unsuitable for cultivation in the double-cropping areas of the country. A separate breeding program was needed for selection of double-cropping varieties.

Double cropping of rice began in West Malaysia around 1942 when the Japanese introduced off-season varieties, such as Ryushu, Taichu 65, and

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Pebifun from Taiwan. Only Pebifun became popular. It was used as the only off-season variety until 1964. The breeding and selection of off-season varieties was formally begun in 1951 when West Malaysia became a participant of the International Hybridization Scheme set up by the International Rice Commission in 1950. Under this program, F_2 seeds from indica x japonica crosses made at the Central Rice Research Institute (CRRI), India, were received for selection and identification of strains suitable for double-cropping areas in the country (Van, 1966).

VARIETAL IMPROVEMENT (1961-1971)

Beginning in 1960 additional personnel and new or improved equipment accelerated the breeding and selection of double-cropping varieties. Links with rice research centers in Asia, particularly the International Rice Research Institute, were established; thus began the exchange of research findings and the increase in quantity of valuable genetic materials introduced into the country. Early-generation hybrids from CRRI and IRRI proved most useful and made possible the selection of four varieties that eventually were officially released to the farmers.

Two double-cropping varieties, Padi Malinja and Padi Mahsuri, resulted from the selections made with a group of 13 crosses (F_2) received in 1956 from CRRI under the International Hybridization Program of the International Rice Commission. Malinja, a selection from the cross, Siam 29 x Pebifun, was released in 1964, while Mahsuri, a selection from the cross, Mayang Ebos 80/2 x Taichu 65, was released in 1965 (Samoto, 1965; Van, 1966). By 1966 these varieties had replaced Pebifun.

After the establishment of the Rice Research Unit of the Department of Agriculture in 1966, rice varietal improvement programs were expanded and incorporated a large number of hybrid selections and parent materials from IRRI to supplement the local hybridization programs. From 303 IRRI hybrid selections received in 1965, one selection, IR8-288-3 (Peta x Dee-geo-woo-gen), was identified and named Padi Ria, and recommended for release to farmers in 1966. Padi Ria, because of its short culms and poor grain quality, is cultivated only on a small scale in areas where there is adequate water control. By 1968, all these varieties had become susceptible to blast. Hence in 1968 a new variety, Padi Bahagia, a sister strain of IR5 (Peta x Tangkai Rotan), possessing good grain quality and better resistance to blast, was released to supplement and gradually replace the susceptible strains. A program to incorporate blast resistance into Malinja and Mahsuri was started in 1965 and concluded in 1969 with the development of a blast-resistant Mahsuri (Sigadis x Mahsuri/3).

Programs for breeding and selecting glutinous varieties were started in 1969. Concurrently as an interim measure, hybrid selections from IRRI were obtained in 1969 for local testing and selection. Of these selections two, IR789-59-3 (IR8 x Muey Nahng 62M) and IR827-24-1 (IR8 x Niaw San Pah Tawng), were selected and are now being tested in farmers' fields. A few of the selections have also been used as parents in crosses relating to the improvement of local glutinous varieties.

Table 1. Comparative agronomic, disease, and quality data on recommended varieties and promising lines at Bukit Merah Padi Experiment Station, 1970/71 main season.

Variety or selection	Maturity (days)	Plant height (cm)	Panicles (no./hill)	Grain yield (t/ha)	Reaction to blast[a]	Eating and cooking quality
Malinja	135	135	14.1	4.50	HS	Fair
Mahsuri	130	135	14.1	5.06	HS	Good
Ria	124	84	14.6	7.64	MS	Poor
Bahagia	133	119	15.7	4.90	MS	Fair
Mahsuri x Ria 1038-1-1-3-2-9-9	118	104	15.4	5.07	MR	Good
Radin Ebos x Ria 753-3-2-4-3-10	125	101	14.6	5.80	MR	Fair
Ria x (Engkatek x Sachupak) 257-3-7-6	128	110	15.9	6.16	HR	Fair
Bahagia x Ria 67009-50-7	130	93	15.4	6.78	MR	Fair

[a]HS, highly susceptible; MS, moderately susceptible; MR, moderately resistant; HR, highly resistant.

CURRENT INVESTIGATIONS AND PROGRAMS

Since the release of Padi Bahagia (IR5-278), several promising local hybrid selections from crosses such as Mahsuri x IR8 and IR8 x (Engkatek x Sachupak), secondary selections of IR8 with improved grain quality, and introduced strains such as C4-63, IR20, IR22, and IR24 are being evaluated at numerous locations in the major rice areas of the country. In addition, two Thai varieties, RD 1 and RD 3, are being evaluated in the double-cropping areas.

At present IR8, Sigadis/2 x Taichung Native 1, and local hybrid lines, such as Bahagia x Ria and Radin Ebos 33 x Ria, are widely used as parents in programs aimed at improving the plant type of local indicas that possess such desirable traits as good grain quality, wide adaptability, and tolerance to pests and diseases. Blast-resistant parents, such as Tadukan and Tetep, are being used to incorporate blast resistance into promising selections, and all breeding materials, including parents, hybrids, and introductions are systematically tested in upland uniform blast nurseries. In addition, programs to incorporate resistance to bacterial leaf blight into promising local hybrid selections are in progress. They include crosses involving resistant parents such as Zenith and TKM-6. Screening for resistance to virus diseases and leafhoppers is limited at present to identifying resistant varieties for use as parents. Entomologists and pathologists actively participate in this work.

The current breeding programs are aimed towards the selection of varieties possessing photoperiod insensitivity (maturation under 130 days); yield potential of over 5 t/ha; good plant type; culm height between 80 to 100 cm; moderate resistance or tolerance to common diseases; good grain shape, size and milling quality; and good eating quality.

Table 1 shows the characteristics of the four recommended double-cropping varieties and some promising local hybrid selections.

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Discussion: Progress of rice varietal improvement in West Malaysia

T. T. CHANG: Are the bulu varieties grown in Malaysia?

B. H. Chew: No. The bulus have poor grain quality.

B. R. JACKSON: Is glutinous rice important to Malaysia?

B. H. Chew: It is grown in small acreage particularly in the Northern States such as Kedah. It is mainly used to prepare rice cakes during certain festivals and ceremonies.

Progress in rice breeding in East Pakistan

S. M. H. Zaman, M. A. Choudhury, M. S. Ahmad

East Pakistan has four distinctly different crop seasons in a year. These seasons have extremely variable temperature, water availability, and solar radiation. Rice breeders in East Pakistan are expected to develop improved varieties that are adapted to these seasons. They also are expected to incorporate into these improved varieties resistance to diseases and insects which have a high incidence in the province. Between 1960 and 1965, the varietal improvement division in East Pakistan tried to breed high yielding varieties from indica x japonica crosses but achieved little success. None of the introductions from many countries that were tested proved to be well adapted. Since 1966, however, considerable progress has been made with the more than 7,000 selections and varieties that have been introduced and tested. Several varieties have been obtained and are now being produced commercially. Improved varieties well adapted to 5.6 of the 10 million hectares of rice grown annually are available. An intensive program of crossing local varieties and improved plant type lines is showing good progress. Several selections from advanced hybrid lines are being evaluated for varietal status in performance trials at different locations.

INTRODUCTION

There are so many varieties in East Pakistan that almost all villages have some different forms. These varieties are grouped into four distinct types, according to crop season: aus (2.5 million hectares, April to August), transplant aman (3.5 million hectares, June to December), deep water rice or broadcast aman (2.5 million hectares, April to December), and boro (800,000 hectares, November to May). The growing seasons of these four crops overlap. Boro and aus varieties are insensitive to photoperiod, others are sensitive. Rice breeders in East Pakistan not only must breed for yield and grain quality, disease and pest resistance, tolerance to low temperature, drought resistance, flood resistance, and varying photoperiod sensitivity, but also must face the additional problems of wide variations in temperature and light intensity in each growing season of the year, and the possibility of the effect of interaction between the photoperiod sensitivity and thermo-sensitivity of rice varieties.

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THE INTERIM PERIOD: 1960-1965

In the early 1960's, the main breeding objectives were to reduce the plant height, to introduce lodging resistance, and to improve the response to fertilizers. By the mid-sixties, the damaging effect of virus and bacterial diseases was recognized and breeding for disease and insect resistance, in addition to high yielding potential, was emphasized.

Indica x japonica hybridization

To incorporate the fertilizer responsiveness and the plant type of japonica varieties into local varieties, and thus break the low yield ceiling, rice breeders made many indica x japonica crosses and studied their progeny. The indica x japonica program, which included the local aus and transplant aman varieties as parents, was conducted during the aus and aman seasons, but limited improvement was achieved (Alim et al., 1962). During the same period many varieties introduced from Japan, Australia, Italy, Egypt, Spain, Iran, Taiwan, and the U.S. were tested for adaptation with little success. The breeders in East Pakistan successfully planted japonica varieties, such as Norin 1, Norin 17, Taipai 177-1, and Yabani M-7. The average yield ranged from 5 to 6 t/ha during the boro season. All these varieties, however, had low amylose content and were not acceptable for local consumption. On the other hand, Taipai 177-1 had slightly better cooking quality and was grown to some extent (Alim et al., 1962).

USE OF NEW SEMIDWARFS: 1965-1971

Rice research began to stagnate because of the serious shortage of trained personnel and working facilities in East Pakistan. Deeply concerned scientists and administrators, with the help of the International Rice Research Institute and the Ford Foundation, initiated a modest but somewhat integrated rice research scheme in 1966. This scheme was expanded and the autonomous East Pakistan Rice Research Institute (EPRRI) was established in 1970.

Short-term program

With the development of IR8 by IRRI, the concept of the improved plant type was recognized. IR8 was introduced in East Pakistan in 1966 and many farmers who planted it harvested 8 t/ha in the boro season. The short-term program emphasized the introduction of IRRI hybrid lines and selections for superior performance under local conditions. So far, more than 7,000 lines covering several generations have been introduced and screened. Three promising selections besides IR8 and IR5 have been proved high yielding and resistant to diseases and insects: IR20 (Irrisail), IR532-1-176 (Chandina), and IR272-4-1. Several other IRRI lines are showing promise and are in advanced stages of testing. They include IR442-2-50, IR442-2-58, IR442-2-71, IR442-36, IR579-48-1, IR626-1-36, IR474-25-1, IR747B2-60-1, and IR667-98-2.

The IR442 lines are moderately flood resistant and can be grown in low areas where the flood level does not exceed 90 cm. They are moderately susceptible to bacterial leaf streak at mid-stages of growth and moderately susceptible to

Table 1. Performance of Irrisail (IR20), IR5, and Latisail in aman season, 1969.

Variety	Growth duration (days)	Grain yield (t/ha)
Irrisail	134	4.67
IR5	146	4.09
Latisail	140	2.67

bacterial leaf blight at later growth stages. Because they are insensitive to photoperiod, they cannot be widely grown in East Pakistan. Hence, selected IR442 lines have been crossed with the best deep-water rices of East Pakistan to incorporate higher levels of tolerance to deep water, increased disease resistance, and some degree of photosensitivity (M. A. Chowdhury and Z. M. H. Zaman, *unpublished*). An introduction from the People's Republic of China in 1967 showed good adaptability in boro and aus seasons. It was renamed "Purbachi" and has become quite popular (S. M. H. Zaman, M. S. Ahmad, and M. A. Choudhury, *unpublished*). It is susceptible to tungro and bacterial leaf blight, but when it escapes disease infection, it yields 4 to 6 t/ha. Its growth duration varies from 140 days in boro season to 115 days in aus season.

Three of the new varieties developed from IRRI breeding materials are briefly described below.

Irrisail is the name given to IR20 in East Pakistan. Irrisail is best adapted to the aman season. It is weakly photoperiod sensitive and has satisfactory levels of resistance to tungro and bacterial leaf blight. The grains are of medium length and have good milling and cooking quality. Irrisail takes about 130 to 140 days to mature (Table 1). In 1970, about 67,000 hectares planted to it had an average production of 3.75 t/ha. In 1971, the area planted to Irrisail may reach 400,000 hectares.

IR532-1-176 has been named "Chandina" in East Pakistan. It was released as a commercial variety for boro and aus crops in 1970. It can be planted any time from mid-November to mid-June, but the sowing in mid-November to mid-December gives the best yield. Chandina takes 136 to 154 days from sowing to maturity, depending on the time of planting in boro season and 112 to 117 days in aus season (Table 2). Like IR20, it is fairly resistant to tungro and bacterial leaf blight but susceptible to leaf streak. The average yield of Chandina from different seasons at different locations is about 5.0 t/ha. Its grain quality is better than that of IR8, Purbachi, and some local varieties.

EPRRI recommended the slightly taller (102 to 114 cm) IR272-4-1 line for commercial production in boro and aus seasons in 1971. IR272-4-1 is an improvement over IR8, Purbachi, and Chandina (Table 3). It can be planted any time from mid-November to May. If sown from mid-November to mid-December, IR272-4-1 yields about 7 t/ha in about 152 days. The yield gradually decreases in subsequent plantings as the growth period decreases. Mid-April sowings yielded 6.2 t/ha in 117 days. When directly sown in rainfed aus

Table 2. Performance of IR532-1-176 (Chandina) and three varieties in boro season, 1968 and 1969 (average of three locations) and aus season, 1970 (average of two locations).

Line or variety	Growth duration (days)	Grain yield (t/ha)
	Boro	
IR532-1-176	145 to 154	5.9
IR8	161 to 172	5.5
Purbachi	144 to 158	4.2
Habiganj B. VI	145 to 153	3.3
	Aus	
IR532-1-176	108 to 115	4.3
IR8	120 to 125	3.3
Dular	101 to 107	2.6

conditions, it produced 3.2 t/ha in 102 days. IR272-4-1 is resistant to tungro and bacterial leaf blight. Grains are medium fine and have acceptable milling and cooking qualities.

Long-term program

At EPRRI, breeding materials are being developed and studied for their yield potential and disease and insect resistance. A collection of indigenous and introduced breeding materials, including IRRI lines, are being tested. Besides the short-term program, EPRRI has a long-term program with the following objectives.

1) To develop superior varieties adapted to various edaphic and agro-ecological situations. Most of the well-adapted IRRI lines have been crossed with the best local varieties. 2) To introduce genes for resistance to rice tungro virus, bacterial leaf blight, sheath blight, stem borers, leafhoppers, planthoppers, and gall midge into these new varieties. 3) To obtain photoperiod-insensitive varieties with shorter life cycle for the boro and aus seasons and photoperiod-sensitive varieties for the aman season. 4) To increase the yield potential of deep-water varieties without lowering the flood resistance of the improved local varieties. 5) To increase milling, cooking, and nutrient quality.

Table 3. Grain yield of two lines and two varieties at two locations, transplanted, aus season, 1970.

Variety or line	Yield (t/ha) Comilla	Joydebpur	Mean
IR272-4-1	6.20	3.34	4.77
IR532-1-176	—	4.84	4.84
IR8	5.76	3.65	4.70
Dular	3.89	2.78	3.34

Table 4. Yield performance of six promising selections from advanced hybrid lines of EPJI (DA-31 x IR8) at Joydebpur, East Pakistan, aus season, 1970.

EPJ number	Life cycle (days)	Yield (t/ha)	Yield per day (kg/ha)
1-6-B-9	116	5.0	43.4
1-13-B-55	121	5.0	41.3
Chandina	117	4.7	40.6
1-2-B-53	113	4.7	42.0
1-4-B-20	116	4.7	40.9
1-2-B-19	112	4.7	42.0

EPRRI HYBRIDS AND THEIR PROSPECTS

EPRRI started its hybridization program in 1966 to improve yield by using the new semidwarfs and the best local varieties. Progeny of 46 crosses are in F_4 and advanced generations and 87 crosses are in F_2 and F_3 generations. During 1970-71 (July-June), 75 new crosses were made. In almost all the crosses, an IRRI material was one of the parents for plant type and disease resistance. All the known good local germ plasm were used for either photoperiod-sensitivity or grain quality. Some progeny of earlier crosses are now being evaluated for yield and for disease and pest reaction in three or four locations.

In 1970-71, selections were made from 4,175 EPJ hybrid lines and 1,049 promising lines were screened for disease and insect resistance. All these have good plant type and appear to have a high yield potential. From the advanced hybrid lines of EPJ1 (DA-31 x IR8) six selections appear very promising (Table 4).

Both EPJ1-6-B-9 and EPJ1-2-B-19 are superior to Chandina in yield per day. But they will not be released for commercial production until they are tested thoroughly in farmers' fields through the trials conducted jointly by the Soil Fertility and Soil Testing Institute and EPRRI. EPJ1-4-B-30, EPJ2-B-24, and EPJ1-17-B-14 have shown good performance in boro seasons. They will also be tested in farmers' fields. All these EPJ selections are moderately resistant to rice tungro virus and to bacterial leaf blight disease. During the last aman season, EPJ3-63-B-5, EPJ3-72-B-14, EPJ3-72-B-20, and EPJ5-4-B-12 showed high yield potential. These lines will be tested in different regions to evaluate their real potentiality under varied agro-ecological conditions.

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High yielding rice varieties in West Pakistan

A. A. Soomro, Gordon W. McLean

High yielding semidwarf varieties, notably IR8 and Mehran 69, are planted on over 40 percent of West Pakistan's rice area. Current breeding work focuses on combining basmati grain characteristics with the high yielding ability of the semidwarf varieties.

The irrigated Indus Valley of West Pakistan has little resemblance to the rice growing areas typical of tropical monsoon Asia. This area is hot (often exceeding 45 C), arid (less than 10 cm annual precipitation) and in the temperate zone (27°N to 35°N). Yet some IRRI-developed semidwarf rices appear to be particularly well adapted here. Since the introduction of IR8 in 1968 rice production has increased by nearly 1 million tons. This increase has largely resulted from the higher yields of semidwarf varieties.

Rice farmers with only minimal inputs are now getting yields twice those they had been achieving with the traditional varieties. The total rice area of West Pakistan, 1.6 million hectares, produced 1.5 million tons of milled rice in 1967 and 2.4 million tons in 1969. In 1967 there were no semidwarf rices on farmers' fields. In 1969 over 40 percent of the total rice area was planted to IR8 and Mehran 69 (a selection from an IRRI line). In 1970 and 1971 the area planted to semidwarf, high yielding rices continued to increase but at a reduced rate.

By 1970 rice yields in West Pakistan had increased 56 percent compared with yields during 1960-64. The North West Frontier Province has had an increase of 47 percent, the Punjab 36 percent, and the Sind 83 percent for the same time period.

The North West Frontier Province has only 47,000 hectares of rice land with all but 10,000 hectares in mountain valleys. Irrigation water is nearly always from melted snow and water temperatures seldom exceed 18 C. Consequently, the tropical varieties developed at IRRI perform poorly because of low water temperatures. Recently, local workers have begun a cooperative breeding-screening program with IRRI to develop high yielding, fertilizer-responsive rices that have high amylose content, long grains, and tolerance to cold water.

The Central Punjab Province has 721,500 hectares of rice. About half is planted to basmati, a variety-group with aromatic, long grains. Basmati rices

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command a premium price in some world markets and are the preferred rices in West Pakistan. IRRI-developed, high yielding varieties introduced into the Punjab (particularly IR8) produced much higher yields than basmati rices, but the IR8 grain is not as long as that of basmati rices and the quality and head-rice yields of IR8 are so low that both the millers and the local consumers pay considerably less for IR8. As a result the area planted to IR8 reached a peak soon after it was introduced and then the area declined. The identification of Mehran 69 from IR6-156-2 (Siam 29 x Dee-geo-woo-gen), a long-grain, high yielding variety, has recently reversed the drop in area planted to high yielding varieties. Now the area planted to basmati in the Punjab is declining. A short basmati selected from the IR424 cross (Basmati 370/3 x Taichung Native 1) has been developed and is in the final stages of testing. It combines the basmati grain characteristics with shorter stature and fertilizer-responsiveness.

The Sind Province comprises the lower Indus Valley and has the most arid conditions in West Pakistan. It is in the Sind rice area of 680,000 hectares that the semidwarf varieties have been most readily accepted because of their greater yield. High temperatures and high light intensity coupled with a low incidence of diseases and insects have resulted in some of the highest rice yields on record. Yields of semidwarf rices of 10 to 11 t/ha are common at the Dokri Rice Research Station. The farmers, however, average about one-fourth to one-fifth of this yield because of low plant populations, improperly levelled fields, weed competition, and low levels of fertilization. Salinity has become a major problem in much of the rice growing area of the Sind.

The breeding and selection program in West Pakistan in the early years was confined to improving grain characteristics. Particularly in the Punjab, there was increased emphasis on producing long, slender, and aromatic basmati type rices. A serious outbreak of blast in 1958 prompted some breeding for blast resistance in the Punjab. In the Sind province breeders attempted to produce earlier maturing varieties that would fit into peak periods of canal flow. The Sind area is developing a variety of basmati that will maintain the distinctive aroma under the extremely high temperatures found in this province. The narrow genetic base of the breeding materials used resulted in only relatively minor increases in yields in the breeding programs before 1967. Other problems of recent concern to the rice breeders are stem borers, kernel smut, bacterial leaf blight (in the Swat Valley), and zinc deficiency.

With the introduction of 303 varieties and selections from IRRI in 1966, there was a major change in the concept of rice breeding. The semidwarf factor stimulated interest in increasing yields. The earlier success of the high yielding, semidwarf wheats in West Pakistan paved the way for the rapid acceptance of semidwarf rices. The Government of Pakistan was actively promoting a program to make Pakistan self-sufficient in food grains concurrent with the release of IR8.

Although the grain type of IR8 was not preferred by consumers in West Pakistan, it was acceptable in East Pakistan. The increase in rice production resulted in major policy changes from compulsory procurement of milled rice in 1966 to voluntary procurement in 1970. West Pakistan presently produces 600,000 to 800,000 tons of milled rice more than its domestic needs.

Once self-sufficiency was achieved the emphasis in breeding shifted from yield to improved grain types, earlier maturity, and resistance to diseases and insects. With the potential of increasing foreign exchange earnings with rice exports, there is more emphasis on producing a high quality rice suitable for export. The problem of improving rice quality reaches beyond the breeding program and into harvesting and processing.

Recent yield increases have changed rice growing from a subsistence operation to a cash crop enterprise. The more profitable production from high yielding semidwarf varieties bred at IRRI have been responsible for this shift. The West Pakistan farmer is able to produce rice cheaper than most rice exporting countries and Pakistan should exploit this production advantage. Rice researchers in West Pakistan have launched a hybridization program between locally accepted quality varieties and the more recent semidwarf varieties from IRRI. This program may provide the next quantum increase in yields.

Discussion: High yielding rice varieties in West Pakistan

R. F. CHANDLER: How does West Pakistan handle the surplus rice of IR8?

G. McLean: They parboil it and ship the rice as parboiled milled rice to East Pakistan.

G. SATARI: How hot does it get in the Sind district?

G. McLean: 50 C in the shade.

Rice varietal improvement in the Philippines

Esteban C. Cada, Pedro B. Escuro

Rice varietal improvement in the Philippines is a cooperative undertaking of both the government and the private sector. During the past three seasons, 18 upland and 50 lowland selections were selected from breeding nurseries and entered in the National Cooperative Performance Tests in which there were 135 entries in the rainy season and 90 in the dry season. The most outstanding new selections and recently recommended varieties were included on "farm" trials each season. Based on these tests, five varieties of upland rice developed through hybridization were recommended for commercial production during the period 1960 to 1971. In 1970 one new selection yielded almost 50 percent more than the check variety at three sites. During this same period 12 lowland varieties obtained from hybrid progenies have been recommended. The highest yielding variety in 1969 (IR20) had an estimated yield increase of almost 60 percent and was 3 weeks earlier than the best early-maturing commercial variety (Peta) at the start of the period. During the 1968-69 crop year, about 21 percent of the total lowland rice area was grown to the new improved Seed Board varieties which yielded about 30 percent more per hectare than those previously recommended and more than doubled the yield of the unselected varieties. In the past crop year the improved varieties were grown on approximately three-fourths of the 1,000,000 hectares programmed for intensified rice production.

INTRODUCTION

The main objectives of the national rice breeding program are to satisfy the demand of farmers for high-yielding varieties to increase production per hectare at minimum cost, and to meet the demand of millers for high milling recovery and of consumers for desired culinary qualities. Other characteristics desired are short plant stature; short growth duration; insensitivity to photoperiod; resistance to lodging, pests, and diseases; high yield response to fertilizer application; medium threshability; and adaptability to a wide range of farm conditions.

Before 1960 practically all commercial rice varieties grown in the Philippines were tall, weak-strawed, lodging-susceptible and, except for upland varieties, late-maturing. Yields on irrigated land seldom exceeded 4 t/ha even during seasons of favorable weather. Having found in previous tests that early lodging

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and long growth duration affect yield adversely, breeders searched for sources of lodging resistance and earliness for use as parents in a hybridization program (Umali, Castillo, and Castillo, 1956).

STATUS OF VARIETAL IMPROVEMENT

Upland rice breeding and testing programs are cooperative projects of the Bureau of Plant Industry (BPI), U.P. College of Agriculture (UPCA), International Rice Research Institute, and Central Mindanao University. In addition to the general objectives, the upland rice breeding work aims to develop varieties which are adapted for direct seeding in relatively dry soil and possess reasonable drought tolerance.

The lowland rice breeding and field testing programs are joint undertakings of BPI, UPCA, IRRI, Central Philippine University, and Visayas Agricultural College. An additional objective of this program is to produce medium- to high-tillering varieties which are adapted to transplanting. About 100 crosses each were made in 1969 and in 1970. The hybrid progenies were advanced from F_2 through F_8 in pedigree rows. The more promising lines were entered in preliminary yield trials. During this period, 18 upland and 50 lowland selections selected from preliminary yield trials were entered in the national cooperative performance tests.

Promising selections developed by the BPI, UPCA, IRRI, and lately the Philippine Atomic Research Center, 135 entries in the wet season and 90 in the dry season, are entered in the national cooperative performance tests at five to eight stations. This project is coordinated by the Varietal Improvement Group of the Seed Board. The entries are screened for resistance to stem borers, blast, and bacterial leaf blight diseases at three to four locations. The most promising lines selected after two to three seasons in the cooperative tests, together with recently recommended varieties, totalling 14 selections, are grown in about 50 cooperative trials in farmers' fields under the guidance of BPI seed inspectors. Data obtained from these two types of trials are used to evaluate new selections for release and seed increase.

PROGRESS IN DEVELOPING VARIETIES

Progress in varietal improvement can be estimated by comparing the performance of commercially grown varieties over a period of years. Table 1 shows the progress from 1960 to 1970 by making an indirect comparison of the performance of varieties grown during the decade through the medium of the common check varieties used in separate trials.

Upland rice

During the past 10 years five varieties of upland rice developed through hybridization were released by the Seed Board. One was subsequently dropped. All these varieties have long grains with fairly high head rice yields and excellent

Table 1. Improvement in variety yields, 1962-70.

Variety	Days to heading[a]	Grain yield (t/ha)
	Lowland rice (rainy season) 1962, 1964	
Tjeremas	110	3.61
Peta	117	3.66
Acc. 440 Dr. 260	119	3.98
Nang Thay	140	4.19
Bengawan	122	3.75
BPI-76	128	3.70
Norelon 340	134	4.24
C-18	109	3.92
BPI-121	140	4.38
Seraup Kechil 36-482	173	4.16
BE-3	153	4.28
Raminad	169	4.06
BPI-76 (NS)	96	4.17[b]
FK-178A	124	4.78
	1968[c]	
FK-178A	124	3.31
C4-137	104	4.27
C4-63	100	3.80
IR5	110	3.92
IR8	101	4.00
	1969[c]	
IR8	101	4.20
IR20	96	4.55
IR22	89	4.38
IR24	101	4.49
BPI-121-407	102	4.32
	Upland rice (rainy season) 1962, 1964, 1966	
Azucena[d]	91	2.70
Dinalaga[d]	98	2.48
Mangarez[d]	94	2.82
Palawan[d]	96	3.16
HBDa-2	91	2.98
Milpal-4	94	2.58
Azmil 26	92	3.12[e]
BPI-9-33	80	3.52[e]
BPI-1-48	86	3.14
	1970[f]	
BPI-1-48	86	2.62
C22-51[g]	89	3.88
C12-30[g]	86	3.11
BPI-76 (NS)	88	3.47

[a]One to two locations. [b]1965, two locations. [c]Two locations. [d]Selection from local collections. [e]2 years. [f]Three locations. [g]Highly promising selection.

cooking and eating qualities. HBDa-2 and Azmil 26 are 4-month varieties. They are tall but moderately resistant to lodging. HBDa-2 is somewhat susceptible while Azmil 26 is somewhat resistant to both blast and bacterial leaf blight diseases. BPI-1-48 (Syn. M1-48) and BPI-9-33 (Syn. M9-33B) mature in a little over $3\frac{1}{2}$ months, are medium statured, and are resistant to lodging. Both are moderately resistant to blast and bacterial leaf blight. The important agronomic and grain characteristics of the older upland Seed Board varieties are found in "1963 Seed Board Rice Varieties" (UPCA, 1963).

Of the selections tested until 1966, only two yielded as well as BPI-1-48, the common entry in the upland rice yield trials since 1962. BPI-1-48 had a 3-year average of 3.14 t/ha in 1966. In 1970, the highest-yielding line, C22-51, yielded an average of 3.88 t/ha which was roughly 48 percent higher than the yield of BPI-1-48 (2.62 t). C22-51 is only 3 days later than BPI-1-48 in growth duration. Compared with Palawan, the highest yielding commercial upland variety before 1966, this selection is 48 percent higher yielding and 1 week earlier. It is interesting that a variety recommended for lowland planting, BPI-76-NS, yielded 32 percent more than BPI-1-48 when grown under upland conditions during 1970. These results suggest that promising and early-maturing lowland selections should be screened for adaptability to upland conditions.

Lowland rice

Within a 10-year period, the cooperative breeding projects resulted in the release of 12 high-yielding varieties for commercial production. The agronomic and grain characteristics of the older Seed Board varieties are found in "1963 Seed Board Varieties" (UPCA, 1963). Those of the newer Seed Board varieties (BPI-76-NS, C4-137, and IRRI varieties approved between 1966 to 1970) are summarized in the 1969 and 1970 issues of "The Philippines Recommends for Rice" (Escuro et al., 1969; Cada et al., 1970).

In 1971, BPI-121-407, a selection from progeny of irradiated seeds of BPI-121, a late-maturing and photoperiod-sensitive variety, and IR24, a selection from IR8 x IR127-2-2, were approved by the Seed Board for release to farmers. In 1970, C4-63G was released to replace the original seedstocks of C4-63, a selection from Peta x BPI-76. C4-63G has a green base and yields about 10 percent more than C4-63. It is a 4 to $4\frac{1}{2}$ month variety which is non-sensitive to photoperiod, medium-short statured, medium-high tillering, resistant to lodging and to many common field diseases, and upright leaved. It has long grains with a 1-month grain dormancy period, has high head rice recovery, intermediate amylose content, and excellent eating qualities. BPI-121-407 has many of the characteristics of C4-63G. BPI-121-407 is, however, shorter in stature, and a few days earlier than C4-63G. It also has slightly lower head rice yield.

In 1968, multiplication of pure seed of 12 lowland varieties recommended previously by the Seed Board was stopped due to one or more of the following defects: lateness of maturity, tallness, susceptibility to lodging, sensitivity to photoperiod, and low fertilizer response.

Many high yielding commercial lowland varieties grown in the country were included in yield trials until 1966. Compared with FK-178A, the highest yielding entry with 4.78 t/ha in 1966, Peta, the most popular variety until then, yielded about 23 percent less. In 1968 four early-maturing, non-seasonal selections out-yielded FK-178A, the best of which (C4-137) yielded 29 percent more and was 2 weeks earlier. Compared with Peta through the common check variety (FK-178A), this represents a total yield improvement of about 60 percent in a 4-year period. In 1969 the highest yielder was IR20, with 4.55 t/ha, or 8 percent more than IR8, which in 1968 yielded 21 percent more than FK-178A. The overall yield improvement of IR20 over Peta, by way of the check varieties IR8 and FK-178A, was also about 60 percent plus a saving of 3 weeks in growth duration.

PROGRESS IN THE USE OF IMPROVED VARIETIES

Available data on selected improved Seed Board varieties in priority areas established by the National Food and Agriculture Council in 1966 show that during the 1968-69 crop season 597,300 hectares, which is one-fifth of the land planted to rice in these areas, were planted to IR8, BPI-76 NS, IR5, and C4-63 (Table 2). Another fifth was planted to former Seed Board varieties, while the remaining land was planted to the old unselected varieties.

Table 2. Areas of present Philippine commercial lowland rice varieties in priority locations.

Variety	Area (000 ha)
Crop year 1968-69 — Philippines	
Improved Seed Board varieties	597
Old Seed Board varieties	585
Other varieties	1,671
Total	2,954
Crop year 1970-71 — programed areas (partial)	
Improved Seed Board varieties	
IR8	203
IR5	169
IR20	80
IR22	16
BPI-76 (NS)	40
C4-63 and C4-63G	178
C-18	9
Old Seed Board varieties	116
Other varieties	121
Total	932

The new improved varieties had the highest average yield, 3.21 t/ha. The former varieties recommended for planting such as Peta, Intan, Tjeremas, and BE-3, yielded 2.22 t/ha and the old unselected varieties grown by the farmers yielded 1.42 t/ha. The new improved varieties yielded 45 percent more than those formerly recommended which in turn yielded 56 percent more than the old unselected varieties. The total yield improvement over the old unselected varieties was about 126 percent in 1969.

The partial report on the areas grown to the improved and other varieties in the programmed areas during the crop year 1970-71 showed that 203,000 hectares were grown to IR8, 178,000 hectares to C4-63 and C4-63G, 169,000 hectares to IR5, and 154,000 hectares to five other improved varieties. The total planted to these varieties, 704,000 hectares, is equivalent to about three-fourths of the programmed area. The old Seed Board recommended varieties occupied 13 percent and the other varieties, 12 percent of the total programmed area.

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Discussion: Rice varietal improvement in the Philippines

T. T. Chang: What mutagen was used in developing BPI-121-407?

E. C. Cada: Gamma rays.

A. O. Abifarin: It was pointed out that C4-63(G) has resistance to field diseases. Does it possess more resistance to blast than C4-63? The latter has come down with blast in Ghana where it is being used on a large scale as an upland variety.

P. B. Escuro: C4-63(G) is a more advanced selection which has replaced C4-63. It is similar to C4-63 except that it is more uniform in plant characters. It has about the same resistance to blast in the Philippines, as far as we know, as the original C4-63. It is somewhat susceptible in certain other areas of the world especially with high nitrogen fertilization.

Progress in rice breeding in Thailand

Sermsak Awakul

When the rice breeding program in Thailand began in 1950, it primarily involved selection within indigenous varieties. In 1960, intensive work was begun on breeding for resistance to blast. Six years later, the breeding objectives were redefined and a vigorous hybridization program was carried out. During the past 10 years, breeding for increased yields and higher resistance to endemic diseases and insects has been emphasized. More recently, improvement of deep-water rice, grain quality, and protein content have been added to the breeding objectives. The breeding program has resulted in the release of three semidwarf, high yielding varieties: RD1, RD2, and RD3. A semidwarf variety that is resistant to gall midge, a tall, stiff-strawed, disease-resistant variety, and a semidwarf type tolerant to deep water may soon be released.

INTRODUCTION

In Thailand in the early 1950's, emphasis was placed on improvement of the yield of indigenous, tall, photoperiod-sensitive varieties through pure-line selections from traditional varieties.

Many crosses were made in the early 1960's, but most involved intercrosses of local varieties which were carried as bulk populations to the F_6 generation with little attention paid to plant type or fertilizer responsiveness. In 1960, breeding materials were screened for blast resistance by the upland-bed, short-row method. This produced good results.

Attacks by the tungro virus (known as yellow-orange leaf in Thailand) in 1965 and 1966 and the concept of plant type fostered by the International Rice Research Institute caused a great change in the breeding program. New semidwarf types were used extensively in crosses with the tall, photoperiod-sensitive, recommended Thai varieties in an effort to combine virus resistance and stiff straw with greater responsiveness to fertilizer.

DEVELOPMENT OF RD1, RD2, RD3

RD1 and RD3 were officially named and released in 1969. They were selected from the cross, Leuang Tawng x IR8, by the pedigree method at Bangkhen Rice Experiment Station. Leuang Tawng, then the only photoperiod-insensitive

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variety recommended by the Rice Department, had long clear grains but was susceptible to lodging and diseases such as blast and tungro virus. It was crossed with IR8 mainly to obtain lines similar to IR8 in plant type but with the long slender, clear grain of Leuang Tawng. RD1 and RD3 are photoperiod-insensitive, non-glutinous, resistant to tungro, have stiff straw and long, translucent grain, and mature in about 120 to 130 days. In yield trials conducted throughout the country they consistently produced yields similar to those of IR8 at all levels of soil fertility.

RD2 originated from a cross of Gam Pai 15 x Taichung Native 1 backcrossed to Gam Pai 15. Gam Pai 15 is a glutinous variety recommended for northern Thailand. The cross and initial selections were made at IRRI, but reselection within segregating F_4 and F_5 pedigree lines was made in Thailand and resulted in the identification of RD2.

The performance of RD1, RD2, and RD3 in yield trials under conditions of reasonably good soil fertility and water control suggests that, depending upon the cultural conditions, they can yield from 15 to 100 percent more than the conventional varieties.

DEVELOPMENT OF OTHER NEW SEMIDWARF VARIETIES

New semidwarf varieties that are highly resistant to blast, bacterial leaf blight, and tungro virus, and superior in grain quality to RD1, RD2, and RD3 are expected to be developed soon. Some of the most promising lines have been found in crosses between Niaw San Pah Tawng x IR262 lines, Khao Dawk Mali 105 x IR262 lines, and Muey Nawng 62 M x IR262 lines.

Niaw San Pah Tawng is a tall, glutinous, photoperiod-sensitive recommended variety that is popular in the north and northeast regions where glutinous rice is a major part of people's diets. It has excellent grain quality and wide adaptation. The objectives of the cross of Niaw San Pah Tawng x IR262 lines were to obtain short-statured, photoperiod-insensitive types with good glutinous quality and more resistance to blast, bacterial leaf blight, and tungro virus than RD2 has. As a result of strong selection pressure, 16 promising lines have been identified and are now undergoing tests at several rice experiment stations.

Khao Dawk Mali 105 is considered by many local consumers to be the best non-glutinous recommended variety on the basis of eating quality. The variety tends to lodge under high soil fertility and it is susceptible to blast, bacterial leaf blight, and tungro virus.

Khao Dawk Mali 105 has been crossed with an IR262 line to combine its grain quality with the IR262 plant type. Through vigorous selection, a few promising lines from this cross have been identified. These are being checked carefully at various rice experiment stations for yielding ability and resistance to diseases. Pedigree selection was practiced in the cross, Muey Nawng 62 M x IR262 lines, and two promising lines are now in the advanced stage of testing. Muey Nawng 62 M is a glutinous variety recommended for the north. It is moderately resistant to the rice gall midge and tungro virus.

BREEDING FOR TALL, DISEASE-RESISTANT, PHOTOPERIOD-SENSITIVE, HIGH YIELDING VARIETIES

The major weaknesses of the indigenous, photoperiod-sensitive, tall, recommended Thai varieties have been their susceptibility to lodging and to diseases, especially under good cultural practices. But many farmers still prefer the taller varieties probably because of tradition and also because they fear that the new short-straw types will be inundated periodically during the monsoon season. The most promising results to date have come from a cross between Puang Nahk 16 and Sigadis. Puang Nahk 16 is a long-grain, late-maturing, strongly photoperiod-sensitive, disease-susceptible type which originated as a pure-line selection and was recommended for the Central Plain region for many years until it suffered severe damage from blast. In the absence of diseases, it yields well with good cultural practices because it is relatively short and it has stiff straw and narrow, erect, dark-green leaves. Puang Nahk 16 and Sigadis were crossed to incorporate the disease resistance of Sigadis with the grain quality of Puang Nahk 16. Intensive selection within this cross has resulted in 13 high yielding lines which combine most of the good qualities of both parents.

BREEDING FOR DEEP-WATER TOLERANCE

Deep-water rice varieties are planted on approximately 1 million hectares, mostly in the Central Plain of the country where water levels cannot be controlled in the wet season. The major characteristics of deep-water rice that distinguish it from ordinary varieties are the ability to elongate rapidly under rising water conditions (up to 10 cm/day starting as early as 6 weeks after planting), formation of adventitious roots at the upper nodes which are capable of absorbing nutrients from the flood water, and the floating appearance of the leaves on the water surface. Its general defects are a rather chalky grain, susceptibility to major diseases, weak straw, and low yields.

Since floating varieties always lodge regardless of water depths, high yields cannot be attained with such types. A type is needed which remains relatively short and lodging resistant during years when flooding is minor and yet are capable of rapid elongation when severe flooding occurs. This important phase of breeding is presented by Jackson et al. elsewhere in this book.

BREEDING FOR INSECT RESISTANCE

During the past 4 years increased attention has been given to breeding for resistance to insects, particularly the rice gall midge and stem borers. At least 20 promising lines have been identified and are undergoing intensive selection and testing. Details of the testing for resistance to gall midge are presented by Pongprasert et al. elsewhere in this book.

MUTATION AND PROTEIN WORK

Other recent developments in the breeding program include the treatment of promising lines which are defective in one or two simply inherited characters with ionizing radiation and chemical mutagens. Considerable success has been attained in inducing higher blast resistance and changes from non-glutinous to waxy endosperm.

Collection and screening of about 1,800 indigenous lines for protein content has been completed and work is under way to eliminate environmental effects to identify genetically high protein lines that show promise as parents in the hybridization program.

Discussion: Progress in rice breeding in Thailand

S. S. VIRMANI: Since IR8 and Leuang Tawng, the parents of RD 1 and RD 3, are susceptible to tungro, how could RD 1 and RD 3 have resistance to this disease?

S. Awakul: RD 1 and RD 3 are primarily resistant to the green leafhoppers but not to the virus. IR8 is also resistant to the leafhoppers. Both Luansark Wathanakul and K.C. Ling have stated that RD 1 is more resistant to the virus than IR8, but this does not mean that it is immune. It may become susceptible under Thai conditions.

S. K. SINHA: You mentioned a semidwarf variety or type tolerant to deep water. Does the plant type of this variety differ from IR8?

S. Awakul: It is similar to IR8 in plant type but has slightly wider leaves. The major difference is that it can elongate 5 cm/day as water level increases up to 130 cm, while IR8 cannot.

B. H. CHEW: I noticed that the grains of RD 1 and RD 3 are partially awned, does this trait affect the acceptability by the farmers?

S. Awakul: So far, we have no complaint from Thai farmers about this minor defect.

Rice breeding in Australia

Donald J. McDonald

Some IRRI varieties have given high yields in the north of Australia but are not produced commercially because of unattractive grain quality. An attempt is being made to improve cooking quality in the most productive lines. High yielding, long-grain varieties have been bred at Yanco Agricultural College and Research Station for the temperate southwestern regions of New South Wales. The variety Kulu, released for commercial production in 1967, has yielded well in all but the southernmost areas. This variety has a slender, long grain that is rather soft when cooked. Its milling quality has been poor in some years. Three new advanced lines are undergoing extensive tests before their release to growers. YR6-100-9 is early maturing and exceptionally high yielding. Its medium-long grain has good appearance and milling quality and it cooks slightly firmer than the grain of Kulu. YR6-54-10-5/7 and YR13-89-9/11 are slender, long-grain types with superior appearance and milling quality. They are lower yielding than Kulu and YR6-100-9 and their cooking quality is similar to that of Kulu. An early-maturing glutinous variety, YR 140, that has been developed for southwestern New South Wales, is expected to be grown on a limited scale commercially.

INTRODUCTION

Rice improvement programs are operated in three widely separated locations in Australia: the Coastal Plains Research Station in the Northern Territory, the Milaroo Research Station in Queensland, and the Yanco Agricultural Research Station in New South Wales.

COASTAL PLAINS RESEARCH STATION

In 1969 the local breeding program was suspended to permit concentration on the introduction and evaluation of IRRI varieties. These varieties, and lines selected from them, yielded as much as 10.5 t/ha in the dry season and 8.5 t/ha in the wet season (E. Langfield, *personal communication*). Weed control has proved particularly difficult with the semidwarf varieties. New crossbreeding work has been started to improve the grain quality of the most productive lines.

This program has been seriously hampered by quarantine restrictions. Introductions must be grown in strict isolation so it is possible to process only

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small numbers of lines at one time. A great deal of time has been lost that could otherwise have been used for seed increase and observation. The wisdom of quarantine regulation is not questioned, but ways must be found to allow a faster flow of scientific material.

MILAROO RESEARCH STATION

The rice industry on the Burdekin River is in its infancy. Less than 2,000 hectares are under rice and Bluebonnet 50 is the only variety grown commercially. Improvement work is limited to testing of varieties introduced from IRRI and elsewhere. IR8 and IR5 have yielded well but they lack the grain quality of Bluebonnet 50. Other IRRI varieties have been introduced and are now being tested together with several U.S. varieties. Belle Patna and Starbonnet have also performed well, the latter having stronger straw than Bluebonnet 50, but it is unlikely that either will be grown commercially (D. Seton, *personal communication*).

YANCO AGRICULTURAL COLLEGE AND RESEARCH STATION

This research station is located in the semi-arid, temperate region of southwestern New South Wales. It services rice-growing areas along the Murrumbidgee, Murray, and Edwards Rivers. The local industry is the largest in Australia with approximately 38,500 hectares sown to rice annually.

The objectives of the breeding program at Yanco are to breed high yielding, long-grain varieties adapted to the temperate environment and having superior grain quality; to develop varieties that combine strong seedling vigor, rapid vegetative development, and early maturity with high yield; to breed nonpubescent, lodging resistant, semidwarf varieties otherwise similar to currently adapted genotypes; to breed early maturing, cold tolerant, long- and short-grain varieties for the cooler southern region; to develop a high yielding, high-quality glutinous variety adapted to the area; and to breed a high yielding scented variety with superior milling and cooking quality.

High yields have been obtained from the progeny of crosses of the adapted japonica varieties, Calrose and Caloro II, with U.S. long-grain varieties, particularly Bluebonnet 50 and Century Patna. In 1967 the variety Kulu was released for commercial production. It was selected from a Bluebonnet 50 x Calrose cross and has given high yields in all but the southernmost rice-growing areas. Its milling quality has been poor in some years and the grain is rather soft cooking. The characteristics and early performance of Kulu have been described by McDonald et al. (1970).

Four advanced selections, YR 6-100-9, YR 6-54-10-5/7, YR 13-89-9/11, and YR 140, are in the final stages of evaluation for release to growers in the near future.

The seedlings of YR 6-100-9, a selection from Century Patna x Caloro II, are pale and only moderately vigorous. YR 6-100-9 tillers rather poorly. Its culms are thick, strong, and erect; its leaves, erect and broad. It matures in

Table 1. Grain yield of adapted varieties and advanced selections in three seasons 1968-69 to 1970-71.

Variety	Yield (t/ha)				
	Northern area[a]			Southern area[b]	
	1968/69	1969/70	1970/71	1969/70	1970/71
Calrose	10.04	10.91	11.36	6.32	8.36
Kulu	9.28	10.06	10.35	3.94	7.04
YR 6-100-9	11.71	9.41	12.28	5.06	8.88
YR 6-54-10-5	9.85	9.20	9.62	4.18	7.45
YR 6-54-10-7	8.72	8.60	9.89	3.84	7.13
YR 13-89-9	—	—	9.80	--	6.70
YR 13-89-11	8.23	8.81	9.24	1.82	6.26
YR 140	—	—	8.92	—	6.88

[a]The Coleambally Irrigation Area and areas north of the Murrumbidgee River (latitudes less than 35°S). [b]Irrigation areas along the Edwards and Murray Rivers (latitudes greater than 35°S).

approximately 160 days (2 weeks earlier than Calrose). The panicles are very large. The grain is medium-long, has good appearance and high milling quality. It cooks slightly firmer than Kulu. It has experimental yields exceeding 13 t/ha, and has outyielded Calrose by as much as 20 percent in some locations. Average yield data on this selection are in Table 1.

YR 6-54-10-5 and YR 6-54-10-7 are selections from the same cross that produced YR 6-100-9. They are lower yielding (Table 1) but have attractive, long, slender grain of high milling quality. The cooking quality is similar to that of Kulu. These selections mature in approximately 170 days.

YR 13-89-9 and YR 13-89-11 are sister selections from a Century Patna x Calrose cross. They have excellent seedling vigor, moderate tillering, and strong straw. They have a rather late maturity (approximately 180 days). Their slender, long grains have excellent appearance and milling quality. Cooking quality is the same as that of Kulu. Their yields are lower than those of other lines, particularly in the cool southern areas (Table 1).

YR 140 is a glutinous selection from (Caloro II)/3 x Delitus Str. YR 140 has a plant type similar to that of Caloro II but its yield is lower (Table 1). It matures in approximately 165 days. It has excellent glutinous quality.

The failure to obtain high yield in combination with superior (firm, non-sticky) cooking quality is the most notable shortcoming of the program. U.S. long-grain varieties have proved unsuitable as parents from this point of view though progeny with excellent appearance and milling quality have been selected from crosses with them. Other varieties having much higher amylose content, including IRRI semidwarfs, have been crossed extensively with the best long-grain selections to improve cooking and milling quality.

Progress in combining early maturity with strong seedling vigor and rapid vegetative development has been slow. Sufficient vigor has not yet been obtained in appropriate plant types, and yields have been rather low. Low yields in early-maturing selections appear to be due to inadequate vegetative development and not to excessive leafiness with resultant mutual shading. Satisfactory earliness has been derived from U.S., Japanese, and Hungarian varieties. Some long-grain selections from the program that have recently performed well in the cooler southern areas will be further tested there.

It has been difficult to find sources of superior hardiness and cold tolerance for incorporation into varieties for southern areas. Japanese varieties have not proved more cold tolerant than the adapted varieties, Early Caloro and Calrose. They have been poorly adapted to the rather harsh environment and have not yielded well.

Attempts to breed semidwarf stature and increased lodging resistance into the best adapted varieties have been intensified. Taichung Native 1, I-geo-tze, and Dee-geo-woo-gen have been used extensively as parents. At least five backcrosses appear necessary to recover yield potential in this environment. Semidwarfs, similar in most other respects to Calrose and Kulu, have been developed and will be tested for productivity in the near future.

Little emphasis has so far been placed on selection for smooth leaves and hulls, but the advanced line YR 6-100-9 is of this type. Modification of adapted pubescent varieties is being attempted by incorporating genes for smoothness from U.S. varieties by backcrossing. Several backcrosses will be necessary to restore yield potential.

A small demand on the domestic market has stimulated attempts to develop suitable glutinous and scented varieties. The glutinous selection YR 140 will be evaluated commercially in 1971-72 and is expected to be grown on a limited scale in the future. It is still too early to evaluate the prospects for scented varieties.

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Rice breeding in Surinam

P. A. Lieuw-Kie-Song, C. W. van den Bogaert

Before 1966, 11 varieties were released for mechanized cultivation in Surinam. Since then numerous crosses have been made with introduced material to develop varieties with short and stiff straw, early maturity, improved plant type, and nitrogen responsiveness. Acorni, Apani, and Awini, which were released in 1971, resulted from this program.

INTRODUCTION

Rice breeding started in Surinam during World War II. The main purpose was breeding for mechanized cultivation. At that time the most important objective was to develop non-lodging varieties suitable for combine harvesting. Other objectives were high yielding capacity, resistance to diseases and pests, suitability for culture in both seasons, tolerance to adverse soil conditions, short growth duration, rapid early growth, smooth leaves and hulls, extra-long grains, ease of threshing, desirable milling and cooking characteristics, and moderate seed dormancy.

In Surinam, rice breeding is mainly done by the Rice Research and Breeding Station (L.O.N.) of the Foundation for the Development of Mechanized Agriculture in Surinam (S.M.L.). In the early days of L.O.N., breeding material was imported from 32 countries. Up to 1966, 11 varieties were released. They were the pioneer varieties of mechanized cultivation in Surinam (Have, 1967). These varieties induced many small holders to change their traditional rice cultivation system to direct sowing and combine harvesting. Double-cropping increased rapidly. To many rice breeders these varieties are well known because of their extra long grain and unique leaf types. Yields from direct sowing vary between 3 and 5 t/ha.

To raise yields and to meet other requirements of farmers, a new breeding program was set up in 1966. Its main objectives were short and stiff straw, very early maturity, improved plant type, and high response to high levels of N fertilization.

Since 1965 a great deal of breeding material has been introduced and observed at the L.O.N. breeding station. The most suitable material [illegible]eding with S.M.L. varieties were Taichung Native 1, IR8, CP-SLO, Dee-ge[illegible]-gen, I-geo-tze, Bluebelle, (CP dwarf x Rexoro), IR22, and several IRRI lines such as IR278, IR279, IR532, IR154, IR480, and IR454.

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Every year about 125 crosses are made, while about 18,000 lines are evaluated in pedigree nurseries. The promising lines may be divided into two groups: very early material and early material. The very early material varies from 95 to 115 days from sowing to harvest and has a plant height of 75 to 90 cm from the stem base to the tip of the panicles. The early material varies from 116 to 125 days and is from 60 to 90 cm tall.

To combine earliness and short stature, crosses are made between the two groups. In 1971, L.O.N. released three varieties, Acorni, Apani, and Awini. These varieties differ greatly from the other well-known Surinam S.M.L. varieties such as S.M.L. Magali (S.M.L. 81b), S.M.L. Alupi (S.M.L. 242), and S.M.L. Apura, in growth duration, plant height, and plant type. Acorni and Apani were derived from backcrosses between S.M.L. Magali and Bluebelle. They are very early maturing and yield 6 to 7 t/ha from direct-seeded plots. Awini came from the backcross of (Taichung Native 1 x S.M.L. Apura/3). It matures in 120 days from direct sowing to harvest, or about 15 days later than Acorni and Apani. Yield from directly sown plots is 7 to 8 t/ha.

A future objective is to raise the protein content and output of head rice after milling the extremely long grains while attention will be paid to juvenile growth vigor, and complete insensitivity to daylength.

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International cooperation in conserving and evaluating rice germ plasm resources

T. T. Chang

The IRRI germ plasm bank illustrates the contribution that useful genes from diverse sources can make toward rapid progress in rice breeding. The bank also represents a successful example of international cooperation in conserving and utilizing commercially important varieties and obsolete varieties. Promising features are also found in a smaller number of exotic stocks, breeding lines, types reported to have special merit, primitive varieties, and wild forms. The identification of useful genes should be continued. Common features in the composition of several major rice collections point to the need for national agencies in tropical Asia to immediately collect and evaluate indigenous germ plasm which now faces the threat of extinction because of rapid advances in varietal improvement and seed distribution. International collaboration will be needed to facilitate surveys of existing collections, to plan and implement systematic field collection and evaluation, to improve preservation and exchanges, and to standardize documentation.

THE IRRI RICE GERM PLASM BANK AND WORK PROGRESS

When varietal improvement work began at IRRI, the staff recognized the need for access to diverse sources of rice germ plasm. By systematically contacting national and international agencies in major rice-producing countries, a rice germ plasm bank was started in 1961. The rice researchers in Asia and other officials at the U.S. Department of Agriculture and at FAO gave enthusiastic assistance. By the end of 1962, the IRRI varietal collection contained 6,867 accessions from 73 countries and territories.

The collection has grown steadily. It now has 14,600 accessions of which about 13,500 are viable. Recently, certain IRRI breeding lines that have special merits have been added to the collection. A second collection includes the cultivated rice of Africa (*O. glaberrima*), wild species of *Oryza* and related genera, and genetic testers and mutants. This collection has 1,600 accessions. A number of wild forms and *O. glaberrima* varieties were collected by Japanese and Chinese workers in Africa with funds provided by IRRI.

The germ plasm bank project was conceived in 1961-62 1) to assemble at one international center the world's available stock of rice germ plasm for basic and applied studies to improve the crop; 2) to produce and preserve sufficient seed of each accession at IRRI and elsewhere to help conserve the world's dwindling stock of rice germ plasm; 3) to develop a morphological and

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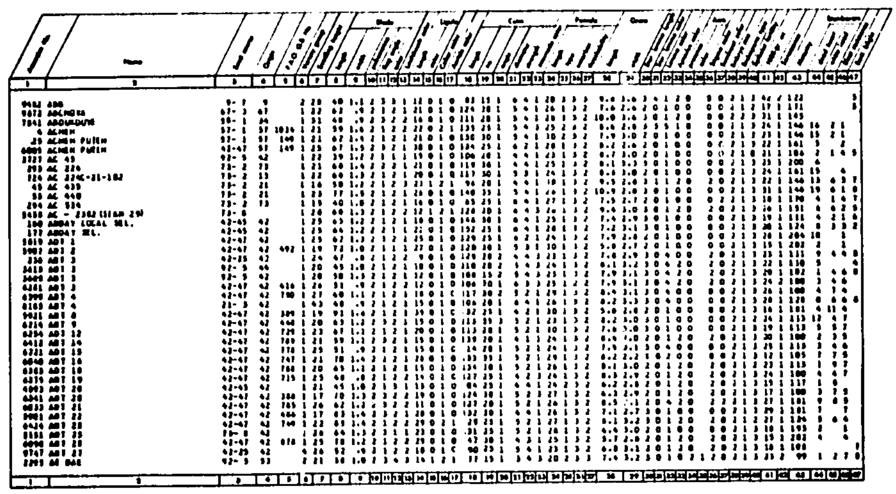

1. A sample sheet from the IRRI Catalog of rice cultivars (IRRI 1970*a*).

agronomic description of accessions in the IRRI collection for a detailed catalog; and 4) to supply rice researchers with needed seed, plant material, and technical information.

Systematic planting and recording of the varietal collection for morphological and agronomic traits was started in 1962. This was soon followed by systematic screening of varieties by plant pathologists and entomologists.

Each viable accession is grown in a three-row plot, 5 meters long. Plants are spaced 30 x 25 cm apart and transplanted at one seedling per hill. A vacant row separates adjacent plots, facilitating identification and harvesting. From 1963 to 1970, records on seedling height, 11 leaf characters, four culm characters, four panicle features, and 14 grain characteristics were completed for 10,330 accessions (supported from 1964 to 1968 by U.S. National Science Foundation grant GB-2417). Quantitative data such as tiller and panicle counts, leaf angle, culm length and strength, days to maturity, and grain weight are recorded in the wet season, which is representative of tropical monsoon weather. Records on pigmentation, pubescence, and other highly heritable traits are sometimes taken in the dry season to distribute the work load. Plant characteristics are recorded according to the method described by Chang and Bardenas (1965). Data on plant characters, diseases, and pests were entered on IBM punch cards. The first catalog (IRRI, 1970*a*) which describes 8,628 accessions was printed in 1970 with a grant from International Business Machines Corp. About 600 copies were distributed to research institutions and rice genetic-stock officers throughout the world. A sample sheet from the catalog is shown in figure 1.

Seeds increased from two or more successive plantings are placed in cold storage (3 to 5 C, 30 to 50% RH). Duplicate seed samples of 9,800 accessions are stored at the U.S. National Seed Storage Laboratory, Ft. Collins, Colorado. Seed viability is checked periodically at both locations. Facilities for long-term storage need to be further improved, however.

Table 1. Number of seed packages sent to requesting agencies and researchers from the IRRI rice collections, 1962-1970.

Year	Varieties		Genetic testers and wild taxa	
	Seed pkg	Requests	Seed pkg	Requests
1962-63	400	17	111	10
1964	2,355	67	228	16
1965	1,608	56	122	6
1966	1,052	41	461	12
1967	1,764	121	789	7
1968	5,286	147	241	18
1969	5,800	101	287	19
1970	5,660	106	91	8
Total	23,925	606	2,330	96

From 1962 to 1970, 24,000 seed packages from the varietal collection were distributed to hundreds of institutions in more than 80 countries and their territories (Table 1). Seeds of genetic testers and wild taxa were sent to 40 institutions in 16 countries.

The IRRI varietal collection has been screened repeatedly to identify sources of desired traits. The first screenings led to the identification of the parents that were used in developing the widely adaptable, nitrogen-responsive, high-yielding, short-statured varieties, IR8 and IR5.

Various research departments of IRRI have also systematically screened thousands of varieties in the collection. The chemists have analyzed the whole collection for protein and apparent lysine contents. Plant pathologists have uncovered outstanding sources of resistance to the leaf blight bacteria, the tungro virus, and races of the blast fungus (IRRI, 1967, 1968, 1970*b*, 1971). By screening thousands of varieties, entomologists have found sources of resistance to the stem borers, green leafhoppers, and brown planthoppers (IRRI, 1967, 1970*b*, 1971). In controlled feeding tests, IRRI virologists have been able to separate IR8's inherent susceptibility to tungro virus from its moderate resistance to the green leafhopper, the vector of the virus (IRRI, 1968). Similarly, the simply inherited nature of varietal resistance to the green leafhopper and to the brown planthopper has been elucidated (IRRI, 1970*b*; Athwal et al., 1970). The information and the resistant sources obtained from the screenings have been used in recent hybridization programs at IRRI (IRRI, 1971). More than 50 papers based on experiments with plant material drawn primarily from the collection have been published by IRRI staff members.

IRRI plant pathologists have tested strains of the wild taxa in the second collection for reactions to fungus, bacterial, and virus diseases. One significant finding is the identification of several plants in a strain of *Oryza nivara* from India which is the only known source of resistance to the grassy stunt virus (Ling, Aguiero, and Lee, 1970).

The initial objectives of the germ plasm bank at IRRI have been largely achieved. Further screening of the collections are expected to reveal additional or new sources of desired traits. The value of the collection will be fully appreciated when rice researchers in further screenings find additional sources of desired genes that will meet the ever expanding demands of rice breeding.

CONTRIBUTIONS TO NATIONAL AND INTERNATIONAL RESEARCH PROGRAMS

Some varieties in the collection have been identified as promising in adaptability and yielding ability. Because seedstocks of promising varieties from the collection have been distributed internationally, several have become important commercial varieties in some countries. Taichung Native 1, Tainan 3, and a few other varieties from Taiwan gained wide acceptance in India from 1966 to 1968. Two U.S. selections were tested and named varieties in the Dominican Republic. In addition, the semidwarf varieties from Taiwan and from IRRI have been widely used recently in the hybridization programs of Ceylon, Colombia, India, Indonesia, Surinam, Thailand, and the U.S.

Mutants and varieties selected from the IRRI collections formed part of the entries in the uniform trials for promising mutants sponsored by FAO and the International Atomic Energy Agency in 1966 to 1968 at 13 locations in Asia, Europe, and South America. Several groups of varieties chosen from the IRRI collection have also been tested in the Rice Adaptability Trials initiated in several countries in 1968 under the sponsorship of the International Biological Program.

Seeds and plant cuttings of wild taxa from the IRRI collection have been used in biosystematic studies in India, Japan, Philippines, and Taiwan. About 10 articles, based partly on plant material from the collection, have appeared in scientific publications.

Seeds drawn from the IRRI collection have restored hundreds of varieties to the national collections of South Vietnam and Tanzania. This clearly indicates the usefulness of the collection in preserving the dwindling stock of rice varieties.

Perhaps the most significant effect of the IRRI activities is that several national research agencies have been encouraged by the identification of useful traits in the IRRI collection to start their own systematic screening activities. Testing programs for resistance to diseases and insect pests are under way in Ceylon, India, Indonesia, and Taiwan. Extensive exchange of promising information and seed material are made at the annual international research conferences of IRRI and at other international meetings.

Screening and testing at IRRI and elsewhere have indicated that many highly desirable characters that improved varieties lack are present in unimproved varieties that otherwise have poor agronomic features. If such varieties were not included in national and international collections, valuable gene-pools would be overlooked and lost from cultivation. The extinction of many primitive types of rice is imminent as varietal improvement and large-scale seed multiplication and distribution proceed at an accelerated pace in tropical Asia.

Interestingly, the outstanding blast resistance found in Tadukan (Philippines), Tetep (Vietnam), and Carreon (Philippines), and the resistance of PI 215936

Tainan Yu 487 from Taiwan) to hoja blanca would not be available to rice reeders if these varieties had not been preserved by researchers in foreign lands.

COMPOSITION OF VARIETY COLLECTIONS AND PROBLEMS IN MAINTENANCE

he varieties in the IRRI collection come largely from Asian nations and the .S. Table 2 shows the distribution of IRRI accessions among major rice-owing countries in Asia. It also presents the results of a recent survey conducted determine the number of native varieties existing in each of the countries.

The IRRI collection can be divided into four major categories: 1) leading mmercial varieties in major rice production areas, including both recent leases and principal varieties of the past (most of the old varieties have been urified or reselected by experiment stations); 2) minor varieties collected ecause they were reported to have special merits, such as tolerance to deep ater, low temperatures, or resistance to disease, insect, salinity, or drought; obscure and unimproved varieties collected recently by national agencies in forts to preserve indigenous germ plasm; and 4) breeding lines of some romise which did not reach the stage of release to farmers.

Table 2. Varieties in the IRRI collection compared with national collections and estimated number of indigenous varieties existing in Asian countries.

Country	Accessions maintained in IRRI collection[a]	Accessions maintained in National collection	Estimated number of indigenous varieties
Burma	146	200	1,000+
Cambodia	65	[b]	[b]
Ceylon	550	1,500+	[b]
China (mainland)	1,417	[b]	[b]
China (Taiwan)	766	1,216[c]	1,700
India	1,780	20,000[a,e]	[b]
Indonesia	604	180	[b]
Japan	755	1,804	2,000+
Korea	294	1,674	[b]
Laos	587	250	[b]
Malaysia (incl. Brunei)	500	1,244+	[b]
Nepal	51	[b]	[b]
Pakistan (East)	804	2,600	4,000
Pakistan (West)	70	[b]	[b]
Philippines	1,059	800	[b]
Thailand	162	1,200+	3,500+
Vietnam (North)	9	[b]	[b]
Vietnam (South)	300	387[d]	940+

[a]Including a number of duplicate samples of the same variety from different sources. [b]No information. [c]Including 682 mainland varieties. [d]Including 16 varieties from North Vietnam. [e]Including collections in 14 states.

Like many national collections, the IRRI collection has good coverage of major varieties. It includes a small number of minor varieties, some of which in further testing have failed to show their reported merits. A few unimproved varieties have been collected by national agencies mainly from Ceylon, India, Indonesia, Malaysia, Pakistan, Taiwan, Thailand, Laos, and South Vietnam. The collection has many of the U.S. and Taiwan breeding lines. On the other hand, there are many duplicate accessions. Some retain identical names; others either were given different names or have evolved into different eco-strains. Most of the accessions received from tropical areas either contain mixtures or variants. Some tropical varieties in the collection contain two morphologically distinct populations in nearly equal proportions. A small number of accessions might have been mislabelled in the prior process of seed increase and distribution because they ceased to breed true to the indicated name or category (e.g. glutinous).

Table 2 shows that the IRRI collection can be considered to be a representative segment of the varietal diversity present in countries like Japan and Taiwan but not of that present in most tropical countries.

In developing countries of the tropics preservation of genetic stocks is not easy. If cold storage facilities are lacking, seed stocks must be renewed every year or two by planting seed plots. But if seed is increased yearly, accessions are more likely to be lost because of pest damage or poor growth of unadapted strains. Mixtures may result from contaminations due to early lodging or to dropped seeds. Mis-identification may arise from errors in handling during harvesting and recording. The maintenance of wild forms is even more difficult because of their high frequency of out-crossing, low spikelet fertility, extreme shattering, persistent seed dormancy, heterogeneous populations, susceptibility to diseases and insect pests in a new habitat, and low adaptiveness to a different environment, and because of disputed questions in taxonomy and nomenclature (Chang, 1970). If competent personnel, facilities, or funds are lacking, the laborious maintenance program may collapse. In addition, to be useful to a national breeding program, the collection must be adequately screened for the traits required by the nation's breeders. Before 1960 systematic planting and recording of national collections were mainly designed for perpetuation and description.

RECENT ACTIVITIES IN COLLECTING, EVALUATING, AND PRESERVING RICE GERM PLASM

A gratifying step toward conserving rice germ plasm is the recently renewed interest of national agencies in collecting and using indigenous germ plasm. Ceylon, India, and Pakistan started projects during the 1960's to preserve primitive types of rice collected from farmers' fields.

International conferences held in 1970 at Los Baños and at Hyderabad, led to the start of the International Rice Collection and Evaluation Project (IRCEP) to coordinate and strengthen national efforts on field collection, evaluation, and preservation on a systematic and international basis (minutes of the IRCEP meeting are available from me). The conferees at the Hyderabad meetings recommended:

—Field collections in Burma, Cambodia, Ceylon, remote areas of India, Indonesia (especially Kalimantan), East Malaysia, Laos, Vietnam, Nepal and adjacent areas, East and West Pakistan, remote areas of the Philippines, and mountainous parts of Thailand.

—Selection of sites and materials for collection on the basis of present availability, genetic diversity, and future needs.

—Development of systematic plans for successive stages of testing and evaluation on a national scale and on an internationally coordinated basis.

—Provision of medium-term seed storage facilities at national centers.

—Storage of duplicate sets of collected materials in international centers to provide maximum security while initial testing is under way at national centers.

—Coordination of field collections, testing operations, pooling and alloting of available funds, and exchange of seed and information, guided by a technical committee and assisted by an international agency such as IRRI.

—Planning for long-range seed storage.

A technical committee has been organized to coordinate the field and laboratory operations, to develop training manuals and record books, and to assist national efforts. Field collections were planned during 1971 in Ceylon, India, Nepal, Pakistan, and South Vietnam.

FUTURE WORK

The conventional way of conserving genetic variability used by rice research institutions is the maintenance of reasonably pure strains to preserve the individuality of original accessions, an approach called "museum collections" by Simmonds (1962). This maintenance method is quite efficient for homozygous materials, though it is laborious and does not exploit the full genetic potential. With unadapted strains, long-range preservation by repeated seed renewal is both inefficient and uncertain. At IRRI we have experienced difficulty in multiplying seed of varieties from high latitudes or high elevations in the tropics. For heterozygous populations, a large number of plants per line should be maintained separately to preserve the subpopulations (Oka, 1969). For the more primitive forms, outcrossing and changes in population structure are more likely to occur under field conditions. Long-term seed storage under optimum conditions is one way to reduce losses of poorly adapted types and to minimize changes in genetic composition.

Alternative ways of conserving and exploiting variability in small grains have been suggested: 1) compositing a selected group of lines with similar genetic and ecological features and perpetuating the mixture (Simmonds, 1962); 2) compositing a group of F_2 progenies from diverse crosses and maintaining the composite as an unselected bulk population (Harlan and Martini, 1929) to provide "mass reservoirs of variability" (Simmonds, 1962); or 3) a cooperative scheme to pool surplus F_2 seeds from different sources and redistribute portions of the composites to other plant breeders as a supplement to the above schemes (Jensen, 1962; Reitz and Craddock, 1969).

While the immediate concern of rice breeders and geneticists is to save indigenous germ plasm from extinction, researchers should also study ways to provide long-term conservation of genetic variability that will also meet the practical demand for maximum performance through close adaptation. I suggest that discussions and cooperative efforts be started on the following phases:

—A systematic survey of genetic stocks in existing collections to facilitate the culling of obvious duplicate accessions and to determine geographic areas where further collections should be made.

—A cooperative scheme to grow and increase the unproductive exotic types under favorable environments at selected centers and to preserve heterozygous, primitive, or wild populations in environments similar to their natural habitats.

—Improved methods and facilities for long-term storage of seeds.

—Appraisal of various methods of conserving genetic stocks.

—A uniform system of documentation for all stages from field collection to evaluation to seed distribution and storage.

—A cooperative scheme to store seed stocks at international centers.

Some of the technical discussion on the above subjects were covered in IBP Handbook 11, Genetic Resources in Plants (Frankel and Bennett, 1970).

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Discussion: International cooperation in conserving and evaluating rice germ plasm resources

H. I. OKA: It is a problem in seed storage that a fraction of genetic stocks is lost on account of decay. How much is the percentage loss per year in IRRI?

T. T. Chang: We have no precise information on this point. Before 1966 when we stored seeds in metal cans containing silica gel, some of the defective cans did result in seed decay. But now the situation is much improved because the seeds are stored in large glass jars containing "indicating" silica gel as well as plain silica gel. Visual inspection tells us if the seeds remain dry and viable. We did lose a small number of accessions due to either poor adaptability or extreme disease susceptibility. On the other hand, we "lost" many more accessions on the books because the original seed samples failed to germinate upon arrival. These are the dead accessions in our books.

B. B. SHAH: Have you devised some simple and standard methods for screening or evaluating of rice collections, so as to have uniformity throughout all countries besides your cataloging system?

T. T. Chang: The suggested methods for uniform measurement or description of plant characters are given in IRRI Technical Bulletin 4 and in the Catalog of Rice Cultivars and Breeding Lines in the World Collection of the IRRI. It is up to a country's rice researchers to choose the traits which are considered essential to the country's specific needs.

K. TORIYAMA: In Japan, we collected rice varieties in farmers' fields. We found that some local varieties had a wide variability within a variety. For example, we have a variety named "Some-wake." The name of this variety indicates that the variety shows many colors at harvesting time. But "Some-wake," which we have now, showed only one color, purple. I think it is essential to include all the variation within a variety.

T. T. Chang: The point is covered in my paper.

S. C. LITZENBERGER: Collections should be of two types. One might be known as a working collection which every worker, agency, or program maintains and the other is the germ plasm bank. The latter should be primarily involved with the sampled material from the areas wherever rice is in existence. Included in this would be the wild or related species of the cultivated rice as we know them agronomically.

In making collections no attempt should be necessarily made to get everything. This is impractical. It is, however, essential that most areas are sampled. The samples from a specific area having the same elevation, soil type, etc., could be bulked and maintained in the collection as such. That helps in reducing numbers handled. And it preserves the genetic diversity that may be present that has made this type of plant survive and flourish in that particular area or environment, regardless of what factors existed to keep its population in check by other organisms, pests included. I believe this method is also being suggested for sorghum. In wheat, for example, if one bulk population were developed from the spring wheats as grown in the remote areas of Tunisia, I would be satisfied that the area was represented in the germ plasm bank. The same would be true for barley from that area. Similar situations may or may not exist in rice.

In making collections it may be satisfactory for untrained personnel to assist in making regular collections where collections are to be made from the farms. But, for the wild types and related species trained men should be involved.

T. T. Chang: In principle I agree with your suggestions. For the self-fertilized rice crop, we hope to carry out a better job of field collection.

Germ plasm conservation and use in India

R. Seetharaman, S. D. Sharma, S. V. S. Shastry

Rice germ plasm collections in India have over 20,000 accessions. These accessions represent sporadic collections made from different localities, specific regional accessions obtained through surveys, entries in the FAO catalog, and others obtained by exchange from rice-growing countries. The national collection of rice germ plasm is maintained at the Central Rice Research Institute, while state collections exist at most rice breeding stations. Recent surveys in northeast India provided over 6,000 indigenous primitive varieties. These collections have contributed greatly to varietal improvement by providing, through screening, sources of resistance for major pests and diseases. Screening of the collection has also revealed a wide spectrum of resistance in some of the donors, mostly in varieties that were hitherto considered of no economic importance and that were collected in areas where rice breeding has not made any headway.

INTRODUCTION

The earliest records of the rich varietal diversity in the cultivated rices of India dates back to Roxburgh (1832) and Watt (1891). The early emphasis was primarily on morphology. It was only in the second decade of this century that crop improvement was the motivation for collecting and maintaining rice germ plasm. Every main rice experiment station had a collection of local varieties that was subjected to pure-line selections leading to a large number of recommended varieties. This collection thus played a critical role in crop improvement over the past half century. The earliest and most extensive collections of germ plasm were at Coimbatore, Dacca, Raipur, Karjat, and Kanpur.

THE NATIONAL COLLECTION

With the establishment of the Central Rice Research Institute (CRRI), the assembly of a national rice collection began. Rice varieties from different experiment stations in India were collected and varieties from other countries were obtained by request. The national collection was further enriched through a survey of indigenous varieties in Jeypore tract (Orissa), a putative secondary center of origin of cultivated rices in India (Ramiah and Ghose, 1951). More

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recently, CRRI collected a number of local varieties from Manipur. CRRI is one of the centers for preservation of the indica germ plasm cataloged by FAO.

At present the national collection at CRRI contains approximately 6,500 accessions including 1,344 from Jeypore tract and 904 from Manipur. The FAO catalog has 970 indica accessions including 47 varieties from Indonesia. The seed stocks of about 6,100 accessions are available for distribution.

OTHER COLLECTIONS

A live collection of wild species and their ecotypes is also maintained at the CRRI. This collection includes extracted types obtained from different crosses as well as chromosomal variants.

The state experiment stations maintain their own smaller collections. These collections include local varieties, improved strains, and introductions. Together the state collections have nearly 25,000 accessions including some duplicates (Table 1).

SURVEY AND COLLECTION OF VARIETIES IN NORTHEAST INDIA

Between 1967 and 1971, the Indian Agricultural Research Institute and the All-India Coordinated Rice Improvement Project, with funds from PL-480, conducted an extensive survey and collection of rice in northeast India. The

Table 1. Collections maintained at some major rice research stations in India.

State	Research station	Source of varietal collections			
		Local	Other States	Exotic	Total
Andhra Pradesh	Maruteru	659	—	62	721
	Rajendranagar	250	328	498	1076
	Tenali	25	9	16	50
	Nellore[a]	—	—	—	326
	Adilabad[a]	—	—	—	
	Machilipatna[a]	—	—	—	
	Rudrur[a]	—	—	—	
Assam	Karimgunj	1127	160	628	1915
	Raha[a]	—	—	—	125
	Titabar[a]	—	—	—	605
Bihar	Dholi	219	246	—	465
	Pusa	800	—	—	800
	Sabour	637	—	191	828
Gujarat	Nawagam[a]	—	—	—	632
Jammu & Kashmir	Khudwani	58	187	181	426
Himachal Pradesh	Nagrota Bagwan	100	—	—	100

Continued on next page.

Table 1. *Continued.*

State	Research station	Source of varietal collections			
		Local	Other States	Exotic	Total
Kerala	Kayankulam	83	41	—	124
	Kottarakkara	60	—	—	60
	Mannuthy	330	85	21	436
	Moncompu	52	39	29	120
	Pattambi	410	257	—	810
Madhya Pradesh	Raipur	750	—	100	850
	Rewa	500	—	—	500
	Waraseoni	400	—	—	400
Maharashtra	Karjat	387	522	210	1119
	Panwel	144	46	11	201
	Sakoli	60	46	—	106
Mysore	Mandya	1563	10	232	1850[b]
Orissa	Bhubaneswar	389	38	64	491
	Berhampur	250	—	—	250
	Jeypore	61	—	—	61
Punjab	Kapurthala	51	30	44	125
	Ludhiana[a]	—	—	—	450
Rajasthan	Banswara	37	13	—	50
Tamil Nadu	Aduthurai	507	—	—	507
	Coimbatore	307	1000	578	2306[b]
Uttar Pradesh	Garampani	146	90	20	256
	Faizabad	530	270	100	900
	Nagina[a]	—	—	—	—
	Gograghat[a]	—	—	—	400[c]
West Bengal	Chinsurah[a]	—	—	—	3500
	Bankura	1000	—	150	1150
	Kalimpong	138 (hill)	238	—	426
	Gosaba[a]	—	—	—	—
	Goskora[a]	—	—	—	—
	Hathwara[a]	—	—	—	86

[a]Detailed information not available. [b]Includes some extracts from breeding lines. [c]Flood and deep water varieties.

need to preserve the genetic diversity of this region was urgent since high yielding varieties were soon expected to replace local types.

The region in which the survey and collection was made extends approximately from 22°N to 30°N and covers the states of Assam, Meghalaya, Nagaland, and the Union Territories of Manipur, Tripura, and the North East Frontier Agency (NEFA). Elevation ranges from 150 to 3,500 meters. In the past, ethnic groups from many countries immigrated to the region and probably brought diverse plant materials with them. Poor communications and tribal rivalries restricted the exchange of seeds so the distinctiveness of the varieties

Table 2. Particulars of rice collections made from different areas of northeast India.

State	District	Collection
Assam (Plains)	North Lakhimpur	658
	Sibsagar	15
	Kamrup	231
	Goalpara	27
	Research Station (Titabar)	182
Assam (Hills)	Mikir Hills	518
	North Cachar Hills	75
NEFA	Kameng	138
	Subansiri	383
	Siang	330
	Luhit	374
	Tirap	302
Meghalaya	Garo Hills	808
	Khasi and Jaintia Hills	548
	Research Station (Upper Shillong)	43
Nagaland	Tuensang	270
	Mokokchung	349
	Kohima	230
Manipur	Manipur East	172
	Manipur West	61
	Manipur North	70
	Manipur South	109
	Manipur Central	586
Tripura	Tripura North	109
	Tripura South	137
Total		6730

was preserved. Hilly regions grow varieties with cold tolerance, an attribute of the japonica ecotype which is not common to the plains. The hilly terrain itself provides a great diversity of climatic conditions within relatively short distances.

The survey was conducted by direct collection from the farmers' fields in the plains and indirectly with the assistance of local revenue and agricultural officials from the inaccessible hilly regions. The latter system was used to avoid violation of local traditions. The collection which includes 6,730 varieties can be claimed to be exhaustive in the locations covered (Table 2).

USE OF THE NATIONAL COLLECTION

The accessions in the national collections vary considerably in morphological characters and the earliest classification of the collection was by such things as occurrence of pigmentation, grain characters, maturity, awning, and spikelet arrangement (Graham, 1913; Beale, 1927; Bhide and Bhalerao, 1927; Thadani and Durga Dutt, 1928; Sethi and Saxena, 1930; Mitra and Ganguli, 1932; Hector et al., 1934; Alam, 1935; and Kashi Ram and Ekbote, 1936). The knowledge gained in these studies formed the basis of later agricultural investigations aimed at crop improvement.

The occurrence of anthocyanin pigmentation in various shades and hues in the different plant parts led to inheritance studies on the occurrence of pigmentation in various plant parts. These studies enabled preparation of schedules, charts, and photographs to distinguish the pattern of anthocyanin and non-anthocyanin variation in rice (Hutchinson and Ramiah, 1938). Information on rice genetics collected during the period was summarized by Ramiah (1953, p. 10-13, 103-170). A tentative scheme on gene symbolization in rice was proposed by Kadam and Ramiah (1943). An economic classification on the basis of characters other than anthocyanin distribution was suggested by Ramiah and this was later modified and adopted by the FAO.

As early as 1914, varietal improvement was achieved through single plant selections in the bulk material collected from cultivators' fields. The ADT strains 1 to 6 and CO strains 1 to 8 were evolved through this approach. Subsequently, the trial of the japonicas was conducted at Coimbatore. It was then concluded that as direct introduction these japonicas would not usually be successful. The more promising of the Chinese varieties identified from 1935 to 1940, such as Ch-2, Ch-10, Ch-45, were later made available to other states in India in the mid-1940's.

Varietal improvement through hybridization and from natural cross material was attempted in a limited scale. Development of CO 1, MTU 16, blast-resistant strains, and non-lodging varieties are examples.

In 1948 studies on the genetic stock collection were started at CRRI. This program is still under way. Material for disease resistance is screened under natural infection; subsequently, the promising ones are tested under artificial epiphytotics to confirm the degree of resistance. Earlier, screening for tolerance to insect pests was done under natural conditions by including several dates of planting and locations. At present, multilocation screening and tests under laboratory conditions are also used. Donors for resistance to diseases and pests identified are given in Table 3 (CRRI, 1960, 1961; Padmanabhan and Ganguly, 1959; Ganguly and Padmanabhan, 1959; Padmanabhan, Ganguly, and Chandwani, 1964, 1966; P. S. Prakash Rao, *unpublished*). Studies on blast also resulted in the identification of races of the pathogen.

Twelve varieties from the Jeypore collection were also found to be resistant to blast (AICRIP, 1969). In preliminary tests 33 varieties were found to possess varying degrees of resistance to bacterial leaf blight (Chakrabarthi and Devadath, 1971).

JBS 446 and JBS 673 were found to be highly tolerant to gall midge. P. S. Prakash Rao (*unpublished*) identified tolerance to stem borer in Mnp 242, to leafhoppers in Mnp 245, and to stem borer and gall midge in Mnp 119. Recently 247 varieties were found to possess a good degree of resistance to gall midge (P. S. Prakash Rao, *unpublished*). Tolerance to leafhoppers was noted in 164 accessions.

Other important features studied are represented by T 141 from Orissa and Sonachuri from Bihar and Vijaya. These varieties possess a high photosynthetic efficiency under low light intensity (K. S. Murthy and S. K. Nayak, *unpublished*). Tolerance to drought at the tillering phase and at heading was noted in MTU17 and Lal Nakanda-41, respectively (K. S. Murthy *personal communication*).

Table 3. Sources of resistance to pests and diseases identified from the CRRI collection of rice germ plasm.

Resistant/ tolerant to	Varieties		
Blast	CO 4	SM 9	Seluz 44
	BJ I	Ch-48	Tetep
	S 67	Aichi-Asahi	Tadukan
	SM 6	AC 1613	Zenith
Helminthosporiose	Ch-13	BAM 10	
	Ch-45	AC 1351	
	T 141	AC 2041	
	T 498-2A	AC 2045	
	CO 20	AC 2559	
Bacterial leaf blight	Lacrosse x Zenith-Nira		
	Wase Aikoku		
	Early Prolific		
	BJ 1		
Stem rot	Basmati 370		
	Bara 62		
Stem borers	TKM 6		
	Ch-67		
	W 1263		
	CB 1		
	CB 2		
	BU 3		
Gall midge	Ptb 10	AC 1368	
	Ptb 18	Leaung 152	
	Ptb 21	Peykeo E 53	
	Ptb 27	Peykeo P 129	
	BU 3		

In addition, 17 varieties from Jeypore collection were identified as possibly being tolerant to drought (AICRIP, 1969). A selection from Taichung 65 x Taichung Native 1 obtained from the International Rice Research Institute was also found to perform well under drought conditions.

The evaluation studies also resulted in the identification of varieties for direct introduction—Shinei from Japan, Ch-1039 and Ch-988 from China; Kaohsiung 22 from Taiwan; Ptb 10 of Kerala and MTU15 of Andhra Pradesh into Orissa; Bam 12 from Tamil Nadu into Punjab; N. 136 from Uttar Pradesh to Bihar.

The next phase was the development of new varieties by hybridizing the useful types from the collection. CR 906 and 907 (CO 13 x CO 25) which are resistant to blast and three strains possessing combined resistance to blast and helminthosporiose were evolved from a cross between CO 25 and Bam 10. CR 1014, a late-maturing and fine-grained variety, was developed from the cross T 90 x Urang-Urangan 89. Crosses were also made between Ptb 18 and GEB 24 to combine resistance to gall midge with yield potential (CRRI, 1965).

Studies pertaining to genetics of anthocyanin pigment distribution in plant parts (Misro, Seetharaman, and Richharia, 1960, 1961; Ghose, Butany, and Seetharaman, 1963), pubescence of the glumes (Richharia and Seetharaman, 1964), notching in kernels (Seetharaman, 1967*b*), development and expression of ligule, auricles, and junctura (Ghose, Butany, and Seetharaman, 1957; Seetharaman, 1967*a*), clustering of spikelets (Butany and Seetharaman, 1960), and semidwarf habit (Seetharaman and Srivastava, 1969) were made possible by the CRRI collection of rice germ plasm. These studies contributed significantly to the understanding of the genetic system in rice. Interrelationships between *O. sativa* and *O. glaberrima* were hypothesized by the studies on parallel variation and by interspecific hybridization (Seetharaman, 1962; Richharia and Seetharaman, 1962). In addition, Misra and Misro (1969) recognized subspecific variation in *O. glaberrima*.

The *glaberrimas* had been only of casual interest to Asian rice researchers because of their low productivity even in their native habitat. At CRRI, varieties of this species were inter-crossed and also crossed to varieties of *O. sativa*. Fertile lines have been obtained from one to two backcrosses to the *sativa* parent. Some have smooth hull, characteristic of *glaberrimas*, along with characters of Taichung Native 1. The utility of such lines carrying genes both from *O. glaberrima* and *O. sativa* is still under study.

A good account of the regional differences in diversity of cultivated rices from Jeypore tract is given by Govindaswami, Krishnamurty, and Sastry (1966). Moderately tall varieties with japonica-type grains were collected from this area. Conspicuously absent in the collection were varieties with purple pericarp and those with glabrous hull. The studies of variation pattern for pigmentation, shattering, sterility, and panicle characteristics indicated the involvement of *O. rufipogon* in the origin of cultivated rices.

The collection from Manipur provided 50 varieties with glutinous endosperm and semidwarf plant types with normal panicles. Varieties with long outer glumes or notched kernels were not obtained in the region, however (Krishna Murty and Sharma, 1970).

Unlike cultivated rices, wild types have not been extensively used. The first attempt was at Coimbatore where *O. longistaminata* was crossed to GEB 24. In another instance a *spontanea* form was hybridized with GEB 24 and the drought-tolerant variety CO 31 was developed (Rajagopalan, 1957).

Assessment of the wild collection is difficult, but an attempt was made at CRRI using the *spontaneas* of diverse origin i.e., from Assam and Madhya Pradesh in India, Badeggi in Nigeria and Sudan. Seeds were subjected to chemical mutagenesis and selection was made for semidwarf habit (Sampath and Jachuck, 1969). Several lines were isolated that had reduced culm length. One culture derived from a Nigerian *spontanea* yielded 8 t/ha during the dry season. The value of these semidwarfs as alternative sources in the breeding programs and the possibility of isolating lines adapted to water-logged conditions from the wild rices and their hybrids are also being explored.

Identification of plants resistant to grassy stunt virus in a population of *O. nivara* and its use in the development of resistant varieties with high yield potential constitute a significant example of the productive use of wild species (IRRI, 1971). Genotypes resistant to other diseases and pests may occur among wild rices.

The collection of wild species had also been used to determine the species relationship, genome analysis, and evolutionary pattern in the genus *Oryza*. These studies made independently by Sampath (1962) and Sharma and Shastry (1965) using interspecific crosses enabled a revision of the taxonomy of *Oryza* and an understanding of the evolutionary pattern in this genus.

STATE COLLECTIONS

The Indian states have been involved in varietal improvement in rice since the turn of the century. Research in the main rice breeding stations, in the early days, centered around collection of local varieties and their improvement by pure-line selections. An analysis of the rice varieties released by different states reveals that 418 out of 547 improved varieties trace their origin to this procedure. Even the 48 varieties developed by hybridization are exclusively from indigenous collections from different locations in India. In the current breeding program in developing dwarf, nitrogen-responsive varieties, some of the local varieties, because of specific traits of adaptation and other desirable characters, are very useful.

ASSAM RICE COLLECTION

Collections made from different localities in northeast India were grown at Hyderabad under uniform conditions. The transplantation of genotypes under a new environment doubtless causes several changes in phenotypic expression that affect agronomic characters, but not in reactions to pests and diseases.

Varieties collected from the hills resemble the japonica type in round grain type, highly pubescent spikelets, dark green foliage, and thermosensitivity reflected in low tillering and early maturity when grown at Hyderabad. The varieties collected from the Brahmaputra valley, on the other hand, are mostly tall indicas with poor plant type and various degrees of photoperiod sensitivity. Several varieties with short stature were collected. The height of these varieties ranges from 70 to 110 cm. Some varieties had glabrous glumes and smooth leaves. The varieties from the plains vary widely in many respects: plant height, 70 to 180 cm; maturity, 110 to 165 days; number of tillers per hill, four to 20; number of grains per panicle, 50 to 385; 1,000-grain weight, 12 to 32 g. Variation in pigmentation in different plant parts covers a wide spectrum (Sharma et al., 1971).

The quality characteristics of the grains, particularly the amylose and protein contents, were determined by A. K. Kaul (*unpublished*) at the Indian Agricultural Research Institute. The grain protein ranged from 6 to 13 percent in different varieties and amylose content ranged from 0 to 27 percent (Sharma et al., 1971).

SCREENING FOR PEST AND DISEASE REACTIONS

A significant feature of the collection project of northeast India has been the simultaneous assessment of the collection for reaction to pests and diseases.

Table 4. New donors for resistance to pests and diseases identified from Assam Rice Collections as a result of AICRIP screening tests.

Pest or disease	Varieties (no.) Tested	Varieties (no.) Resistant	Locations of test
Blast	927	18	Anakapalle, Maruteru, Ponnampet
Bacterial leaf blight	3,459	17[a]	Cuttack, Maruteru, Hyderabad
Rice tungro virus	200	22	Hyderabad
Gall midge	1,261	43	Warangal
Stem borers	1,349	17	Warangal
Leaf hoppers	550	11	Hyderabad
Helminthosporiose	618	1	Pattambi

[a]Moderately resistant.

The screening tests are conducted by the AICRIP coordinating center at numerous locations under natural infestation for stem borers and gall midge and under natural infection for blast, bacterial leaf blight, and helminthosporiose. Reactions to leafhoppers and rice tungro virus were determined under the greenhouse conditions at AICRIP employing two to three viruliferous and non-viruliferous leafhoppers in the individual plant caging technique (Everett, 1969). The number of varieties screened in each case together with the number of varieties suspected to be resistant for each pest or disease is summarized in Table 4. Shastry et al. (1971) described the screening techniques adopted and the varieties found resistant.

Screening for resistance to rice gall midge and stem borer in Warangal during kharif 1969 and kharif 1970, respectively, was under natural infestation that was so severe that no susceptible hosts survived. The identification of resistant varieties was therefore considered reliable. Reaction to blast was based upon the Uniform Blast Nursery data from three locations which exhibited severe incidence of the disease. Even so, the data must be confirmed over a greater number of seasons and locations, since the pathogen is known to be differentiated into several races. Screening for bacterial leaf blight was by pin-prick inoculation using the most virulent isolate available. None of the varieties were resistant to bacterial leaf blight, but some were scored as moderately resistant under these rather severe disease conditions. Reactions to leafhoppers and rice tungro virus were determined by individual plant caging technique (Everett, 1969). They were based on a single test and need to be confirmed.

SCREENING FOR MOISTURE STRESS CONDITIONS

Andhra Pradesh Agricultural University organized a screening test to determine varietal resistance to moisture stress conditions. Three locations were chosen — Rajendranagar, to represent heavy soil with high pH and good water retention, but with limited availability of Fe because of the high pH; Tirupati to represent light soils; and Garikapadu, to represent light soil with low content of Fe. The nursery, composed of 1,644 Assam varieties, was grown in the 1970 dry season at Rajendranagar under lightly irrigated conditions, with 12 days of stress 1 month after sowing. The test was repeated at Tirupati and Garikapadu during kharif 1970. The varieties were scored for leaf tip drying, leaf discoloration, and rolling and rejuvenation of tillering after irrigation. Seven varieties were resistant to iron chlorosis resulting from high soil pH, and five varieties were tolerant to moisture stress at all locations. In addition, 15 varieties were resistant to drought at one location or more. Resistant varieties matured in 120 to 150 days and produced yields of 4 to 6 t/ha while the susceptible varieties gave yields of 1 to 2 t/ha under comparable conditions. Varietal differences in reaction to adverse soil conditions is an important aspect of rice breeding for upland conditions.

VARIETIES WITH GOOD PLANT TYPE

While most of the varieties collected in northeast India have poor plant type like most varieties in the tropics, 98 varieties were short (70 to 110 cm). Current breeding programs in most countries accent semidwarf plant types—employing the plant type gene from Dee-geo-woo-gen (Dgwg). New donors may offer alternative sources of genes for desirable plant type. S. D. Sharma and K. L. Hakim (*unpublished*) attempted nine crosses involving nine different Assam semidwarfs and Dgwg. All F_1 and F_2 plants were semidwarfs. Thus the plant-type genes of these nine varieties are allelic to that of Dgwg. Three crosses between Assam semidwarfs and talls revealed that semidwarfism is a monogenic recessive, similar to Dgwg dwarf gene. H. W. Li (*personal communication*) likewise, found that the genes of the short mutants obtained by irradiation are allelic to the Dgwg gene. It remains to be seen whether the remaining semidwarf varieties from Assam carry the same gene as Dgwg.

DISTRIBUTION OF PEST AND DISEASE-RESISTANT VARIETIES

Have the donors identified for pest and disease resistance originated randomly from different localities of the survey? Are resistant varieties distributed in specific localities? An analysis of this type has several recognized limitations. First, the number of varieties collected from various districts differs widely, from 15 in Sibsagar to 548 in North Lakhimpur (Table 2). Second, the entire collection is not yet subjected to all the screening tests. Third, some of the collections made from the research stations at Titabar and Upper Shillong represent varieties collected outside the district: and this question may be true of some collections from the farmers' fields, too. In spite of these limitations, available data permit some general comments.

Collections from Garo and Mikir Hills account for 22 out of 43 gall midge resistant varieties collected by the survey team from different districts. Likewise, 10 of 17 varieties resistant to stem borers and seven of 11 varieties resistant to leafhoppers originate from the Garo Hills. Blast resistant varieties are predominantly included in the collections made from North Lakhimpur, Garo Hills, and K and J Hills. All the varieties exhibiting some resistance to bacterial leaf blight originate from the four districts of NEFA. Mikir Hills collections contributed 13 of 22 tungro resistant varieties. In contrast, the distribution of plant type mutants was random. The glabrous type and japonica-like varieties were collected only from the hilly districts of NEFA, Meghalaya, and Nagaland.

PROBLEMS IN PRESERVATION

The preservation of the germ plasm presents certain difficulties. For example, low seed set and loss of viability are problems in maintenance of japonicas in the tropics. Another difficulty is the verification and maintenance of purity of the types especially in a large collection that contains identical phenotypes. The lack of a good facility for seed storage in several centers affects the viability of seed to a great extent. Without cold storage the whole collection must be grown year after year. Slight errors in handling of the material during sowing, planting, harvesting, drying, and storage can lead to difficulties. The maintenance of purity in wild types poses a problem considering the extent of out-crossing. The simultaneous maintenance at more than one center leads to duplicate maintenance; but this procedure is desirable. Duplicates in the improved varieties can be traced; duplicates in older varieties are hard to assess, but estimates vary from 5 to 10 percent.

THE FUTURE

Past experience leads to the observations: 1) the value of a germ plasm collection increases with the amount of information available on each accession. In this connection the pioneer work at IRRI in cataloging after laboratory and field studies constitutes a major step. 2) The breeder needs specific detailed information on characters like resistance to races of *Piricularia* and other diseases or to insect pests. Therefore, the publication of information by various rice breeding institutes should be encouraged. 3) Breeders who have transferred pest resistance to productive genotypes are contributing substantially to the new germ plasm. This germ plasm should be maintained. 4) The productive varieties of the world brought under FAO catalog have not been fully exploited. These varieties should be screened in the light of present breeding objectives. Such a study may also reveal a geographic pattern in varietal variation. 5) Greater attention needs to be paid to the collection of varieties, wild types, and those closely related to the cultivated types from the remaining uncollected areas. 6) Setting up of a national agency for the exportation and introduction of germ plasm would accelerate the progress in the collection, assessment, and use of the material.

In a country rich in varietal diversity there has been little systematic survey and collection. Early collections were through individual efforts from limited areas. There still exist vast areas which have been only incompletely surveyed.

Regions in India which could be considered for future survey are *Konkan* region of Mysore and Maharashtra; Kerala and "Agency" tracts in Andhra Pradesh; Bengal and eastern and northern Bihar; and sub-montane areas in the Himalayan range.

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Discussion: Germ plasm conservation and use in India

H. I. OKA: Did you find "semi-wild" types in the northeast territory?

S. D. Sharma: Northeast India is hilly except the Brahmaputra valley, central Manipur, and Barak valley. The perennial wild rice (*O. rufipogon*) and hybrid swarms (*spontaneas*) that could be intergrades of natural hybrids between the wild form and the cultivated rices were observed in Brahmaputra valley. The perennial form was also found in the Logtak Lake area of Manipur. Probably the hybrid populations can also be found in this area. I do not know about their occurrence in the Barak valley. The annual wild form, *O. nivara*, probably does not occur in this region. The wild forms and spontaneas are found only on the plains and not in the hilly areas.

T. H. JOHNSTON: The USDA collection includes more than 5,000 accessions. About 4,400 varieties and selections were described in a 1968 report by Webb, Bollich, Adair, and Johnston. A more detailed publication is under preparation. As new entries are included in the USDA collection, they are first grown under quarantine in the greenhouse at Beltsville, Maryland or, more recently, in the field at El Centro, California. The latter location is remote from the normal rice-producing area. Several thousand introductions were grown at El Centro in 1970 for evaluation. Seed stocks of varieties in the USDA collection are replenished and maintained by growing the varieties periodically at one of the major rice stations.

Disease resistance

Genetics of blast resistance

Shigehisa Kiyosawa

Through gene analysis of the blast resistance of rice varieties, 13 genes for resistance have been found. These genes are located on seven loci. Linkage relationships have been found between some genes. Some linkages have also been recognized between genes for resistance and ones for other characters. The gene-for-gene relationship between host and pathogen found by Flor can be applied to the relationship between "true resistance" of rice varieties and virulence of blast fungus. How to apply the gene-for-gene theory for breeding is described. The causes of breakdown of resistant varieties may be mutation from avirulence to virulence in the fungus and selective multiplication of virulent fungus strains. A simple method for comparing the longevity of resistant varieties grown in mixture cultivation and rotational cultivation has been developed. For this purpose the relation between daily increase and yearly increase of virulent fungus strains on a resistant variety must be known. Varietal resistance must be viewed from two standpoints, degree of resistance at the time of release of the variety and its stability. For the former, "true resistance" plays an important role, and for the latter, "field resistance" of a non-specific nature is critical.

INTRODUCTION

Blast resistance is one of the most important breeding objectives in rice growing areas. Breeding for blast resistance generally began with the use of native varieties but recently exotic varieties or wild species have been used.

Gene analysis of blast resistance was begun by Sasaki (1922). Investigations in this field have been reviewed by Takahashi (1965) and Yamasaki and Kiyosawa (1966). Introduction of exotic genes for resistance induced the occurrence of new races of blast fungus in the field. The discovery of pathogenic races annulled the old investigations on the inheritance of blast resistance in which pure fungus strains with known pathogenicity were not used. Thus, gene analysis of blast resistance using pure fungus strains was begun by Niizeki (1960) and Iwata and Narita (Japan Ministry of Agriculture and Forestry, 1961) and advanced by me and my co-workers in Japan. Modern breeding for blast resistance started at that time or at the time that an extensive study on races of blast fungus was begun by Goto and his co-workers (Japan Ministry of Agriculture and Forestry, 1961, 1964).

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Table 1A. Classification of Japanese rice varieties on the basis of reaction patterns to seven fungus strains of blast and gene constituents of resistance of representative varieties in each group (Kiyosawa, 1970*e*).

Type of variety*	Genotype of representative variety	Reaction						
		P-2b	Ken 53-33	Ina 72	Hoku 1	Ken 54-20	Ken 54-04	Ina 168
Shin 2	*Pi-k*[s]	S	S	S	S	S	M~S	S
Aichi Asahi	*Pi-a*	S	S	R	S	S	M~S	R
Kanto 51	*Pi-k*	MR	S	S	R^h	R^h	R^h	R^h
Ishikari Shiroke	*Pi-i, Pi-k*[s]†	M	S	M	S	MS	MR	M
Yashiro-mochi	*Pi-ta*†	S	S	M	MR	M	MR	S
Pi 4	*Pi-ta*^{2}	S	M	R^h	R	R	R	MR
Fukunishiki	*Pi-z*†	M	M	M	MR	M	MR	M
Toride 1	*Pi-z*^{t}	R^h	R^h	R^h	R^h	R^h	R^h	R^h
To-to	*Pi-k, Pi-a*	MR	S	R	R^h	R^h	R^h	R^h
Shinsetsu	*Pi-i, Pi-a*	M	S	R	S	MS	MR	R
Shimokita	*Pi-ta, Pi-a*	S	S	R	MR	M	MR	R
Zenith	*Pi-z, Pi-a*	M	M	R	MR	M	MR	R
K 2	*Pi-k*^{p}*, Pi-a*	S	S	R	R	R	R	R
K 3	*Pi-k*^{h}	MR	S	S	R	R	R	R
BL 8	*Pi-b*	MR	M	MR	MR	M	MR	MR
K 59	*Pi-t*	M	MR	M	M	MS	M	MS

*We are now using Shin 2 (*Pi-k*[s]), Aichi Asahi (*Pi-a*), Kanto 51 (*Pi-k*), Fujisaka 5 (*Pi-i, Pi-k*[s]), K 1 (*Pi-ta*), Pi 4 (*Pi-ta*^{2}), Ou 244 (*Pi-z*), Toride 1 (*Pi-z*^{t}), K 2 (*Pi-k*^{p}*, Pi-a*), K 3 (*Pi-k*^{h}), BL 8 (*Pi-b*), and K 59 (*Pi-t*) for determining genotypes of fungus strain for virulence. †Reactions shown in these rows are of Fujisaka 5, K 1, and Ou 244, respectively, which belong to each group.

Table 1B. Specific relations between differential strains of fungus and virulence gene in strains of blast; Av = alleles for avirulence and V = alleles for virulence corresponding to the resistance gene, *Pi-a*.

Genotype of fungus strains	Differential fungus strain						
	P-2b	Ken 53-33	Ina 72	Hoku 1	Ken 54-20	Ken 54-04	Ina 168
Av-a	V	V	Av	V	V	V	Av
Av-k	Av	V	V	Av	Av	Av	Av
Av-ks	V	V	V	V	V	V	V
Av-kp	V	V	V	Av	Av	Av	Av
Av-kh	Av	V	V	Av	Av	Av	Av
Av-i	Av	V	Av	V	Av	Av	Av
Av-ta	V	V	Av	Av	Av	Av	V
Av-ta2	V	Av	Av	Av	Av	Av	Av
Av-z	Av	Av	Av	Av	Av	Av	Av,
Av-b	Av	Av	Av	Av	Av	Av	Av
Av-t	Av	Av	Av	Av	Av	Av	Av

CLASSIFICATION OF RICE VARIETIES BASED ON BLAST RESISTANCE

Modern genetic study of rice blast was begun by classifying rice varieties and breeding materials based on resistance to the disease. Some classificatory studies were made in the process of finding differential varieties for testing the virulence of blast fungus (Japan Ministry of Agriculture and Forestry, 1961; Shimoyama et al.. 1965; Nakanishi and Nishioka, 1967; Yamanaka, Shindo, and Yanagita, 1970). After determining the Japanese differential varieties, Yamasaki and Kiyosawa (1966) classified rice varieties and breeding materials into five groups by using seven fungus strains which were chosen to analyze the blast resistance of Japanese rice varieties. At present, 16 groups have been identified with these seven fungus strains as shown in Table 1 (Kiyosawa, 1967*d*, Yokoo and Kiyosawa, 1970; Kiyosawa, 1972*a*), and this method of classification has generally been used in Japan (Ezuka et al., 1970*a*; Yamada, 1969). However, all varieties and breeding materials in Japan cannot be differentiated in relation to their genotypes for blast resistance with only the seven fungus strains. Yamada (1969) added some fungus strains to differentiate genotypes which cannot be differentiated by the seven fungus strains.

GENE ANALYSIS OF BLAST RESISTANCE

From each group classified as mentioned above, representative varieties were selected to analyze their blast resistance genetically, and the results are shown in Table 1. To date, 13 genes have been found. Among them, *Pi-k* (Yamasaki and Kiyosawa, 1966), *Pi-k*^{s} (Kiyosawa, 1969*a*), *Pi-k*^{p} (Kiyosawa, 1969*b*) and *Pi-k*^{h} (Kiyosawa and Murty, 1969) are allelic and located on the *Pi-k* locus; *Pi-ta* (Kiyosawa, 1966*b*, 1969*c*) and *Pi-ta*^{2} (Kiyosawa, 1967*b*) on the *Pi-ta* locus; and *Pi-z* (Kiyosawa, 1967*a*) and *Pi-z*^{t} (Yokoo and Kiyosawa, 1970) on the *Pi-z* locus. The results of gene analyses have been reviewed before (Kiyosawa, 1967*a*, *d*, 1972*a*). The distribution of genes found to date are shown in Table 2.

Linkage relationships among resistance genes have been found as shown in figure 1. Besides them, *Pi-k* and *Pi-m* are linked with crossing over value of 11.3 percent (Kiyosawa, 1968*a*).

All the genes mentioned above confer "true resistance" (i.e. no susceptible-type lesions will form—as opposed to "field resistance" which allows a few susceptible lesions to form) and act against specific (but not all) fungus strains. In contrast, resistance which seems to be nonspecific in its function for fungus strains was analyzed in Norin 22 (Kiyosawa, Matsumoto, and Lee, 1967), Homare Nishiki, and Ginga (Kiyosawa, 1970*c*) which show field resistance, with a weakly aggressive fungus strain. We found that this type of resistance was controlled by one major gene and a few minor genes.

I have reviewed gene analysis of blast resistance before 1970 (Kiyosawa, 1967*d*, 1971*b*), especially gene analyses of blast resistance introduced from exotic varieties into Japanese varieties.

GENE-FOR-GENE RELATIONSHIP AND ITS APPLICATION

Yamasaki and Kiyosawa (1966) revealed that host-pathogen relationships of blast disease coincide with those in flax rust found by Flor (1956, 1959). In further studies I showed that the gene-for-gene theory can be applied to host-pathogen relationship of blast disease with the exception of field resistance

Table 2. Resistance genes identified in some exotic varieties.

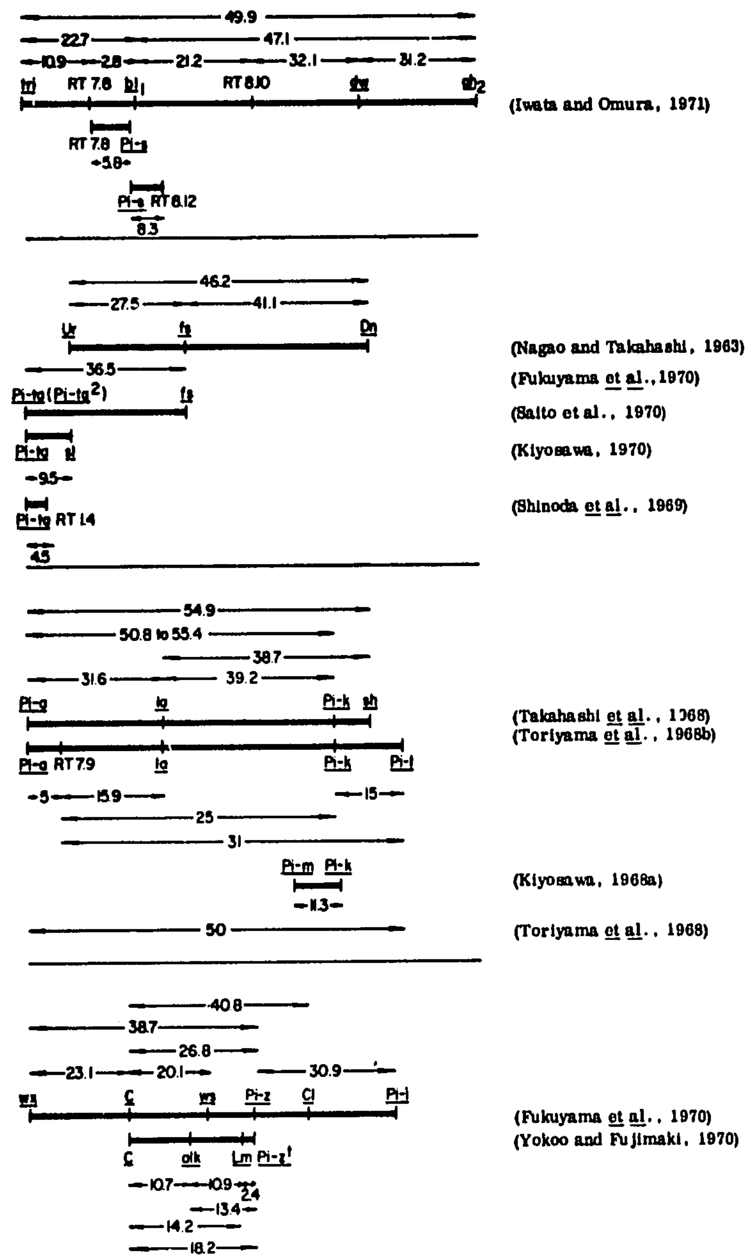
Origin	Variety	Genes identified
Korea	Doazi chall	*Pi-i*
	Jae Keum	*Pi-a*
	Pal tal	*Pi-a*
China	Usen	*Pi-a*, others
	Yakei-ko	*Pi-k*
	Reishiko	*Pi-k*
	To-to (short grains)	*Pi-k*, *Pi-a*
	Choko-to	*Pi-k*, *Pi-a*
	Hokushi Tami	*Pi-k*, *Pi-a*, *Pi-m*
	Pe Bi Hun	*Pi-a*
	To-to (long grains)	*Pi-k*^{s}
	Taichung 65	*Pi-k*^{s}
	Sha-tiao-tsao	*Pi-k*^{s}
	Oka-ine	*Pi-ta*
	Pai-kan-tao	*Pi-ta*, others
Philippines	Tadukan	*Pi-ta* and/or *Pi-ta*^{2}
India	HR-22	*Pi-k*^{h}, others
	CO25	*Pi-z*^{t}, *Pi-a*, others
	TKM.1	*Pi-z*^{t}, others
	Charnack	*Pi-k**, others
	CO4	*Pi-z*^{t}
Pakistan	Dular	*Pi-k**, others
	Pusur	*Pi-k*^{p}, *Pi-a*, others
Vietnam	Te-tep	*Pi-k**, others
	Morak Sepilai	*Pi-z*^{t}
	Kontor	*Pi-z*^{t}
	Leuang Tawing 77-12-5	*Pi-z*^{t}
	Chao Leuang 11	*Pi-z*^{t}
USA	Zenith	*Pi-z*, *Pi-a*
	Caloro	*Pi-k*^{s}
	Lacrosse	*Pi-k*^{s}
	Blue Bonnet	*Fi-a*
USSR	Roshia No. 33	*Pi-k**
Indonesia	Tjina	*Pi-b*, others
	Tjahaja	*Pi-b*, *Pi-t*, others
	Bengawan	*Pi-b*, others
Malaysia	Milek Kuning	*Pi-b*, others

*Any allele at the *Pi-k* locus.

(Kiyosawa, 1971*c*). I speculated that multiple alleles for resistance have a semi-fine structure, based on the gene-for-gene theory (Kiyosawa, 1971*a*). The implications of the theory to breeding can be summarized as follows (Kiyosawa, 1969*d*, 1972*d*):

1) There are many gene pairs for resistance and avirulence.

2) The correspondence between a resistance gene and an avirulence gene is highly specific.



1. Linkage relationship among genes for blast resistance and other traits in four groups (compiled by K. Toriyama and S. Kiyosawa). *alk*: alkali reaction; bl_1: brown mottled discoloration of leaf and panicles; *C*: chromogen for anthocyanin color; *Cl*: clustered spikelets; *Dn*: dense panicle; *dw*: Waisei shiro-sasa dwarf; *fs*: fine stripes of young leaf; gh_2: gold hull 2; *la*: lazy growth habit; *lm*: late maturity; *Pi-a, Pi-f, Pi-i, Pi-k, Pi-s, Pi-ta, Pi-z (Pi-z')*: blast resistance; RT 1·4, RT 7·8, RT 7·9, RT 8·12: reciprocal translocation point between chromosome 1 and 4, chromosome 7 and 8, chromosome 7 and 9, and chromosome 8 and 12, respectively; *sh*: shattering of grains; *sl*: Sekiguchi lesion; *tri*: triangular hull; *Ur*: undurate rachis; *ws*: white stripes; *wx*: waxy endosperm.

3) The number of resistance genes depends upon the number of avirulence genes contained in the fungus strains used, and vice versa.

4) Usually, resistance is dominant over susceptibility, and higher resistance and avirulence are epistatic over lower levels of resistance and avirulence, respectively.

5) The ability to differentiate varieties by host resistance (or fungus strains on avirulence) is highest in a set of fungus strains that have a single avirulence or virulence gene differing from each other (or a set of fungus strains with a single resistance or susceptibility gene differing from each other). If such a set is not collected, complete differentiation of all possible genotypes is not possible.

6) To confirm the accumulation in a single variety of two or more genes that have no additive effect, the same number of fungus strains that have single avirulence genes specifically corresponding to the resistance genes are needed as the number of resistance genes to be accumulated are necessary.

The third point explains why a susceptible variety is often not susceptible in another country as illustrated by the variety Shin 2 which is susceptible to all Japanese fungus strains, but resistant to a Philippine fungus strain (Kiyosawa, 1969*a*).

The fifth point is important for choosing differential varieties. It must be noted that the current differential varieties (Japanese and international) are not chosen from such a point of view (Kiyosawa, 1969*d*).

I established the mutant method for gene identification (Kiyosawa, 1967*a*, 1969*a*, 1971*b*). A given variety is inoculated with a fungal mutant for virulence and with the original fungus strain of the mutant. If the variety shows different reactions to both fungus strains it is concluded that the variety has the resistance gene for which the avirulence of the original strain mutated to virulence.

BREAKDOWN OF RESISTANCE AND ITS CAUSE

In Japan, the use of true resistance in exotic varieties to improve local varieties was begun in 1944 (Ujihara and Nakanishi, 1960). Thus, some varieties that had the gene *Pi-k* were developed. These resistant varieties or breeding materials suddenly became susceptible in a small area in 1952 (Ujihara and Nakanishi, 1960) and in many regions from 1962 to 1964 (Kiyosawa, 1965; Yamada, 1965). From 1962 to 1964, the breakdown of the resistance of varieties carrying *Pi-k* (Ito, 1967; Iwata et al., 1965; Iwata, 1968; Iwata and Abo, 1966; Iwata, Yaoita, and Ozeki, 1969) or *Pi-ta*^{2} (Toriyama, 1965; Nakamura and Ishii, 1968) was widespread. Later, breakdown of the resistance of varieties having *Pi-z* (Mogi and Yanagita, 1967) or *Pi-ta* (Tanaka et al., 1970) were reported. These breakdowns were attributed to the occurrence of new races and their selective multiplication. Furthermore, I consider mutation of avirulence to virulence in a fungus strain a major cause of the occurrence of new races (Kiyosawa, 1965, 1966*a*). A different hypothesis was proposed by Suzuki (1965, 1967) who attributed a large portion of the variability in blast fungus to heterokaryosis. Although the heterokaryosis hypothesis was supported by Chu and Li (1965), many investigators (Yamasaki and Niizeki, 1965; Horino and Akai, 1965; Mogi and Yanagita, 1969; Giatgong and Frederiksen, 1969) found that the mycelium and conidium of blast fungus are uninucleate. That indicates that heterokaryosis is not an important cause of variability in blast fungus.

LONGEVITY OF RESISTANT VARIETIES

The breakdown of resistant varieties mentioned above occurred 2 to 6 years after release of the varieties. We must produce a variety which has high resistance and a long life from release to breakdown—a resistant variety with "longevity." Several factors affect longevity (Kiyosawa, 1965): 1) amount of the pathogen around the field which depends on susceptibility of surrounding varieties and their amount, 2) mutation frequency of avirulence allele to virulence allele, 3) amount of virulent fungus strains at the time of release of the variety, and 4) multiplication rate of virulent fungus strains between years.

We must know how to estimate the quantitative effect of these factors on longevity. The increase of virulent fungus strains in a field where a resistant variety is grown should proceed as shown in figure 2 under the standard conditions that were defined as conditions without yearly fluctuation of environment but with a regular seasonal fluctuation in a year and with an unlimited amount of host.

The number of lesions at the time of first infection each year is used to denote yearly trends of increase of the pathogen (Kiyosawa, 1965). The curve of yearly increase of the pathogen is expressed under the standard conditions by

$$dy/d\tau = y\lambda \quad (1)$$

and solving this equation

$$y = y_0 e^{\lambda\tau} \quad (2)$$

where y is the number of lesions at the initial time of infection in each year, y_0 is that at the time of the release of a given variety, τ is time in years, and λ is the fitness of the pathogen on the given variety. When using equation (2), the longevity of the variety, T_M, is expressed by $T_M = (1/\lambda)(\log_e M - \log_e y_0)$ which is derived from $M = y_0 \exp \lambda T_M$ where M is the maximum number of lesions over which the variety loses utility because the damage becomes very severe (Kiyosawa, 1972*c*). We must breed varieties with a large T_M.

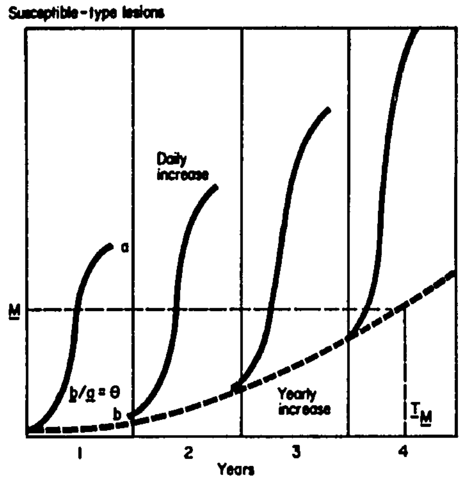
RELATION BETWEEN YEARLY RATE AND DAILY RATE OF DISEASE INCREASE

Equations (1) and (2) can be applied only under the standard conditions mentioned above. What equation can be employed to measure the yearly increase of the disease under substandard conditions with a limited amount of host and no yearly fluctuation of environment? To find out, the relation of the yearly increase to the daily increase of disease must be known. Accordingly, investigations of the daily increase of disease are important for determining the longevity of a new variety.

For the daily increase of disease Van der Plank (1963) used the equations

$$dx/dt = rx \quad (3)$$

and $dx/dt = rx(1-x)$, where x is the proportion of diseased tissue and t is



2. Relationship between daily increase and yearly increase of disease measured by lesion numbers.

time in days. On the other hand, I used the equations (Kiyosawa, 1965)

$$dy/dt = ry \tag{4}$$

and

$$dy/dt = ry[1 - (y/Y)] \tag{5}$$

where y is the number of lesions and Y is the upper limit of lesion numbers. Integrating equations (4) and (5) gives

$$y = y_0 e^{rt} \tag{6}$$

and

$$y = Y/(1 + ke^{-rt}) \tag{7}$$

where $k = (Y - y_0)/y_0$. Equations (4) and (6) are expected under ideal conditions —a constant environment and an unlimited amount of host that has unchangeable resistance. Under sub-ideal conditions where the amount of host is limited, equations (5) and (7) apply. Under natural conditions, an upper limit of lesion numbers is observed in every year and the disease increase shows a good fit to equation (7) (Kiyosawa, 1972*b*). This fit is, however, not due to the nearly ideal conditions because the environment varies and the amount of host is limited. Moreover, the observed disease increase curves (Kuribayashi and Ichikawa, 1952) showed a good fit to equation (7) even in years that did not show severe infections (Kiyosawa, 1972*b*). This means that the factor determining the upper limit of lesion numbers was not the amount of host, at least in such years. The equation, $dy/dt = yr[1 - (t/T)]$, produces a sigmoid curve (Kiyosawa, 1968*b*). Integrating this equation gives

$$y = y_0 \exp r(t - [t^2/2T]) \tag{8}$$

Here, T is the time at which the disease increase ends. The time T should be approximately constant in a specific region, and can be determined *a priori*. Observed curves (cumulative spore numbers) showed a good fit to equation (8) as well as to equation (7). The good fit to equation (8) indicates the possibility that the multiplication rate of the pathogen decreases steadily with time as a result of seasonal change in environmental conditions or increase in the resistance of the host with aging, or both.

The values of r obtained by using equations (6), (7), and (8) depend upon the field resistance of the host and the aggressiveness of the fungus strains, if the field resistance and aggressiveness are nonspecific. The values of y_0 depend upon specific resistance to which resistance controlled by all genes designated to date belongs (Van der Plank, 1963; Kiyosawa, 1965).

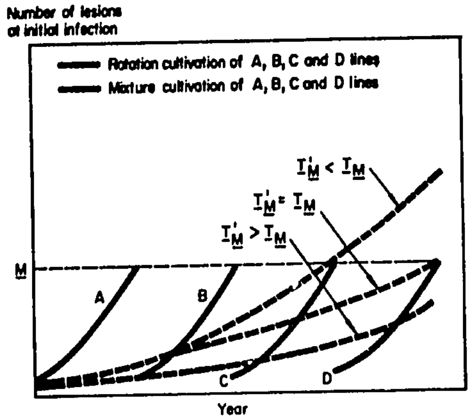
I have investigated mathematically the relationship between r and λ when equations (6), (7), and (8) are applied (Kiyosawa, 1972*c*). For equations (6) and (8), simple relations $rT + \log_e \theta = \lambda$ and $\frac{1}{2}rT + \log_e \theta = \lambda$ were obtained, where θ is overwintering rate expressed by b/a in figure 2. For equation (7), a simple relation was not obtained. This difference seems due to the inconsistency of y_T/y_0; that is, y_T/y_0 is constant in equations (6) and (8) and not in equation (7). If equation (6) or (8) is practically applied, a rectilinear relation is expressed between r and λ, since $\log_e \theta$ seems constant under standard and sub-standard conditions. These studies make clear that equation (2) holds for the yearly increase if equations (6) and (8) can theoretically be applied for the daily increase of disease and if there is no density effect on disease increase; they cannot hold if Y in equation (7) is determined by the amount of host, or if there is a density effect (Kiyosawa, 1972*c*). Therefore, we must study the daily curve of disease increase in detail.

COMPARISON BETWEEN MIXTURE CULTIVATION AND ROTATIONAL CULTIVATION

Multiline varieties have been recommended as a means of disease control by Jensen (1952) and Borlaug (1959). Such varieties have been used in the U.S. (Browning and Frey, 1969; Frey, Browning, and Grindeland, 1970). There is, however, no evidence of whether multiline varieties are the most effective use of resistance genes. We have no practical or theoretical method to estimate the effect of a given means. Mode (1958, 1960, 1961) discussed change of gene frequency in host-pathogen population from the standpoint of population genetics. On the other hand, Leonard (1969*a*, *b*, *c*) approached a similar problem rather epidemiologically. However, these investigations do not allow us to compare multiline variety system with other methods.

I think various methods can be compared by examining the longevity of a multiline variety (mixture cultivation) in relation to the total longevity of component lines (rotational cultivation), as shown in figure 3 (Kiyosawa, 1972*c*). If component lines of multiline variety have equal levels of field resistance and the amount of fungus strains attacking each of the component lines is equal, then the total longevity of the component lines (T_M) and the longevity of a multiline variety (T'_M) are expressed

$$T_M = \sum_{i=1}^{v} T_{Mi} = \frac{v}{\lambda}(\log_e M - \log_e y_0)$$



3. Comparison between rotation cultivation and mixture cultivation. Solid curve: rotation cultivation of A, B, C, and D lines. Broken curve: mixture cultivation of A, B, C, and D lines. Each curve corresponds to the broken curve in figure 2.

and $T'_M = (1/\lambda')(\log_e M' - \log_e y_0)$, respectively, where v is the number of the component lines, λ' is fitness of the pathogen on the multiline variety, and λ is fitness of the pathogen on the component lines in pure stand. If $M = M'$, where M' is the maximum lesion number at the initial infection in a mixed stand over which the multiline variety becomes ineffective, $T_M/T'_M = v\lambda'/\lambda$. Accordingly, if $v\lambda' = \lambda$, the longevity is equal between rotational cultivation (using a second line immediately before breakdown of a first resistant line) and mixture cultivation (use of multiline variety). We can compare the utility of a multiline variety with that of consecutive use of component lines by comparing λ' with λ.

Here again, we must know a relation between yearly rate and daily rate of disease increase. The relation between the rates in pure stand was discussed above. Leonard (1969a) compared the daily rate of disease increase between two fields of oats with all of the plants susceptible to rust in field 1 and only half of the plants susceptible in field 2. Assuming that the distribution of the rust is random, that is, half of the pustules in field 2 will be on susceptible plants, he calculated the relative amounts of rust in the two fields as $x'/x_0 = m^n(x/x_0)$, where x_0 is the proportion of host tissue initially infected, x' is the proportion of infected host tissue in field 2, x is the proportion of infected host tissue in field 1, m is the proportion of susceptible plants in the host mixture, and n is the number of generations of rust increase. From this equation and equation (3), he obtained the equation

$$r_m = r_s + (n/t)\log_e m \tag{9}$$

where r_m is rate of stem rust increase in a mixture of susceptible and resistant plants, and r_s is the rate of increase in a plot composed entirely of susceptible plants. Furthermore, he experimentally obtained

$$r_m = r_s + c\log_e m \tag{10}$$

and noticed a similarity between equations (9) and (10).

However, one of Leonard's assumptions, random distribution of spores on resistant and susceptible plants, is not strictly correct. To determine the influence of non-random distribution of spores we (Kiyosawa and Shiyomi,

1972) first confirmed that spore dispersal from an inoculum plant is $y = \beta e^{-\alpha d} = a\gamma e^{-\alpha d}$, where d is distance from the inoculum plant, a is the initial lesion number on the inoculum plant, and γ and α are constants relating to lesion number on inoculum plant with one lesion after a spore dispersal and dispersal gradient, respectively. When susceptible plants are planted in a row in resistant plants and only a central plant is inoculated with the pathogen, distribution of lesions on the jth plant after the ith generation is calculated by the equation

$$y_j^{(i)} = \gamma[y_0^{(i-1)} e^{-\gamma d} + \sum_{k=1}^{\infty} y_k^{(i-1)} (e^{-|k-j|\alpha} + e^{-|k+j|\alpha})]$$

The total lesion number is

$$y^{(i)} = 2\sum_{j=0}^{\infty} y_j^{(i)} - y_0^{(i)}$$

By using these equations, the increase in lesion numbers in pure stand in which all plants are susceptible was compared with that in a mixed stand in which half the plants are susceptible. The results show that for $\alpha \leqslant 0.2$ the ratio of mixed stand to pure stand agrees with the ratio calculated by the equation, $y'/y_0 = m^n(y/y_0)$, where y' and y are lesion numbers in mixed and pure stands after n generations, respectively. For $\alpha > 0.2$, the effect of a mixture of resistant plants decreases. Accordingly, only when α is 0.2 or less, can equation (9) be applied, and it is limited to occasions when disease increase is according to equation (6).

At present, we have no theoretical way to determine the utility of a multiline variety. It will, however, become possible by advancing such investigations.

FACTORS AFFECTING THE LONGEVITY OF VARIETIES

Varietal resistance must be judged from two standpoints: resistance at the present time and the stability of the resistance. For the former, true resistance plays an important role; for the latter, field resistance, especially the non-specific type, exclusively acts, as expressed by y_0 and λ in equation (2). Accordingly, it is convenient to consider the longevity of variety from the two standpoints.

A decrease of y_0 is brought about by the use of true resistance genes for which few or no virulent fungus strains exist, or by accumulation of true resistance genes. If there is no virulent fungus strain to a developed resistant variety, the first agent causing breakdown of the variety is mutation from avirulence to virulence in the pathogen. The number of mutants attacking the variety depends upon the proportion of mutants and the amount ol pathogen present around the field where the resistant variety is grown. Accordingly, to minimize the occurrence of mutants, it is necessary to choose a resistance gene to which mutation frequency of the pathogen is very low. And it is desirable to replace all the plants with resistant ones to remove the source of the pathogen from which mutants occur. Several studies (Kiyosawa, 1966*a*; Niizeki, 1967; Katsuya and Kiyosawa, 1969) showed that there are genic differences and inter-strain differences in mutation frequency. It was noticed in particular that the mutation frequency for the avirulence allele corresponding to the resistance gene *Pi-k* which controls the resistance of some varieties that have broken down in various regions is higher than the mutation frequency of other avirulence genes. After virulent mutants arise, they can cause the breakdown of a variety only after they have multiplied enough to survive winter losses (Kiyosawa, 1965).

Once the mutants are established or when virulent fungus strains are already present, the fungus strains multiply selectively on the resistant variety. The multiplication rate, daily and yearly, depends upon the non-specific field resistance in the variety. Thus non-specific field resistance plays an important role not only in the decrease of infection in each year but also in extension of the longevity of the variety. The influence on the extension of the longevity is especially important in breeding.

GENETIC RELATION OF RESISTANCE GENES TO OTHER CHARACTERS

Linkage or allelic relationships among resistance genes were mentioned above. Linkage relationships of resistance genes to genes other than resistance genes have been reviewed before (Kiyosawa, 1968*c*), although no linkage between *Pi*-genes for blast resistance and genes for several characters were found except those shown in figure 1. Recently I found a linkage relationship between *Pi-ta* and *sl*, which controls the formation of Sekiguchi lesion induced by some pathogens and chemicals, with a crossing-over value of 9.5 percent (Kiyosawa, 1970*a*).

Yokoo and Fujimaki (1971) reported a close linkage between *Pi-z'* and *Lm* for late maturity. This close linkage often caused the failure of the transfer of the gene *Pi-z'* into Japanese varieties because only early maturing plants were selected.

In breeding resistant varieties, the most important matter is close relationships, including pleiotropic function and linkage, of resistance genes to genes for undesirable characters in agriculture. Particularly in breeding for field resistance, genetic relationship to undesirable characters is important, because it is generally thought that the field resistance is controlled by many minor genes or polygenes, although little information exists (Kiyosawa et al., 1967; Kiyosawa, 1970*c*).

TEST FOR "TRUE RESISTANCE" AND "FIELD RESISTANCE"

The definition of "true resistance" and "field resistance" varies with researchers (Kiyosawa, 1970*b*). In this paper, both terms are employed as resistance that affects y_0 in equation (6) and r in equation (7). It is convenient to express the field resistance by $1/r$.

Varieties have been tested for true resistance by two methods in Japan, injection (Yamasaki and Kiyosawa, 1966) and spraying (Japan Ministry of Agriculture and Forestry, 1961, 1964). Japanese varieties and breeding materials have been divided into 16 groups according to their resistance patterns to seven fungus strains as shown in Table 1.

Field resistance has been tested by field test (Iwano, Yamada, and Yoshimura, 1969; Ezuka et al., 1970*b*; Chiba et al., 1972), upland nursery beds in a field (Ezuka et al., 1970*b*; Asaga and Yoshimura, 1969*a*, *b*, 1970), spraying (Niizeki, 1967), and injection in a greenhouse (Kiyosawa, 1966*c*, *d*, 1969*e*). Two methods for testing field resistance have been devised: use of a weakly aggressive fungus strain (Kiyosawa, 1966*c*, *d*, 1969*e*) and inoculation at a late stage of plant growth (Niizeki, 1967). The relations among resistance measured by these testing methods were schematically described by Kiyosawa (1970*d*).

In the greenhouse and nursery-bed tests, field resistance was evaluated only when virulent fungus strains were used. The entire picture of the field resistance cannot, however, be evaluated by one rating of resistance. Field resistance has two aspects, resistance to formation of susceptible-type lesions and resistance to sporulation of the fungus. In the usual greenhouse test, resistance to lesion formation can be measured, but not resistance to sporulation unless at least a few cycles of infection, lesion enlargement, and sporulation are completed (Kiyosawa, 1969*f*). For testing field resistance in a greenhouse, multiplication of the fungus must be possible in the greenhouse.

In field tests, plants are infected with a mixture of some fungus strains. Therefore, comparison of the field resistance among varieties is not possible by only one rating if varieties with different genotypes for true resistance are included, as shown in equation (6) or (7). Two ratings are mathematically adequate to estimate the value of r from equation (7) or (8). But seasonal variation in environmental conditions does not permit a correct estimation of field resistance if there are varieties with different genotypes.

To eliminate this defect, Ezuka et al. (1970*b*), Hirano et al. (1966), and Suzuki and Iwano (1968) compared field resistance among varieties with the same genotype for true resistance and found varietal differences. I have estimated values of r (Kiyosawa, 1972*b*) with equation (7) and (8) from the data on cumulative spore numbers obtained in Nagano Prefecture by Kuribayashi and Ichikawa (1952). Values of r vary with the equations used, and range from 0.10 to 0.19 in equation (7) and from 0.13 to 0.25 in equation (8) during 12 years.

Chiba et al. (1972) studied the influence of some factors under field conditions on r estimated by equation (8). They found that r was greatly affected by yearly differences in climatic factors and the amount of fertilizer applied. Varietal difference had slight effect. They also found a significant negative regression of r against the lesion numbers at the time of first infection, i.e. the density effect. By correcting r by the regression coefficient, more distinct differences were obtained among treatments. The corrected values of r showed that the range of variation of r by year was 0.32; by variety, 0.20; and by amount of fertilizer applied, 0.31. The average value of r obtained under various conditions for 4 years was 0.36. In recent studies, K. Toriyama (*personal communication*) and H. Niizeki (*personal communication*) found fungus strains that selectively attacked some rice strains possessing field resistance. This indicates that the term "horizontal" resistance which was used by Van der Plank (1963, 1968) is not a suitable substitute for "field resistance" because horizontal means non-specific. The specific nature of some field resistance warns against an indiscriminate use of "field resistance." The addition of field resistance of a specific nature to a variety may decrease y_0, but it may not decrease r as much as expected from the field resistance of non-specific nature.

LOCATING AND SELECTING RESISTANCE SOURCES

Among the 13 genes for true resistance that have been identified, only two have been found in Japanese native varieties and derivatives from hybrids of native varieties. The other genes were found in exotic varieties and derivatives from hybrids of exotic and Japanese varieties. Exotic varieties are more resistant than Japanese native varieties to Japanese fungus strains (Yamasaki and Niizeki, 1964; Kiyosawa, 1967*d*; Kozaka, Matsumoto, and Yamada, 1970). This does not always indicate that Japanese varieties are more susceptible than exotic varieties, however. For example, the Japanese variety Shin 2 which is susceptible to all Japanese fungus strains is highly resistant to a Philippine fungus strain, Ken Ph-03 (Kiyosawa, 1969*a*).

Rice varieties are divided into two groups, japonica and indica. One way rice varieties can be separated into these groups is by their reaction to fungus strains collected from various countries. Fungus strains are divided into two groups: indica and japonica race groups (Morishima, 1969, Kozaka et al., 1970), so indica-type varieties tend to rather be susceptible to the indica race group and resistant to the japonica group, and japonica-type varieties to show the reverse reaction. Thus resistant varieties useful for breeding purposes can be found in distant countries.

In searching for resistant varieties, varieties that have different genes from each other should be selected. This is difficult. For instance, Nagai and his co-workers selected TKM-1, CO 4, Leuang Tawng, Chao Leuang 11, Morak Sepilai, and Kontor as resistance sources. After using these sources, they could introduce only one resistance gene, *Pi-z'*, into Japanese varieties (Nagai, Fujimaki, and Yokoo, 1970; Fujimaki and Yokoo, 1971). Clearly, genes must be identified early in the breeding process. The mutant method provides a way to do so (Kiyosawa, 1967*a*, 1968*a*).

We used this method to analyze Dular and Pai-kan-tao (Kiyosawa, Wu, and Ono, 1971; Kiyosawa, 1972*a*). F_2 or F_3 populations of the hybrids of these varieties with Japanese varieties were inoculated with mutant strains of the blast fungus that attack the resistance genes *Pi-k* and *Pi-ta*, and with original strains. The segregation that resulted showed a significant difference between the mutant and its original strain, indicating that these varieties carry the genes *Pi-k* and *Pi-ta* or similar genes. To use this method, gene analysis of resistance must be made and mutants must be available. An effort must particularly be made to get mutants of the fungus.

Gene analysis of the resistance of exotic varieties to domestic fungus strains is generally difficult because many genes are found in such combinations

(Kiyosawa, 1971*b*). Therefore, the gene analysis should be made in countries where the variety is common. Through exchange of information among researchers, resistance genes that are lacking in each country can be introduced.

Few investigations of resistance sources in wild rices have been made in spite of numerous such studies in other crops and even though most resistance genes have been transferred from wild species (Kiyosawa, 1967*c*). Yamasaki and Niizeki (1964) tested the resistance of wild rice to blast fungus and found that wild rices are not always more resistant than cultivated rice.

PROBLEMS IN USE OF SINGLE GENES FOR TRUE RESISTANCE

A variety that has a single resistance gene often becomes susceptible suddenly. Such varieties are sometimes damaged more severely than native varieties that do not have true resistance. Van der Plank (1963) called this phenomenon the "Vertifolia effect" since the potato variety, Vertifolia, with true resistance was suddenly damaged by late blight more severely than many susceptible varieties. The high susceptibility of newly developed varieties is assumed to be caused by loss of field resistance genes during the course of breeding or by a pleiotropic decrease in field resistance caused by the true resistance gene. If the latter hypothesis is confirmed, the use of true resistance is hopeless. Van der Plank (1963) supported the former hypothesis.

Asaga and Yoshimura (1969*a*, 1970) compared the field resistance of sister lines derived from hybrids which had true resistance genes. The field resistance of line groups that have a true resistance gene was the same as that of line groups lacking the gene in the hybrids Kanto 77 (*Pi-k*$^+$) x [BR No. 1 (*Pi-k*) x Kusabue (*Pi-k*)] and Yamabiko (*Pi-a*) x Kusabue (*Pi-k*), but different in the hybrids Norin 29 (*Pi-a*$^+$) x Kusabue (*Pi-k*) and Yamabiko (*Pi-a*) x Norin 29 (*Pi-a*$^+$). In the latter two hybrids, *Pi-k*$^+$ and *Pi-a* lines were more resistant than *Pi-k* and *Pi-a*$^+$ lines, respectively. Furthermore Asaga and Yoshimura (1969*a*, 1970) indicated that field resistance is different among lines carrying the same genotype for true resistance. This finding supports the first hypothesis for the Vertifolia effect. No conclusion can be made at present, however.

ADDITION OF FIELD RESISTANCE

The future direction of breeding to control blast disease will be towards addition of field resistance, accumulation of two or more true resistance genes (Kiyosawa, 1965), and use of multiline varieties (Okabe, 1967). The use of multiline varieties was described above. Field resistance is more effective in combination with true resistance. The true resistance to which virulent fungus strains are not present is more desirable. When such a true resistance is combined with field resistance, however, there is no way to test the field resistance which is masked by the true resistance. To test field resistance, a mutant fungus that could overcome the resistance would be necessary. But if we could obtain such a strain it could not be used in the field because it might escape and attack resistant varieties being grown by farmers. Thus a greenhouse test for field resistance would have to be developed. If such a fungus strain cannot be found, the alternative is to raise the probability that field resistance is included in an improved variety. One way to do this is to make repeated backcrosses of a resistant parent to a native variety with field resistance.

PROBLEMS IN ACCUMULATION OF TRUE RESISTANCE GENES

It is generally believed that accumulation of resistance genes in a variety makes it possible to effectively control crop disease. But some problems exist. How do you make genes accumulate? How can you prove that genes are accumulated? Where or how do you find new sources of resistance if the resistance of a variety with accumulated resistance genes breaks down?

The first and second question pertain to essentially the same subject, that is, identification of accumulated genes. The more desirable the gene is for breeding, the more difficult recognition of the presence of another gene in the same plant or line. To find out whether the intended gene is contained in the plant or line, gene analysis or a mutant or fungus strain that will attack a variety that has the resistance gene is needed.

If several genes are to be transferred, several fungus strains are needed for the tests—one for each gene as the gene-for-gene theory explains.

When several genes are accumulated in a variety, the longevity of the variety should be greater than that of a variety with a single gene for resistance, provided mutants attacking the variety do not occur step by step during the breeding process. Such stepwise mutation is possible because during the breeding process, varieties with single genes are grown in the field. A first-step mutation could occur on the varieties with single genes, and a subsequent one-step mutant could attack a variety with two genes, and so on. Therefore, a greenhouse test must be used to prevent the escape of the mutants to the field. If a variety with several genes is overcome by a mutant strain, a shortage of usable genes for resistance will occur.

STABILIZING SELECTION

Van der Plank (1963, 1968) gave some evidence that an unnecessary virulence gene lowers the ability of the fungus strain to survive. He called the selection caused by such a function "stabilizing selection". If this hypothesis is generally true, mutants attacking a variety with a single gene or many genes for true resistance should have a low fitness for survival. If so, the value of a variety with many genes should be higher than that mentioned above: a resistant variety which breaks down might become useful again after a few years. For this reason, studies on stabilizing selections are vital.

Few investigations have been made on the stabilizing selection of the blast fungus, however. Causes of stabilizing selection may be that an avirulence gene itself plays a pleiotropic role in the fitness of pathogen or an avirulence gene stabilizes, structurally or functionally, the gene or genes relating to the fitness in the fungus (Kiyosawa, 1972*d*). I have compared the aggressiveness of some mutants that changed their virulence with their original strain, and did not find any difference in aggressiveness between them immediately after isolation of mutants. On the other hand, I have found that mutants that attack varieties with true resistance change to a lower aggressiveness a few months after their isolation. These results seem to support the second hypothesis; however, more extensive studies are needed.

DIFFERENTIAL VARIETIES AND DIFFERENTIAL FUNGUS STRAINS

Change in geographical distribution and frequency of races of the pathogen has a profound influence on breeding for disease resistance. Even if a variety has a resistance gene, it is damaged when virulent fungus strains are predominant. The longevity of a newly bred resistant variety is remarkably influenced by selective multiplication of virulent races. Therefore, the identification of pathogenic races and the choice of differential varieties for making the identification are very important for breeding. Various sets of differential varieties have been selected in Japan (Japan Ministry of Agriculture and Forestry, 1961, 1964), the USA (Atkins, 1965; Latterell, Tullis, and Collier, 1960), Taiwan (Chiu, Chien, and Lin, 1965; Hung and Chien, 1961; Kou, Woo, and Wang, 1963), Korea (Ahn and Chung, 1962), India (Padmanabhan, 1965), and the Philippines (Bandong and Ou, 1966). Later, an international set of differential varieties was agreed on by USA and Japanese workers (Atkins et al., 1967; Goto et al., 1967). This international set of differentials was later used in Colombia (Galvez-E. and Lozano-T., 1968), the Philippines (Ou and Ayad, 1968; Ou et al., 1970), the U.S. (Giatgong and Frederiksen, 1969), India (Padmanabhan et al., 1970), and Nigeria (Awoderu, 1970).

As the gene-for-gene theory indicates, ideal differential varieties should each have a single resistance gene which is different from those of the other differential varieties. However, all the sets of differential varieties have not been chosen with due consideration of this point (Kiyosawa, 1967*d*). An ideal set of differential varieties could be selected in the following order: choice of temporary differential varieties, choice of differential fungus strains, gene analysis of varieties, selection of new differential varieties based on the gene-for-gene theory.

In addition the resistance genes of the differential varieties should be those included in commercial varieties and breeding materials in each country. Inclusion of genes that are not present in the varieties and lines in the country is scientifically significant but practically meaningless in breeding. Accordingly, differential varieties must be separately selected in each country. And an ideal set of international differential varieties must be selected from differential varieties chosen in various countries after their gene analyses.

In Japan, I selected seven fungus strains (Kiyosawa, 1967*d*) from races grouped according to reactions on the Japanese differential varieties by Goto and his co-workers (Japan Ministry of Agriculture and Forestry, 1961, 1964) and I classified varieties according to their reaction patterns to the seven fungus strains. After making a genetic analysis of their resistance, I selected a new set of differential varieties to determine the gene constitution of the fungus strains for avirulence. These varieties are shown in Table 1. At present an effort is being made to eliminate unnecessary genes in a few varieties which carry two or more genes.

An ideal set of differential fungus strains for classifying varieties by their genotypes for resistance consists of fungus strains which carry single avirulence alleles or single virulence alleles differing from each other (Kiyosawa, 1969*d*). Collecting such fungus strains is, however, not so easy as collecting ideal differential varieties. If various genes are introduced, most domestic fungus strains often have avirulence genes for the genes introduced. So, it is difficult to collect fungus strains having single avirulence genes. In the field it is easier to collect fungus strains that have single virulence genes each of which attacks only one ideal differential variety. One difficulty, however, is that only fungus strains used for gene analysis on resistance of varieties can strictly be asserted to have avirulence genes corresponding to the resistance genes identified. According to the extended gene-for-gene theory (Kiyosawa, 1969*d*), the number of resistance genes that can be found depends upon the number of avirulence genes included in the fungus strains used for gene analysis. Therefore, if a variety with an identified gene shows an avirulent reaction to a fungus strain that is not used for gene analysis, the fungus strain does not necessarily carry the avirulence gene corresponding to the gene in the variety. In other words, the variety might have an additional resistance gene which is effective against the fungus strain.

The number of fungus strains that can be used for gene analysis is limited. It is impossible to select fungus strains from them that satisfy the condition for differential fungus strains. Moreover, it is not easy to analyze newly collected fungus strains genetically through gene analysis on resistance of varieties. Therefore, I think that use of mutants is better. Mutants that overcome each resistance gene identified must be prepared from fungus strains used for gene analysis of resistance. In Japan, mutants for *Pi-a*, *Pi-k*, $Pi\text{-}k^s$, $Pi\text{-}k^p$, $Pi\text{-}k^h$, *Pi-ta*, *Pi-z*, *Pi-m*, $Pi\text{-}z^t$, and *Pi-b* have been obtained. If a given variety showed a different reaction to a mutant and its original, we can conclude that the variety has the resistance gene which corresponds to the avirulence gene differing between both fungus strains.

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Discussion: Genetics of blast resistance

H. L. CARNAHAN: From your presentation, I gather that you conclude that there is a gene-for-gene relationship between resistance in the host and virulence in the pathogen. However, in Table 1A, I note that *Pi-k*^{h} gives resistance to several isolates to which *Pi-k*^{s} gives susceptible reactions. Is the result consistent with your conclusion?

S. Kiyosawa: *Pi-k*^{h} is included in the Indian variety, HR-22, and *Pi-k*^{s} is included in the Japanese variety, Shin 2. But in Japan, the effective fungal strain to *Pi-k*^{h} is not present. For example, Shin 2 carrying *Pi-k*^{s} is susceptible to all Japanese fungal strains, but this variety is highly resistant to the Philippine fungal strain.

Y. L. WU: In the Philippines, S. H. Ou found Tetep to have stable resistance to rice blast isolates. Could you tell us how many varieties or which varieties show more stable resistance to rice blast in Japan?

S. Kiyosawa: T. Kozaka said that Pai-kan-tao from Taiwan is more resistant than Tetep. But in my studies, Tetep is the most resistant variety in Japan.

R. A. MARIE: Are we sure that blast isolates or races used till now in experiments are sound, healthy, and not themselves infected by any pathogenic virus?

S. Kiyosawa: According to Yora and his co-workers, most blast fungi are infected with a virus, but I have no such experience in my experiments. It has not been demonstrated that a virus present in the blast fungus affects the pathogenicity of the fungus.

Studies on stable resistance to rice blast disease

S. H. Ou

Few or no lesions are produced on varieties from the International Blast Nurseries that have a broad spectrum of resistance to blast, even when they are inoculated with pathogenic isolates of the blast fungus. Single-conidial subcultures of six pathogenic isolates from Tetep, one such resistant variety, when inoculated back to the variety, differentiated into many races with variable pathogenicities. Most of the new races that developed could not reinfect the original host variety. Since the blast fungus continues to change, no special race can build up its population, and varieties with a broad spectrum of resistance remain resistant. This new type of host-parasite relationship promises stable resistance to blast.

INTRODUCTION

Disease resistance in plants that depends on one or a few major genes usually is unstable. The resistance breaks down when a new virulent race appears. This type of resistance has been referred to as "vertical resistance," "specific resistance," or "major gene resistance." Another type of resistance is not affected by the variation in the pathogenicity of races—it is stable. This type of resistance has been called "horizontal resistance," "field resistance," "general resistance," "race non-specific resistance," "tolerance," and other terms. Many genes usually control this type of resistance (Van der Plank, 1963; Caldwell, 1968; Robinson, 1969).

Most efforts in breeding for disease resistance in the last few decades have involved vertical resistance. When a resistant variety loses its resistance, a new resistance gene is sought, identified, and incorporated into new improved varieties. Efforts have to be repeated and the useful life of a resistant variety is short.

When dealing with variable pathogens, stable or horizontal resistance is obviously more desirable than vertical resistance, but it is more difficult to assess because of its complex nature and because it requires extensive field testing. Horizontal resistance is recognized as a phenomenon, but its genetic mechanism is obscure.

The "vertical resistance" of a variety against a specific race breaks down when a new virulent race multiplies its population increases and all individuals are pathogenic to the variety, i.e. they breed true to the new race. If, however,

S. H. Ou. International Rice Research Institute.

the new race does not breed true and produces other races in its progeny and if the variety has a strong gene (or genes) for resistance, or a broad spectrum of resistance against most of the new races that develop, a severe outbreak will not occur because the population of the original pathogenic races in the progeny is small. This seems to occur with varieties that have a broad spectrum of resistance to the blast fungus, *Pyricularia oryzae*. The resistance of the varieties does not seem to break down even when pathogenic races are present. This type of stable resistance appears to be "horizontal resistance," but it does not coincide with the strict definition of the term by Robinson (1969). We are also trying to find out if typical "horizontal resistance" to blast can be found in rice varieties.

IDENTIFYING BROAD SPECTRUM RESISTANCE THROUGH THE INTERNATIONAL BLAST NURSERIES

During the past half-century, many tests have been made in several countries to identify blast-resistant varieties. These resistant varieties have been used in breeding programs with limited success. The new varieties are resistant only for a few years. One reason is that the tests for varietal resistance in the past have been limited to relatively few varieties, few seasons, and few geographic areas. But the blast fungus varies greatly from locality to locality, and from season to season. Thus the varieties selected as donors of resistance have not been exposed to many pathogenic races and consequently they do not have a broad base of resistance.

Work in the Philippines illustrates the change of varietal reaction between localities and seasons. From 1962 to 1964, 8,214 varieties of the world collection of IRRI were tested in a blast nursery. Of these, 1,457 were highly resistant in the first test. When these resistant varieties were further tested in the same blast nursery for seven repeated trials, only 450 remained resistant. These 450 varieties were tested in seven stations in different regions of the Philippines and after a few repeated tests, only 75 showed resistant reactions in all tests at all stations.

A close examination of changes in races in a blast nursery during a 21-month period (Quamaruzzaman and Ou, 1970) showed that races differ in both composition (different races) and frequency (population of each race) each month. Of the 363 samples tested, 60 races were identified. Though the number of samples was smaller than the actual number of conidia and races that might have been present in the nursery, changes in races took place in the blast nursery. It is conceivable that such changes also occur in the field. This may explain why certain varieties, though resistant as seedlings, are susceptible to neck blast.

To identify material that has a broad spectrum of resistance, blast resistance must be tested repeatedly over a wide range of geographic regions. Thus, an international program is necessary. The International Uniform Blast Nurseries (IBN) were started in 1963. Testing materials included 258 leading commercial varieties and the varieties used by three countries for differentiating races. In 1966 another 321 resistant varieties selected from the IRRI blast nursery were added to constitute the group II of testing varieties. In 1969 groups I and II were consolidated to form one group of 356 varieties, which excluded most of the susceptible varieties and included a few other varieties. By 1970, more than 200 test results had been obtained from 50 stations in 26 countries, mostly in Asia, but some in Latin America and Africa. Detailed data are reported biannually (Results of the FAO-IRC 1962-1963 uniform blast nursery tests, 1964; International uniform blast nurseries, 1964-1965 results, 1966; IRRI, 1968, 1970).

The results of the IBN showed that many rice varieties that are resistant in one region or country are susceptible in other regions or countries where different races exist. Many varieties tested in a new region are resistant, at least initially. For example, many japonicas are resistant in tropical Asia while many indicas are resistant in Japan and Korea. The blast fungus apparently is capable of producing new races all the time. The new races, however, can survive only when there are susceptible host varieties. Thus, after a long time, races prevailing in Japan or Korea are those that are virulent on japonicas while in the tropics prevailing races are virulent on indicas.

The most valuable information obtained from the IBN is the identification of many varieties that have a broad spectrum of resistance, although no variety has been resistant in all tests. Some of the most resistant varieties are shown in Table 1. Varieties such as Tetep are consistently more resistant than others. Tetep was resistant in 97.5 percent of the tests made. The susceptible variety Fanny was resistant in only 19 percent of the tests.

STUDIES ON STABLE RESISTANCE

A variety has horizontal resistance if it consistently has 1) small lesions of the intermediate type (type 3 on the IBN scale) and 2) few lesions on each plant. Both types of reaction limit the production of conidia and reduce the possibility of an epiphytotic. Studies are being made to find out if any variety can consistently maintain such resistance against all races.

Resistance involving small lesions

Of the 8,214 varieties we have screened, over 400 varieties had the small-lesion type of reaction. We tested these varieties to find out if any of them had stable partial resistance, like resistance to late blight of potato. New races produced large, susceptible-type lesions on many varieties, but by the fourth and fifth tests about half of the varieties still were resistant. Starting in 1969, 212 varieties have been sent to various countries. These varieties constitute another group of testing varieties in the IBN. So far only 18 results from tests have been obtained from Colombia and IRRI. Fifty-one of the 212 varieties have shown one or more susceptible reactions. These and earlier tests show that many of the varieties are affected by fungus races, and do not possess horizontal resistance. Whether any of the remaining varieties possess horizontal resistance will be determined by further tests in the IBN.

Resistance involving few lesions

Even though Tetep and other varieties in Table 1 have a broad spectrum of resistance, they are infected by a few races, as shown by the few susceptible

Table 1. The most resistant varieties selected from the International Uniform Blast Nurseries, 1964-1970.

Variety	1964-65 Total	1964-65 Susceptible	1966-67 Total	1966-67 Susceptible	1968-69 Total	1968-69 Susceptible	1970 Total	1970 Susceptible	1964-1970 Total	1964-1970 Susceptible	Resistant (%)
Group I											
Tetep	22	2	59	0	62	2	23	1	199	5	97.5
Nang chet cuc	39	2	49	2	63	3	23	0	176	7	96.0
Tadukan	56	3	57	2	63	5	23	0	201	10	95.0
R 67	51	4	51	2	63	1	21	3	188	10	94.7
C46-15	56	2	60	3	63	4	22	4	203	13	93.6
CI 7787	50	4	59	2	63	4	20	2	194	12	93.9
Pah Leuad 29-8-11	47	4	59	4	59	4	20	2	187	14	92.5
D25-4	31	3	60	6	64	3	23	2	180	14	92.3
Trang Cut L. 11	27	4	50	5	64	2	23	0	166	11	94.0
Pah Leuad 111	18	2	55	5	63	3	22	2	160	13	91.9
Fanny(susceptible)	54	51	49	34	47	32	23	23	173	140	19.0
Group II											
Mamoriaka	—	—	32	0	62	0	22	1	117	1	99.1
Huan-sen-goo	—	—	32	1	63	1	21	0	116	2	98.4
Dissi Hatif(DH-2)	—	—	32	0	63	1	22	2	117	3	97.5
Carreon	—	—	31	0	62	3	22	0	115	3	97.4
Pah Leuad 29-8-11	—	—	31	1	61	0	22	2	114	3	97.3
Ram Tulasi	—	—	32	0	60	1	22	2	114	3	97.3
C46-15	—	—	30	1	61	1	23	1	112	3	97.3
Ram Tulasi (sel)	—	—	33	0	60	2	19	1	112	3	97.3
Ca 435/6/5/1	—	—	31	1	62	2	22	1	115	4	97.4
DNJ-60	—	—	29	1	62	1	22	2	113	4	96.5

cases in the IBN. These varieties have also been tested more than 40 times during the last 8 years in our blast nurseries. Under epiphytotic conditions, a few large susceptible lesions occasionally appeared, so these varieties may be considered susceptible in a qualitative sense. Will these varieties break down or will they maintain their level of resistance by producing only a few lesions occasionally?

The possible reasons why few lesions are produced in the blast nurseries are that the conidia population of the pathogenic races specific to these varieties may be low or that interaction between the fungus and the host variety may be genetically controlled. To determine the true reasons, the pathogenic races on Tetep were isolated, cultured, and inoculated back to Tetep, to another resistant variety, Carreon, and to a susceptible control variety, Khao-teh-haeng 17 (KTH).

The results of 37 such inoculations show that few susceptible-type lesions were consistently produced on Tetep while many were produced on KTH (Table 2). The average number of lesions per seedling on Tetep was 2.2 and on KTH, 32.7. One inoculation produced 14.1 lesions on Tetep and another

Table 2. Susceptible-type lesions on varieties Tetep, Carreon, and Khao-teh-haeng 17 inoculated at the same time with isolates and reisolates of *P. oryzae* from Tetep.

Isolates and reisolates	Lesions per seedling[a] (no.)		
	Carreon	Tetep	KTH
FR-1	0	0.0	63.4
FR-4A10	0	14.1	53.3
FR-13-141	0	0.1	67.3
FR-13-1a	0	0.3	42.5
FR-28	0	0.0	39.2
FR-30A2	0	0.4	20.3
-30A3	0	2.5	26.0
-30A5	0	5.8	44.5
-30A6	0	2.6	43.0
-30A7	0	2.1	61.4
-30A8	0	0.2	62.8
-30A42	0	0.4	15.2
-30A43	0	0.0	15.7
-30A44	0	0.9	17.0
-30A45	0	0.5	14.6
-30-1a	0	0.1	38.4
-30B1	0	0.8	14.1
-30B2	0	0.6	29.7
-30B3	0	0.0	14.6
FR-31	0	0.1	58.3
FR-35-1b	0	0.7	38.6
FR-50-1b	0	0.3	30.3
FR-52-1b	0	0.0	24.1
FR-54-1b	0	0.4	17.7
FR-56	0	4.8	55.6
-56A2	0	2.5	15.6
-56A9	0	5.0	16.3
FR-57	0	0.3	35.5
-57-1b	0	0.2	17.2
FR-59A1	0	8.1	34.5
-59-1b	0	0.2	20.3
FR-78	0	0.8	22.4
-78A4(1)	0	3.7	44.0
-78A4(2)	0	3.8	19.9
-78-1a	0	3.1	21.5
-78-1b	0	1.3	9.7
-78-16	–	16.1	44.6
Average	0	2.2	32.7

[a]Counted from 20 plants.

produced 16.1 lesions. Several isolates produced no lesions. These results indicated that the few lesions produced on Tetep were not caused by a low population of conidia of pathogenic races.

The small number of lesions on Tetep and the large number on KTH in the same inoculations suggest that many of the conidia failed to infect Tetep even

Table 3. Pathogenic races derived from isolates FR-1, FR-1-138, FR-78, FR-78-16, FR-79, and FR-80 grouped by the number of the Philippine differential varieties infected.

Differential varieties infected (no.)	FR-1		FR-1-138		FR-78		FR-78-16		FR-79		FR-80	
	Races (no.)	Subc. (no.)	Races (no.)	Subc. (no.)	Races (no.)	Subc. (no.)	Races (no.)	Subc. (no.)	Races (no.)	Subc. (no.)	Races (no.)	Subc. (no.)
1	-	-	-	-	-	-	1	1	-	-	-	-
2	1	1	-	-	-	-	1	1	-	-	-	-
3	1	1	-	-	-	-	6	6	-	-	-	-
4	4	4	-	-	-	-	7	9	5	12	-	-
5	7	15	2	2	-	-	5	7	1	1	-	-
6	5	22	5	11	-	-	7	10	5	17	2	3
7	1	61	1	19	-	-	6	12	2	11	1	37
8	3	34	3	12	2	3	6	13	2	2	2	3
9	3	17	1	4	3	6	7	11	3	5	2	2
10	-	-	-	-	1	33	3	17	1	4	-	-
11	2	3	-	-	2	3	2	13	-	-	-	-
12	1	2	-	-	-	-	-	-	-	-	-	-
Total	28	160	12	48	8	45	51	100	19	52	7	45

though the fungus was isolated from it. To substantiate this idea many single-conidium subcultures were made from six of the pathogenic isolates from Tetep: 160 single-conidium subcultures from isolate FR-1, 48 from FR-1-138 (single-conidial reisolate from FR-1), 45 from FR-78, 100 from FR-78-16 (the most pathogenic single-conidial reisolate from FR-78; it produced 16.1 lesions on Tetep), 52 from FR-79, and 45 from FR-80. All these subcultures were inoculated to Tetep, Carreon, the 12 Philippine differential varieties (Bandong and Ou, 1966), and eight international differentials (Atkins et al., 1967). The numbers of susceptible-type lesions on Tetep, Carreon, and KTH were counted in each inoculation.

By the Philippine differentials, the 160 single-conidial subcultures of FR-1 differentiated into 28 pathogenic races; the 48 of FR-1-138 into 12 races, the 45 of FR-78 into eight races, the 100 of FR-78-16 into 51 races, the 52 of FR-79 into 19 races, and the 45 of FR-80 into seven races. These races differed greatly in pathogenicity. Some infected only one or two varieties, others infected 11 or all the 12 differential varieties. The races were grouped according to the number of the Philippine differential varieties they infected (Table 3). The distribution of subcultures varies among the races developed. Usually a few races have a large number of subcultures.

The numbers of races separated by the international differentials and a combination of the two sets are shown in Table 4. When more differentials are used, more races are differentiated.

The number of races and the number of subcultures that infect Tetep, Carreon, and KTH, as well as the number of susceptible-type lesions on these three varieties are shown in Table 5. Many of the races and many of the subcultures originally isolated from Tetep failed to reinfect Tetep. The numbers

Table 4. Number of pathogenic races differentiated from the single conidial subcultures of seven single conidial parental isolates of *Pyricularia oryzae* by three different sets of differential varieties.

Isolate and total no. of subcultures	Pathogenic races (no.) differentiated by: Eight international differential varieties	12 Philippine differential varieties	20 varieties[a]
FR-1 (160)	20	28	59
FR-1-138 (48)	6	12	22
FR-78 (45)	3	8	11
FR-78-16 (100)	23	51	63
FR-79 (52)	25	19	37
FR-80 (45)	3	7	12

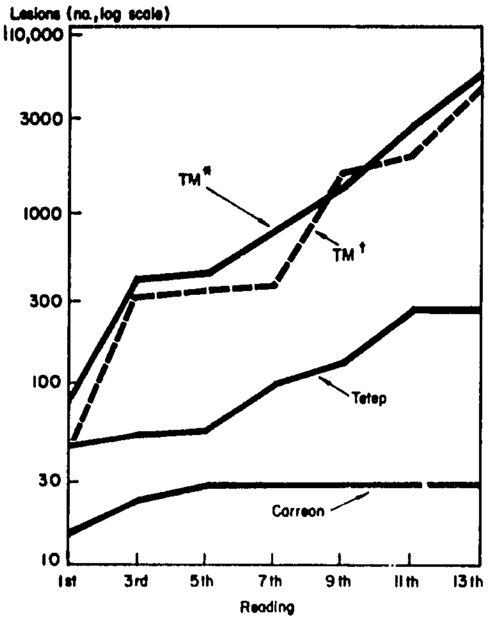
[a]Combination of international and Philippine differential varieties and Tetep and Carreon.

of lesions on Tetep and Carreon were consistently and significantly smaller than those on KTH. Even the pathogenic races or subcultures produced few lesions on Tetep and Carreon.

Tetep and Carreon were planted in our blast nursery with a susceptible variety, Tjeremas, planted as control between every two rows of either Tetep or Carreon. Before any lesion appeared on the young seedlings, they were inoculated with FR-78-16, an isolate from Tetep. The number of lesions on 100 seedlings was counted every other day, about a week after inoculation. Tetep and Carreon had far fewer lesions than Tjeremas (fig. 1). The results agree well with those of greenhouse inoculations.

Table 5. Qualitative (pathogenic races) and quantitative (no. susceptible lesions) pathogenicity of monoconidial subcultures of isolates FR-1, FR-1-138, FR-78, FR-78-16, FR-79, FR-80, isolated from Tetep when inoculated on Tetep (T), Carreon (C), and Khao-teh-haeng 17 (KTH).

Isolate	Races (no.) Total	Races Pathogenic to C	T	KTH	Subcultures (no.) Total	Subcultures Pathogenic to C	T	KTH	Lesions (no./plant) caused by All subcultures C	T	KTH	Pathogenic subcultures C	T	KTH
FR-1	28	11	5	28	160	60	19	160	0.3	0.1	33.9	1.1	1.4	33.9
FR-1-138	12	6	1	12	48	15	3	48	0.8	0.1	56.6	2.8	6.2	56.6
FR-78	8	—	7	8	45	—	44	45	—	5.2	22.6		6.1	22.6
FR-78-16	51	1	17	48	100	1	43	97	0.1	3.6	17.4	8.7	8.9	18.0
FR-79	19	1	11	19	52	1	17	52	0.01	0.7	46.3	0.5	2.5	46.3
FR-80	7	3	1	7	45	7	1	45	0.6	0.2	47.9	4.1	7.9	47.9
All isolates	—	—	—	—	460	84	127	457	0.3	1.5	34.6	1.7	6.6	34.8



1. Number of lesions per 100 seedlings on resistant varieties (Tetep, Carreon) and on susceptible variety Tjeremas adjacent to Tetep (TM*) and adjacent to Carreon (TM†) inoculated with isolate (FR-78-16) from Tetep in the blast nursery.

The pathogenic races from the few lesions on other resistant varieties are being studied in the same manner. Preliminary results show they behave like those on Tetep. Thus the few lesions produced on Tetep and other resistant varieties are probably a genetically controlled reaction between the fungus and the host variety. The original pathogenic fungus races separate into a great number of races in each generation of multiplication and the broad-spectrum resistance of the host operates against most of the races that develop.

DISCUSSION

The preceding experiments confirm the extreme variability in pathogenicity of *Pyricularia oryzae* reported earlier by Ou and Ayad (1968) and Giatgong and Frederiksen (1969). Many races are produced from single lesions and from single-conidial cultures and these races vary greatly in pathogenicity. This phenomenon appears unusual, but it is not unique. Snyder (1933), in studying the variability in *Fusarium*, said, "All evidence from studies upon variation in fungi illustrate the hazard of using single-spore culture in the study of a species exhibiting variation, unless large numbers of monoconidial cultures are employed." Furthermore, "... within a given monoconidial line it was possible to assemble, through the phenomenon of dissociation, a group of cultures almost representative of the range in colony types and virulence exhibited by the entire group of strains. Thus a monoconidial parent has been shown in certain instances by its dissociates to possess the potentialities of most of the type of colony character and virulence of the 15 strains studied." Snyder and Hansen (1954) also said, "Although the principle (variability of fungi) is recognized and accepted, the significance of variability is not yet fully appreciated, nor is it widely utilized." Such statements are quite relevant to the pathogenic variability of *P. oryzae.*

Stakman (1954), after the outbreak of race 15B of *Puccinia graminis tritici*, wrote: "Concepts regarding the dynamics of rust must be broadened and deepened by extensive and intensive investigation." And he observed that, "The number of biotypes of *P. graminis tritici* appears to be comparable to *Ustilago zeae* and *Helminthosporium sativum.* At least 15,000 biotypes of *U. zeae* and at least, 1,000 of *H. sativum* are present in Minnesota and there is no visible limit to numbers."

Because of great pathogenic variability, a particular pathogenic race cannot build up rapidly, and it separates into many races. The population of an original race present in the progeny is small or nil, as indicated by some isolates (Table 2). Since some varieties possess a broad spectrum of resistance, most of the races that develop cannot infect them. Thus only a few lesions, if any, develop. The resistance of such varieties is therefore not broken down by new virulent races.

Tetep and other varieties seem to have stable resistance to blast, but their resistance is neither "race non-specific" nor "horizontal" as defined by Robinson (1969). They react differently to different races; they are resistant to most races but are susceptible to a few, at least in a qualitative sense, though few lesions form on them. This pathogen-host relationship which results in a stable resistance seems to be a new observation.

The level of resistance in such varieties as Tetep depends on how broad the spectrum of resistance is. The more races the varieties can resist, the fewer lesions will develop. As shown in Table 2, Carreon is resistant to the isolates from Tetep. It may be possible to combine the resistance of Tetep and Carreon to further broaden the spectrum of resistance.

Sakurai and Toriyama (1967), and Yunoki et al. (1970) reported that varieties St 1 and Chugoku 31 have "field resistance." In greenhouse and blast nursery tests, both varieties produced a small number of lesions. A genetic mechanism, similar to that described above, may be involved, though they did not study the fungus in detail.

The genetics of resistance in Tetep and other varieties is not known. It would be most interesting to find out whether few strong genes or many genes are involved. The lack of such information demands that extensive and intensive tests be undertaken to select the genotype with broad-spectrum resistance in breeding programs.

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Discussion: Studies on stable resistance to rice blast disease

N. E. BORLAUG: What is the correlation between seedling reactions and the adult plant reactions under field conditions?

S. H. Ou: Generally speaking, seedling reactions expressed as leaf blast and adult-plant reaction expressed as neck blast are the same. We made inoculations several years ago, using 16 isolates and 16 varieties and found the reactions of the young leaves highly correlated to the infections on the neck of the panicle.

N. E. BORLAUG: Are there exceptions to this, such as that the seedlings are susceptible but the adult plants have fairly good field resistance?

S. H. Ou: Yes, one abstract in Phytopathology by U.S. workers indicated the seedlings had different reactions than the adult plants.

N. E. BORLAUG: A vast amount of information has been built up from the rust fungi especially on the wheat stem rust. This information indicates that the seedling type of resistance alone is unreliable from the standpoint of incorporating it into a variety. The obvious approach is to try to combine both types of resistance. But then, you always have the masking effect of seedling resistance genes over the expression of general resistance. The only way of finding out is to grow the variety widely and subject it to the field inoculums. This approach has become more practical as international cooperation has come into being, especially through the international rust nurseries that have been coordinated by the USDA for 20 years.

But still, it is one of the most frustrating problems that faces wheat breeders. I don't think that we are making nearly as much progress as we had expected in maintaining rust resistance. Because so much of our total effort in wheat breeding is devoted to protecting against changes in rust resistance, we cannot find time to improve other characters especially resistance to other diseases.

S. V. S. SHASTRY: If one picks conidia from a susceptible lesion on a susceptible variety such as Tjere Mas, do we expect to find some races which will give a resistant reaction on a susceptible variety?

S. H. Ou: My impression is that the degree of resistance of any variety is the percentage of the potential races that a variety can resist. Take Tjere Mas or Khao-teh-haeng, they are susceptible to, say, 90 percent of the races. If you pick a single spore, it will develop into a number of races also, but most of them will still give a susceptible reaction on Tjere Mas. So you cannot detect the race difference. Only varieties that have a very broad spectrum of resistance are resistant to most new races that develop.

S. V. S. SHASTRY: But do you occasionally get a resistant reaction?

S. H. Ou: Yes, like isolate FR78-16. Out of 100 single conidia, three cannot infect Khao-teh-haeng.

P. WEERAPAT: Would it be possible to combine horizontal and vertical resistance into a single variety by breeding?

S. H. Ou: It is possible. But we don't know if we have horizontal resistance in rice or not.

K. TORIYAMA: In my experience, the progeny of the crosses involving Tetep segregated into a high percentage of highly resistant individuals, and Tetep has many resistant genes. Do you have any plan to determine which individuals have the same stable resistance of Tetep?

S. H. Ou: Since we know so little about genetics of stable resistance, the best way is to test the progenies repeatedly, so as to include all or most of the resistance from Tetep.

L. M. ROBERTS: I know that you have the international blast nurseries project which started around 1963. Do you have corresponding tests for the bacterial leaf blight or tungro virus?

S. H. Ou: For blast, we can do the job easily by sending out seeds. For bacterial leaf blight, it is more difficult because the organism is not air-borne. In certain localities where the disease occurs every year I feel we can carry out cooperative tests. In the absence of international nurseries we have a cooperative project with the University of Hawaii where bacterial isolates from 11 Asian countries were collected and the virulence of these isolates was compared. For tungro, we do not have much information from other countries. We have found three strains of the virus but varietal resistance does not seem to differ greatly. Even with the several strains reported from India in this symposium, the resistant varieties remain more or less resistant. Cooperative testing for tungro, however, is very desirable.

Breeding for resistance to rice tungro virus in India

S. V. S. Shastry, V. T. John, D. V. Seshu

Recent evidence shows that strains of the rice tungro virus vary in virulence, that rice varieties differ in resistance to tungro, that symptomatological polymorphism is determined by the host plant, and that environment influences the expression of disease symptoms and multiplication of the virus. Two new resistant donors, Latisail and Kataribhog, remain resistant even when infected by the most virulent strain; Kataribhog seems to interfere with the multiplication of the virus. If the nitrogen or nutritional status of the plant is favorable, it "recovers" from an initial susceptible reaction. It is hypothesized that the balance between the rate of growth of the host and the rate of viral multiplication determines the final expression of the disease. A breeding program involving the transfer of resistance from Latisail and Kataribhog to the semidwarf indica varieties resulted in the identification of selections combining a high level of resistance, superior grain type, and good plant type. Resistance to tungro in the cross, IR8 x Latisail, is governed by two genes. These genes interact in a complementary way to confer resistance as early as the seedling stage. When either of these two genes are present, an initial susceptible reaction is followed by recovery. This is a phenomenon related to the rate of growth of the host in comparison with the rate of viral multiplication as influenced by the genetic system of the host.

INTRODUCTION

Rice tungro virus, which has been widespread in several southeast Asian countries, was not reported in India until 1967, when a survey team spotted some plants with symptoms of tungro infection (M. D. Pathak, K. C. Ling, J. A. Lowe, and S. Yoshimura, *unpublished*) and Raychaudhuri, Mishra, and Ghosh (1967) reported what was described as a "leaf yellowing" disease. John (1968) conclusively established that the leaf yellowing disease reported by Raychaudhuri et al. (1967) was the same as the tungro virus, on the basis of the vector involved in transmission, the duration of acquisition feeding, non-persistence, and differential reaction on the variety Pankhari 203. Following the establishment of the presence of tungro virus in India, indigenous varieties were screened by the single-plant caging method reported by Everett (1969).

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VARIETAL DIFFERENCES

The typical symptoms of tungro-infected plants are stunting and orange-red foliage. These symptoms are pronounced on a highly susceptible variety like Taichung Native 1. While the symptoms on most of the susceptible indigenous varieties conformed to those on Taichung Native 1, some differed in degree of stunting and in coloration of foliage. In some susceptible varieties, even the symptomatic orange-red foliage did not appear, instead a dark rusty color, leaf rolling, leaf mottling, and necrosis were observed (All-India Coordinated Rice Improvement Project, 1968). Until recently tungro was not recognized as a major disease of rice in India because its symptomalogical polymorphism had not been described and its vector, the leafhopper, was considered a minor pest.

Studies at the International Rice Research Institute identified Pankhari 203 as the most resistant variety to tungro (International Rice Research Institute, 1967), and described Tilakkachary as moderately resistant. Screening tests by the All-India Coordinated Rice Improvement Project confirmed the resistance of Pankhari 203 but not of Tilakkachary—a difference probably attributable to the screening technique used (mass screening vs. single plant caging). Four new sources of resistance were identified: Latisail, Kataribhog, Kamod 253, and Ambemohar (All-India Coordinated Rice Improvement Project, 1968). Resistant varieties showed no stunting or discoloration of leaves after they were infected with tungro by the individual caging technique in which two to three viruliferous leafhoppers (*Nephotettix impicticeps* Ish.) are caged with 14-day-old seedlings.

RICE TUNGRO VIRUS EPIDEMIC IN INDIA

Extensive areas of rice in Bihar and eastern Uttar Pradesh were affected by a leaf yellowing disease in the 1969 wet (kharif) season. Leafhoppers that fed on infected stubbles collected from this region could transmit tungro virus to young Taichung Native 1 seedlings (John, 1970). Under field conditions, the varieties most affected were Taichung Native 1 and Padma, both of which are known to be highly susceptible to tungro. Most local varieties were as infected as Taichung Native 1, with the exception of BR 34, T 9, and NSJ 205 which probably escaped infection. Subsequent tests on T 9 and BR 34 confirmed the susceptibility of these varieties. The only varieties that exhibited relatively satisfactory field resistance were IR8 and Jaya (Table 1). The epidemic brought out several features of tungro that were previously not known. The strain of tungro involved was definitely more virulent than that encountered previously in other parts of the country; furthermore, the male *N. impicticeps*, generally a poor transmitter of the tungro virus, transmitted the virulent strain at least as effectively as the female insect. The more virulent strain was designated as RTV_2 in contrast with the less virulent, RTV_1. A heavy build-up of leafhopper vectors in 1969, the involvement of a more virulent strain of tungro, and extensive cultivation of susceptible varieties resulted in the unprecedented epidemic.

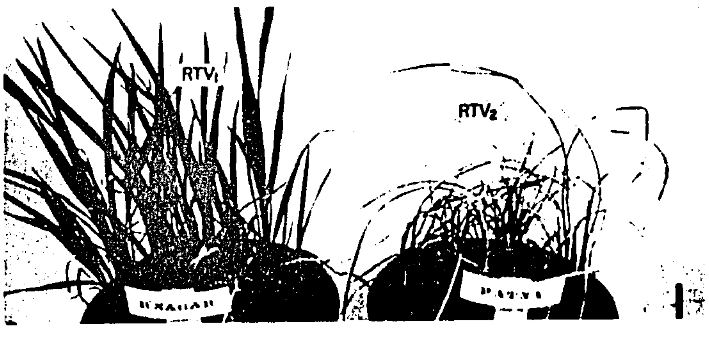
Table 1. Severity of leaf yellowing symptoms as observed in cultivators' fields during the wet season of 1969 in Varanasi, Uttar Pradesh, and Patna and Arrah, Bihar.

Location	Variety	Severity of symptoms [a]	Color of leaves
Varanasi, Patna	Taichung Native 1	++++++	Orange-yellow
Varanasi	Padma	+++++	Orange-yellow
Patna	Padma	++++++	Orange-yellow
Varanasi	Kashi	++++++	Orange-yellow
Patna	N 136	+++++	Orange-yellow
Varanasi	Varuna	+++	Yellow mosaic
Varanasi, Patna	IR8	+++	Light yellow
Varanasi, Arrah	Jaya	++	Light yellow
Varanasi	NSJ 205	+	Light yellow
Varanasi	T 9	0	Green [b]
Patna	BR 34	0	Green [b]

[a]Denotes intensity of symptoms, which include besides leaf color, stunting and necrosis: + = light yellow leaf, less stunting, no necrosis; ++++++ = yellow-orange leaves, greater stunting, and necrosis; 0 = healthy leaves and plants. [b]Escaped infection probably owing to late planting.

VARIATION IN TUNGRO STRAINS

When assayed for tungro virus, samples of infected rice plants collected from different parts of south India between 1967 and 1969, gave a positive reaction on Taichung Native 1. This reaction included orange-red foliage and stunting, but rarely included necrosis of the seedlings or leaves. The strain of tungro virus isolated from the epidemic areas of northeast India, on the other hand, produced severe necrosis on Taichung Native 1 seedlings (fig. 1) and more intensely orange foliage. The varieties Jaya and IR8 did not show necrosis either with RTV_1 or RTV_2. While inoculation of RTV_1 on Pankhari 203, Ambemohar 159, Ambemohar 102, and Kamod 253 failed to produce any symptoms, inoculation with RTV_2 resulted in mild but reversible symptoms. The only varieties which failed to show any symptoms with the two tungro strains were Latisail and Kataribhog (Table 2). All varieties tested and found resistant to RTV_2 were also



1. RTV_2 produces necrosis on Taichung Native 1 seedlings, while RTV_1 produces stunting

Table 2. Differential reactions of some host varieties to RTV_1 and RTV_2.

Variety	RTV_1			RTV_2		
	Foliage	Infection (%)	Necrosis (%)	Foliage	Infection (%)	Necrosis (%)
TN1	Orange	80	20	Bright orange	100	60
Padma	Orange	80	10	Bright orange	100	40
IR8	Dull-orange tips	40	0	Dull-orange tips	40	0
Jaya	Dull-orange tips	40	0	Dull-orange tips	40	0
Pankhari 203	Green	0	0	Reversible light orange	0	0
Ambemohar 159	Green	0	0	Reversible light orange	0	0
Kamod 253	Green	0	0	Reversible light orange	0	0
Ambemohar 102	Green	0	0	Reversible light orange	0	0
Latisail	Green	0	0	Green	0	0
Kataribhog	Green	0	0	Green	0	0

resistant to RTV_1, whereas the converse was not true. From these data, it is evident that RTV_2 is a more virulent variant of tungro virus.

A. Anjaneyulu (*unpublished*) made extensive collections of tungro virus from different regions of India. He found that RTV_1 and RTV_2 could be distinguished on the basis of reactions on Latisail, Pankhari 203, and Taichung Native 1 (fig. 2). For example, the substrain 1A which is more typical of RTV_1 produces mild symptoms only on Taichung Native 1, but not on any known resistant variety. RTV_2, on the other hand, can be further classified into three substrains based on the reactions of the differential varieties and on the degree of virus

Table 3. Reaction of indicator varieties to the substrains of RTV_1 and RTV_2 [I = resistant (immune), virus not recoverable; R = resistant, virus recoverable in traces; S = susceptible; + = severity of symptoms].

Variety	RTV_1 substrain 1A	RTV_2 substrains 2A	2B	2C
Kataribhog	I	I	I	I
Latisail	I	R	I	R
Kamod 253	I	S_{++}	S_{+}	R[a]
Pankhari 203	I	S_{+++}	S_{++}	S_{+}
Ambemohar 159	I	S_{+++}	S_{++}	S_{+}
Ambemohar 102	I	S_{++}	S_{++}	R[a]
Taichung Native 1	S_{+}	S_{++}	S_{++++}	S_{++++}

[a] Unconfirmed.

2. Tungro strains produce symptoms that differ in severity on Taichung Native 1 plants.

recovery on assay. For instance, the substrain 2A, 2B, and 2C produce resistant reactions on both Kataribhog and Latisail with the difference that traces of the virus can be recovered from Latisail after inoculation with 2A and 2C. The substrains 2A and 2B cause almost identical susceptible reactions on the other resistant varieties (Kamod 253, Ambemohar 159, Ambemohar 102) which not only display visible signs of infection, but also contain appreciable quantities of the virus. The substrain 2C seems to differ from 2A and 2B in that it produces a resistant reaction on two varieties, Kamod 253 and Ambemohar 102. Kataribhog is the most distinctive variety. None of the four substrains produces any symptoms on it and the virus is not recoverable from inoculated plants (Table 3). Variation in tungro strains, therefore, seems far more complex than has been recognized (John, 1970).

SYMPTOMLESS CARRIERS

A host's resistant reaction may mean either that the inoculated virus fails to multiply *in situ* or that the genetic system of the host represses the symptoms. Differences in virus strains and symptomalogical polymorphism in host varieties reveal that the tungro syndrome is separable into different components, all of which are seen only in a highly susceptible host. For farmers, a symptomless carrier is as good as a resistant or immune variety which prevents virus from

Table 4. Recovery of RTV_2 after passing through resistant host varieties.

Variety	Symptoms		Recovery of virus[a]
	Stunting	Foliage color	
Kamod 253	Slight	Slightly mottled and/or dull orange	++++
Ambemohar 159	Slight	Slightly mottled and/or dull orange	++++
Pankhari 203	Slight	Slightly mottled and/or dull orange	++++
Latisail	None	Green; rarely tips of older leaves yellow	++
Kataribhog	None	Green	—

[a]As evident from transmission on Taichung Native 1; + = degree of recovery.

multiplying. But the symptomless variety can harbor the virus and communicate it to a susceptible variety. To prevent tungro epidemics a distinction between the symptomless carrier and the resistant variety is particularly important in breeding for tungro resistance.

Resistant varieties were inoculated with RTV_2 and after 3 to 4 weeks of incubation they were tested for the inoculated virus by the acquisition feeding method, with non-viruliferous leafhoppers. These leafhoppers were caged with 14-day-old seedlings of Taichung Native 1. In such tests non-transmission indicates that the titer of the virus is low in a particular resistant variety either because the individual virus multiplied poorly or because it had been inactivated by the host, as in the extreme case of immunity. Tests of this nature conclusively establish that Kataribhog is an unfavorable host for the multiplication of RTV_2, that Latisail is a poor symptomless carrier, and that other resistant varieties are good carriers of virus although they do not exhibit symptoms (Table 4).

MODIFICATION OF SYMPTOMS

When the leaf yellowing problem of northern India was surveyed in the kharif season of 1969, the symptoms of tungro were more pronounced in fields that were poorly managed. At AICRIP, some tungro-infected seedlings apparently recovered after transplanting. Since nutrient supply is the major environmental difference between a crowded seedbed in the greenhouse and the lower plant density of the transplanted field, it was suspected to influence the expression of symptoms. When rice seedlings were reared in nitrogen culture solutions and inoculated with tungro, the symptoms were more pronounced in the low-nitrogen treatments, proving that the nutritional status of the host plant has a decisive influence on the symptomatology of tungro infection.

A pot experiment with nitrogen levels ranging from 0 to 200 kg/ha N was laid out at AICRIP in the 1971 dry season. In all treatments, a 14-day-old seedling

Table 5. Effect of nitrogen level on the development of tungro on Taichung Native 1.

Nitrogen level (kg/ha)	Reaction (%)			
	Necrosis	Diseased[a]	Partially recovered[b]	Fully recovered[c]
0	63	37	—	—
50	22	49	22	7
100	24	55	3	18
150	20	34	23	23
200	16	43	16	25

[a]Foliage: orange, Stunting: extreme, Virus recovery: 40%; excludes those dead and partially recovered. [b]Foliage: orange-green, Stunting: moderate, Virus recovery: 80%. [c]Foliage: green, Stunting: slight, Virus recovery: 0%.

was placed in a cage with two to three viruliferous leafhoppers. All plants, irrespective of nitrogen treatment, produced disease symptoms initially. At later stages, however, disease symptoms were accentuated in the low nitrogen treatments (Table 5). The data confirm those of the preliminary nutrient culture experiment. About 63 percent of the infected plants were necrotic and the rest developed pronounced orange-yellow foliage and severe stunting in the zero-nitrogen treatments; necrosis was low in the high-nitrogen treatments. While all plants without nitrogen showed disease symptoms, even the low nitrogen level of 50 kg/ha N enabled 30 percent of the plants to recover partially or fully At the highest nitrogen level, 40 percent of the plants were apparently normal (fig. 3).

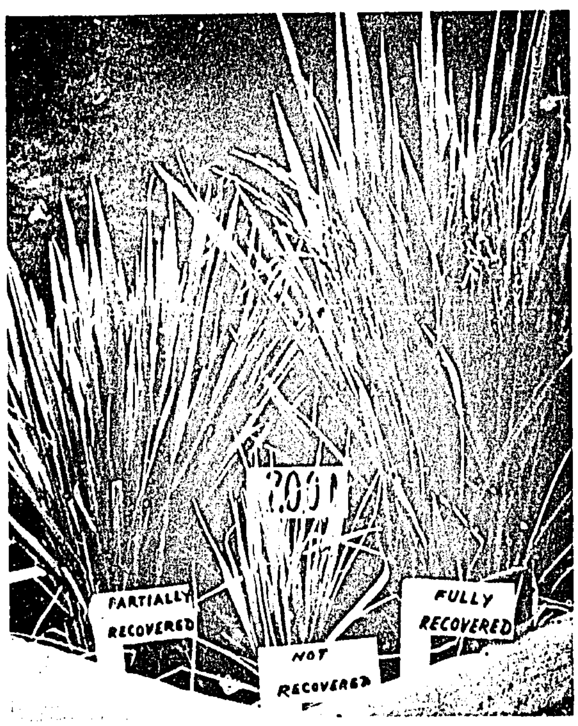
Most plant diseases produce more pronounced symptoms on the host that has better nutrition than on the host that has poor nutrition, but tungro is an exception. Does added nitrogen retard the expression of typical symptoms of tungro or does it reduce the multiplication of the virus *per se*? Plants recovered from high-nitrogen treatments, when used for acquisition feeding, transmitted less virus. This could either mean that virus multiplication is impeded in host plants with higher nitrogen status or that the enhanced growth of the host has a diluting effect on the virus, or both. While the high-nitrogen plots recovered from viral symptoms, they were distinctly later in maturity than the uninfected check plots (fig. 4).

The inference of Y. L. Nene and R. A. Singh (*unpublished*) that the leaf yellowing malady of northeast India is non-infectious was based on their observation that plants affected by the symptoms, when transplanted in Pantnagar, recovered and put out new leaves and tillers that were dark green in color. The observation at AICRIP clearly reveals that tungro-infected plants do recover and that recovery does not refute the viral nature of the malady. The infection studies with the stubbles collected from Uttar Pradesh (John, 1970) clearly establish the viral nature of the problem.

INCORPORATING TUNGRO RESISTANCE INTO SEMIDWARFS

Earlier efforts to transfer tungro resistance from Pankhari 203 into dwarf plant types were relatively unsuccessful (All-India Coordinated Rice Improvement Project, 1968). Consequently, the resistant donors identified at AICRIP were used in breeding. Latisail and Kataribhog were eventually preferred because of their resistant reaction to the more virulent strain of tungro.

Latisail, Kataribhog, and Ambemohar 159 were used as donors for tungro resistance, and Jaya, IR8, and Cauvery as donors for plant type. A large population of F_2 plants from each cross was screened by individual plant caging tests with two to three viruliferous leafhoppers. Plants which exhibited susceptible reaction were discarded and the rest were planted in the field to evaluate plant type and other agronomic characters. Seeds from the selected F_2 plants were divided into two sets, one for greenhouse screening for tungro resistance, the other for field studies. In the screening test, even if only one plant out of 10 in a progeny exhibited susceptibility, the relative F_4 progeny in the field is discarded. About 30 dwarf plant-type selections with near immunity to tungro were identified from the screening of over 5,000 F_2 plants, 578 F_3 progeny, and 493 F_4 progeny of the cross IR8 x Latisail (Table 6). During the dry (rabi) season, 1971, 872 progeny of the cross were intensively screened for resistance.



3. Seedlings of Taichung Native 1, originally infected by tungro "recover" under high nitrogen status.

The cross, Cauvery x Ambemohar 159, was extremely poor and was discarded. Resistant selections from IR8 x Latisail have good plant type and vigor, but their grain type is not so good. On the other hand, selections in the cross, Jaya x Kataribhog, had good grain type, but most of them had poor vigor. Both these crosses produced a high level of resistance in semidwarf plant types. To reciprocally cover the deficiencies of the above primary crosses, a double cross [(IR8 x Latisail) x (Jaya x Kataribhog)] was attempted. Materials with promising plant type, vigor, resistance, and grain type are encountered in this cross. Resistant selections from several crosses are being further improved for grain type by appropriate hybridizations.

INHERITANCE OF RESISTANCE

Genetics of resistance to tungro (RTV_2) was studied in the cross, IR8 x Latisail. The test material included the two parents, the F_1 hybrid, and an F_2 population consisting of 568 plants. Resistance was determined through the single-plant caging technique of artificial inoculation. Individual 14-day-old seedlings were each caged with two to three viruliferous adults of *N. impicticeps* for 24 hours. Test plants were scored for resistance 20 days after inoculation on the basis of orange coloration of the leaves and vein clearing. The seedlings that showed no

4. Initial infection by tungro delays maturity of Taichung Native 1, although a high nitrogen status leads to "recovery" of the host.

Table 6. Reaction of select F_4 progeny in the cross IR8 x Latisail to tungro virus.

Selection no. in F_3	Reaction in F_3		Selection no. in F_4	Reaction in F_4[a]	
	Susceptible	Resistant		Susceptible	Resistant
98	9	20	98-29	0	9
147	4	20	147-5	0	8
173	0	36	173-29	0	9
214	11	20	214-6	0	9
222	1	10	222-1	0	19
222	-	—	222-10	0	10
222	-	—	222-47	0	10
222	-	—	222-56	0	10
222	-	—	222-63	0	10
267	9	20	267-28	0	8
331	0	10	331-3	0	9

[a]Data from single-plant caging technique. Acquisition feeding 24 hours, inoculation feeding 24 hours, scored 20 days after inoculation.

symptoms after the first inoculation were re-inoculated 10 days after the first inoculation to prevent "escapes" from being misclassified as resistant. The single-plant caging technique by itself minimizes the chances of misclassification and hence was preferred to mass screening. After being classified for resistance, the two groups of seedlings, "resistant" and "susceptible," were planted separately. The plants were again observed for resistance 40 days after planting (i.e. about 60 days after inoculation); at this stage, stunting was considered as an additional criterion for susceptibility.

The results indicated that resistance to tungro virus in IR8 x Latisail is dominant (Shastry et al., 1971). The F_1 hybrid showed a resistant reaction. In the F_2 population, the pre-planting scores of seedlings indicated that 339 were resistant and 229 were susceptible, a ratio that fits into the digenic complementary ratio of 9:7 (Table 7). The post-planting observation, however, revealed that 529 plants were resistant and 39 susceptible, conforming to the duplicate gene ratio of 15:1. As mentioned earlier, the distinction between resistant and susceptible seedlings was preserved by planting them separately. This facilitated the detection of the course of changes within each group, which led to an altered ratio for segregation for resistance in the second observation. The resistant group remained normal and healthy throughout, but certain of the plants from the susceptible class "recovered" and were normal green. Thus the segregation ratio changed from the first to the second observation. Some susceptible plants that were susceptible in the early scoring turned out to be resistant later, but those resistant at the beginning did not become susceptible later. When the group that was resistant in the second observation was subdivided into "resistant" and "recovered," the segregation for the three phenotypes fell perfectly into the digenic ratio of nine resistant: six recovered: one susceptible (Table 8). It therefore does not appear that separate genes are involved in resistance at different stages. On the other hand, resistance is basically governed

Table 7. Segregation for resistance to RTV_2 in the F_2 of IR8 x Latisail.

Date of observation (days after inoculation)	Plants (no.) Total	Resistant Observed	Resistant Expected	Susceptible Observed	Susceptible Expected	Expected ratio	χ^2	P
20	568	339	319.5	229	248.5	9:7	2.72	0.10 ~ 0.05
60	568	529	532.5	39	35.5	15:1	0.37	0.75 ~ 0.50

by two dominant complementary genes, recovery from an initial susceptible condition is effected in the presence of either one of these two dominant genes, and the plants remain susceptible only when both genes controlling resistance are recessive.

INTERACTION OF HOST, PATHOGEN, AND ENVIRONMENT

Genetically, when infected even by the least virulent strain of tungro, susceptible hosts like Taichung Native 1 permit establishment of viral infection, rapid multiplication of the virus in the hosts, and expression of severe symptoms of the disease. Resistant varieties—Pankhari 203, Kamod 253, Ambemohar 159, Latisail, and Kataribhog—restrict the establishment of the disease and the reaction of resistant hosts is influenced by the genetic constitution of the viral strains.

The host's growth stage and nutritional status regulate the expression of symptoms. When very young (7-day-old) seedlings are used for inoculation, a susceptible reaction occurs even on a resistant variety. Even when the viral infection is established in a susceptible variety like Taichung Native 1, better nutritional status permits at least part of the population to recover. While two complementary genes interact to inhibit the establishment of the virus even in 14-day-old seedlings, the presence of just one of the two resistant genes of Latisail ensures their recovery into apparently healthy plants.

Table 8. Segregation for three phenotypes at second observation (60 days after inoculation) for resistance to RTV_2 in the F_2 generation of IR8 x Latisail.

	Plants (no.) Resistant	Recovered	Susceptible	Total	χ^2	P
Observed	339	190	39	568	4.02	0.25 ~ 0.10
Expected (9:6:1)	319.5	213.0	35.5	568		

The host's rate of growth is the result of interaction between the host's genetic system and its environment. The rate of virus multiplication is determined by the genetic constitution, the growth stage, and the nutritional status of the host. The balance between the host's rate of growth and rate of virus multiplication determines the final expression of the disease. In 7-day-old seedlings, for example, the host's growth is so overpowered by virus multiplication that even the resistant genes can not function. In 14-day-old seedlings unless both genes for resistance are present in the host, a resistant reaction cannot be seen. At a later stage, during tillering for example, even if the host has one of two resistant genes, the virus activity is low in relation to host growth and the plants recover from an initial susceptible condition.

Segregation for plant height (talls and dwarfs) was studied in the F_2 population, but only the resistant group (first observation) was tested since classifying for plant height is difficult in susceptible plants. The resistant plants segregated in a monogenic ratio of three talls (258 plants) to one semidwarf (81 plants) with a good fit ($\chi^2 = 0.22$; P between $0.75 \sim 0.50$), indicating thereby that plant height is inherited independently of resistance to rice tungro virus. This is borne out by the identification of dwarf resistant plants discussed above.

Preliminary studies at IRRI on the cross, Pankhari 203 x Taichung Native 1, indicated that resistance in Pankhari 203 is governed by two complementary dominant genes (International Rice Research Institute, 1967). In the study of backcross progeny of Pankhari 203 x IR8 and Pankhari 203 x Taichung Native I at IRRI, certain plants identified as resistant became diseased at a later growth stage and *vice versa*. It was, therefore, concluded that resistance at seedling and adult stages may have to be considered separately in the genetic analysis of tungro resistance (International Rice Research Institute, 1968). In the present studies involving IR8 x Latisail, the change from first to second observation was uni-directional, i.e., "susceptible" becoming "resistant"; there were no instances of "resistant" plants becoming "susceptible." Hence, the same genes governing resistance at the seedling stage, as interpreted earlier, could account for the altered ratios at second observation.

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Discussion: Breeding for resistance to rice tungro virus in India

A. TANAKA: How do you differentiate symptoms of nitrogen deficiency from tungro symptoms?

S. V. S. Shastry: Very simple. Nitrogen deficiency cannot be transmitted by leafhoppers. It is possible that rice tungro virus infection reduces nitrogen uptake.

A. T. PEREZ: In a farmer's field, we found that an application of 50 kg/ha N to IR5 infected with rice tungro virus and which exhibited general yellowing, resulted in recovery, but heading was delayed by 1 to 2 weeks. We suspected that nitrogen deficiency aggravated the symptoms of rice tungro virus.

S. V. S. Shastry: Our results are similar. The symptoms of rice tungro virus are enhanced by nitrogen deficiency.

B. R. JACKSON: Do you have problems in obtaining 100 percent infection on susceptible parents?

S. V. S. Shastry: No. The data consistently show that we can produce 100 percent infection on Taichung Native 1.

P. WEERAPAT: You have used leaf yellowing to identify the resistant plants. How do you record the leaf yellowing of infected plants?

S. V. S. Shastry: We use not only the leaf coloration, but also the rice tungro virus content of the leaves so that the symptomless carriers are excluded. For instance, Kataribhog is resistant since it produces no symptoms, but it also does not permit viral multiplication.

M. J. ROSERO: What is more important, resistance to the tungro virus or resistance to the vector? Does the vector cause a direct feeding damage greater than the tungro virus in India?

S. V. S. Shastry: The best strategy is to incorporate resistance to both. The position we take may depend upon the aggressiveness of the biotype of the insect and virulence of the strain of rice tungro virus. It is unsafe to rely upon insect resistance as an insurance for tungro resistance, although this may at best be taken as a starting point.

E. A. SIDDIQ: I understand that resistance to tungro virus and to its vector are governed by different genes. Have you come across any variety showing resistance to both? Are the genes linked?

S. V. S. Shastry: It is true that among the varieties used as donors, we have resistance to either or both the vector and rice tungro virus. The genetic relationships have not yet been completely investigated. Latisail is resistant to both the vector and virus.

Y. L. WU: Varieties Latisail and Kataribhog appear resistant to tungro virus. I would like to know the major agronomic characters of these two varieties. Do you believe that resistance to tungro virus also has some correlation with later maturity and tall plant height?

S. V. S. Shastry: Latisail is a photoperiod-sensitive, high tillering, fair-grained commercial variety grown in West Bengal. It is a reasonably good variety among the tall varieties. Kataribhog has better grain, but has a lower yield potential. It is also a tall variety. In our breeding program we found better plant types in the crosses involving Latisail. I do not think lateness and tallness are correlated with virus resistance. We have been able to combine earliness and short stature with resistance to tungro.

R. FEUER: With your experience in India would you recommend that farmers use nitrogen to reduce the effect of tungro infection?

S. V. S. Shastry: The data from India clearly indicate that plants infected by tungro do "recover." The recovery is best when nitrogen fertilizer is added close to the time of infection.

S. H. Ou: What kind of consistency can you get in determining the percentage of infection of a variety or a hybrid population? You showed that nitrogen level affects the percent of recovery from tungro. Would this affect your readings in your genetic studies?

S. V. S. Shastry: Consistency is very good when one adopts, as we do at AICRIP, the single-plant caging technique. Consistency is not good under mass screening. The fact that "recovery" from an initially susceptible reaction is related to the genetic constitution (plants having one of the resistance genes) clearly illustrates that, instead of interfering with the genetic interpretation, it has added a new dimension to the genotype-environment interaction of the system.

G. S. Khush: Have you verified your results on segregation by progeny tests?

S. V. S. Shastry: Not yet. This is being done.

Breeding for resistance to major rice diseases in Japan

Kunio Toriyama

Since the establishment of scientific breeding in Japan, great efforts have been made to develop the varieties with resistance to various diseases, especially to blast and bacterial leaf blight. Blast resistance genes such as *Pi-k*, *Pi-ta*, *Pi-ta*^{2}, *Pi-z*, and *Pi-z*^{t} have been incorporated into the genetic background of Japanese lowland varieties. Recently, specialization of the pathogenic races of the blast fungus was recognized and emphasis was placed upon "field resistance" in addition to "true resistance." Use of differentiation strains of the pathogen for bacterial leaf blight, revealed the need for resistant varieties that have the wide-range resistance gene of Wase-aikoku 3 or "Lead rice" and resistance to lesion enlargement. Varieties incorporating the stripe resistance gene of indica varieties are now being developed.

INTRODUCTION

The diseases that take a large toll from rice production in Japan are blast due to *Pyricularia oryzae* Cav., bacterial leaf blight due to *Xanthomonas oryzae* (Uyeda and Ishiyama) Dowson, sheath blight due to *Corticium miyabeanus* (Ito *et* Kuribayashi) Drechsler ex Dastur, yellow dwarf due to a mycoplasma-like organism, and the virus diseases such as stripe, dwarf, and black-streaked dwarf.

The most economical protection from diseases is planting resistant varieties. Great efforts have been made in Japan to develop varieties possessing resistance to major diseases, especially to blast and bacterial leaf blight. Although some outstanding work has been done in this field, rice disease investigation in Japan emphasized chemical control after World War II. Recently, use of fungicides has led to some unexpected problems: the direct toxicity to farmers who spray or dust, residual toxicity in food, and environment pollution. Breeding of resistant varieties, therefore, is an urgent agricultural need.

BLAST DISEASE

Progress in breeding for resistance

Progress in breeding for blast resistance in Japan was reviewed by Ito (1965), Ito and Takakuwa (1965), Nagai (1966), Hirano (1967) and, to some extent, by Ou and Jennings (1969). As they have pointed out, the breeding means were classified into four categories as follows: concentration of genes for resistance

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in Japanese native varieties, use of resistance in Japanese upland rice, incorporation of resistance genes from Chinese varieties of japonica type, and incorporation of resistance genes from indica varieties.

Concentration of genes for resistance in Japanese native varieties. Since systematic breeding of rice varieties began, many crosses among native varieties have been made to develop blast resistant varieties. As a result, some outstanding varieties such as Norin 22, Norin 23, and Yamabiko were developed for southwestern Japan, Rikuu 132 and Fujiminori for northeastern Japan, and Ishikari-shiroke for northern Japan.

Of these varieties, Ishikari-shiroke possesses the "true resistance" gene *Pi-i*, and Yamabiko and Fujiminori possess the gene *Pi-a* (Ezuka et al., 1969*a*). The expression of the resistance of the gene *Pi-i* has been moderately effective till now, but the gene *Pi-a* does not express itself because of the widespread virulent fungus races for the *Pi-a* gene.

In general, the resistance of these improved varieties is more stable and higher than those of their parental varieties, but they are often affected slightly by blast due to their moderate degree of resistance. By use of these varieties as parents, some moderately resistant varieties were rather easily developed. The resistance of these varieties was assumed to be controlled by polygenic system, except for the gene *Pi-i*.

Use of resistance in Japanese upland rice. Some Japanese upland rice varieties possess a much higher level of resistance to blast than lowland varieties. In 1912, Iwatsuki attempted to incorporate the resistance of the upland rice Sensho into lowland varieties by single cross, but the cross was discarded in an early generation because no promising offspring resulted (Esaka et al., 1969).

In 1922, Iwatsuki again employed Sensho as a female parent for crossing with a lowland variety, Kinai-ban 33. In this attempt, he planned to use multiple crossing with lowland varieties to eliminate the undesirable characters of upland rice. After crossing four times with lowland varieties, Futaba was developed. It possessed high resistance to blast and the characteristics of lowland rice (Iwatsuki, 1942). From the cross between Futaba and Norin 6, Shuho was developed, and then Shuho was crossed with Norin 22. From this cross, five outstanding varieties, Wakaba, Wase-wakaba, Kogane-nishiki, Ukon-nishiki, and Homare-nishiki, were developed. These five varieties were widely planted in the mountainous region of southwestern Japan because of their stable and moderately high resistance to blast (Ujihara, 1960). They are now being used as the gene sources of blast resistance.

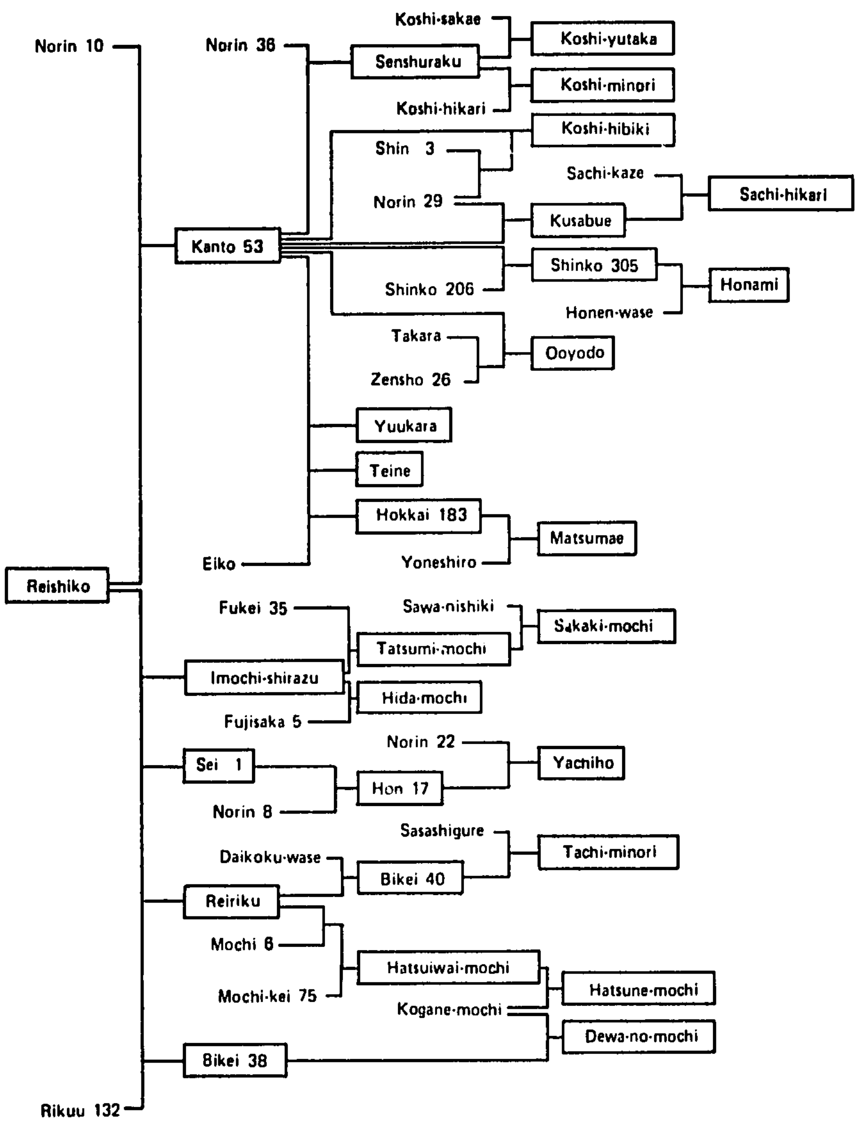
By the injection inoculation method devised by Yamasaki and Kiyosawa (1966), the only true resistance genes found in these varieties derived from Sensho was the *Pi-a* gene (Ezuka et al., 1969*a*). The resistant reaction of these varieties, however, was clearly observed when fungus races C-6 and N-6 were inoculated by the spray inoculation method (Nakanishi and Nishioka, 1967; Yamada, Matsumoto, and Kozaka, 1969). The fungus races C-6 or N-6 were seldom found in the field, so the moderately high resistance of these varieties may not be due to the action of a true resistance gene to C-6 and N-6. The resistance observed in the field may be due to the simultaneous effect of the unknown gene, however.

Incorporation of resistance genes from Chinese varieties of japonica type. By 1917, it had been observed that some foreign rice varieties including Chinese varieties possessed extremely high resistance compared with that of Japanese lowland varieties, but no attempts to use the high resistance of foreign varieties were made until 1930, when a Chinese variety Usen was crossed with a Japanese variety Kyoto-asahi by Nakamori and Kozato (1949). After the second back-crossing in this breeding program, the attempt failed chiefly because of sterility in the progeny.

Reishiko and To-to, two Chinese varieties of japonica type, were found to be highly resistant to blast (Matsuo, 1952). They were used as sources of resistance to avoid the hybrid sterility that often occurred in japonica-indica crosses. Hybridization with these two introductions produced Kanto 51 to Kanto 55 (Koyama, 1952). Thus, several new varieties were developed in the breeding programs with Kanto 51 and Kanto 53 as shown in figure 1 (Sugitani and Hashimoto, 1951; Ito et al., 1961; Kunitake et al., 1962*a*, *b*; Soga et al., 1963; Tohoku Agr. Exp. Sta. Lab. Crop, 1964*a*; Shirakura et al., 1965; Toriyama, Tsunoda, Wada, Futsuhara, Tamura, and Fujimura, 1967; Higuchi et al., 1967*a*, *b*; Ichikawa et al., 1967*a*, *b*, *c*, 1969; Nishio, Esaka, Nakamori, Komura, Ito, and Konomoto, 1968; Samoto and Ouchi, 1968; Tsunoda et al., 1970). These new varieties possess the blast resistance gene *Pi-k* from parental Chinese varieties, and some of them show new gene combinations with the genes of domestic varieties. The genotypes that were recognized are *Pi-k* type, *Pi-a*, *Pi-k* type, and *Pi-i*, *Pi-k* type (Ezuka et al., 1969*a*).

The first varieties derived from Kanto 53 were Kusabue, Yuukara, and Senshuraku. These varieties were not only highly resistant to blast but also had a high yielding ability and good grain quality. Within 3 to 5 years after their release, however, they were affected more severely by blast than Japanese domestic varieties, which had no true resistance genes. The damage on the varieties with *Pi-k* gene was recognized as being due to the rapid propagation of fungus races virulent to *Pi-k* (Iwata et al., 1965; Matsumoto et al., 1965; Kosaka, 1966). When these varieties were bred, there were no fungus races virulent to the *Pi-k* gene. Breeders, therefore, could not determine the degree of field resistance of the materials tested because all the materials with the *Pi-k* gene showed no lesions. The reason why these varieties were severely attacked by new virulent races might be due to a lack of field resistance which is not protected by genes for "true resistance."

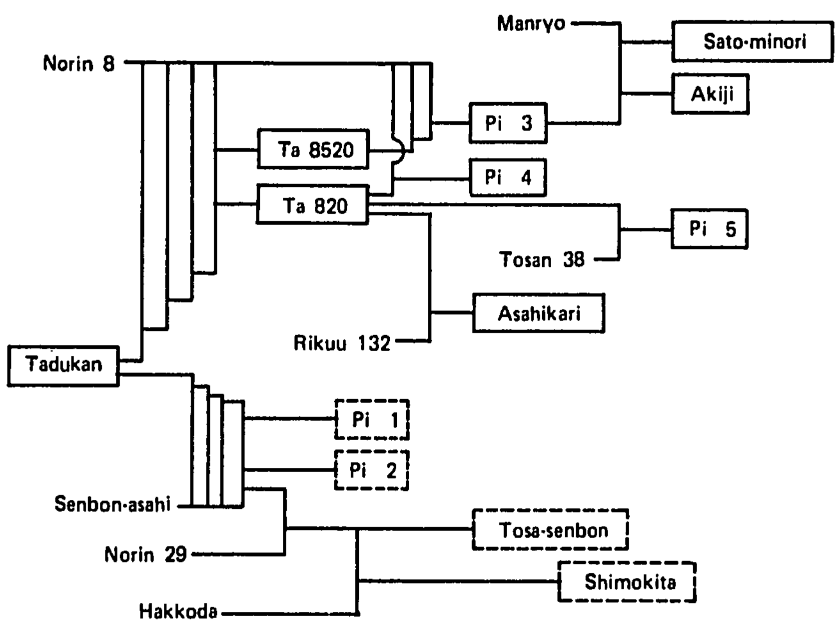
In the field where the varieties derived from Reishiko and from To-to were severely affected by blast, some selections that had a Chinese variety, Hokushi-tahmi, as a parent showed high resistance (Ujihara, Nishio, and Tanabe, 1955; Ujihara and Nakanishi, 1960). Therefore, selections derived from Hokushi-tahmi were employed as a new source of resistance to blast races virulent to *Pi-k* gene. Kongo and Minehikari were developed from these crosses (Ujihara and Tanabe, 1959; Ujihara et al., 1966; Ishizumi, Mizuno, and Kawai, 1965;



1. Lineage of varieties possessing the *Pi-k* gene (names in boxes) derived from Reishiko.

Miyazaki et al., 1966; Nishio, Esaka, Nakamori, Komura, Ito, Konomoto, Takamatsu, and Yanagida, 1968). These newly developed varieties possess not only the *Pi-k* gene but also the *Pi-m* gene (Kiyosawa, 1968*a*), in addition to field resistance from domestic varieties.

Recently, some recommended varieties derived from Reishiko were developed. These varieties, such as Matsumae and Tatsumi-mochi, possess the *Pi-k* gene and field resistance, and show moderate resistance even on exposure to fungus races that are virulent to the *Pi-k* gene (Ezuka et al., 1969*b*).



2. Lineage of varieties possessing *Pi-ta* (names in boxes with broken lines) or *Pi-ta*^{2} (names in boxes with solid lines) derived from Tadukan.

Incorporation of resistance genes from indica varieties. High sterility often occurs in japonica-indica hybrids because of remote phylogenical distance (Terao and Midusima, 1942). Sterility makes it difficult to incorporate resistance genes from indica into japonica varieties.

After many studies on hybrid sterility, it was found that the sterility in backcrossed offspring was caused by the cytoplasmic effect of the maternal indica parent, and that the degree of sterility in hybrids varied with the maternal indica variety employed (Kitamura, 1962*a*, *b*, *c*, *d*). To eliminate hybrid sterility in backcrossed offspring, Kitamura (1961) proposed the use of indica varieties as a male parent in the first hybridization program or the use of japonica varieties as a female parent in backcrosses. Thus, Pi 1 to Pi 5 possessing japonica type and high resistance to blast were developed by the backcross method, in which a Philippine variety Tadukan was employed as a donor (Shigemura and Kitamura, 1954; Kitamura, 1962*a*). The expression of resistance of Pi 1 and 2 is due to the gene *Pi-ta* (Kiyosawa, 1966) and that of Pi 3 to Pi 5 is due to the *Pi-ta*^{2} (Kiyosawa, 1967*c*). Both *Pi-ta* and *Pi-ta*^{2} genes come from Tadukan and are recognized as allelic to each other. As the next step after development of Pi 1 to 5, recommended varieties Shimokita and Tosa-senbon that have the *Pi-ta* gene, and Satominori and Akiji that have the *Pi-ta*^{2} gene were released (fig. 2) (Kariya et al., 1966; Matsuzawa, Maeda, and Yokoyama, 1968; Toriyama, Kariya, Washio, Sakamoto, Yamamoto, and Shinoda, 1968). Yashiro-mochi derived from a Taiwan variety, Oka-ine, was found to have the same gene, *Pi-ta* as Pi 1 (Kiyosawa, 1969). The extension of varieties possessing the *Pi-ta* or *Pi-ta*^{2} gene is now under way, and the change from resistance to susceptibility of these varieties has seldom been reported (Toriyama, 1965).

The resistance of a U.S. variety, Zenith, was also employed. Fuku-nishiki has the *Pi-z* gene of Zenith (Tohoku Agr. Exp. Sta. Lab. Crop, 1964*b*; Kiyosawa, 1967*b*). The virulent fungus races to *Pi-z* have already been found in some places where Fuku-nishiki was recommended (Hirano, Kato, and Hashimoto, 1967; Mogi and Yanagida, 1967).

Some attempts have been made to breed varieties with resistance to all major races of blast in Japan. Two multi-racial resistant varieties of the japonica type, Toride 1 and Toride 2, were selected from the crosses of Norin 8, which was backcrossed four times as a recurrent parent with TKM-1 and CO 25 as donors, respectively (Nagai, Fujimaki, and Yokoo, 1970; Kiyosawa and Yokoo, 1970; Yokoo and Kiyosawa, 1970). Both Toride 1 and Toride 2 show high resistance, due to the *Pi-z'* gene of indica varieties, to all the fungus strains collected from the paddy field. The gene *Pi-z'* is allelic to and stronger than *Pi-z* of Zenith in the expression of resistance (Yokoo and Kiyosawa, 1970).

When breeders try to incorporate the blast-resistance genes of newly introduced varieties, they must identify the kind of resistance gene in given varieties, but identification of resistance genes is difficult because of the complex gene constitution of the varieties (Fujimaki and Yokoo, 1968). Actually, the genes introduced from foreign varieties seem to be located at a few loci because the resistance genes identified to date could be explained by assuming three loci for *Pi-k*, *Pi-ta*, and *Pi-z*.

Recently, a new kind of multi-racial resistance gene or genes was identified in the Indonesian varieties Tjina and Tjahaja and the Malaysian variety Milek Kuning (Fujimaki and Yokoo, 1971). Whether the newly introduced resistance genes are the same is not yet known. Nevertheless, they will be used as new sources of blast resistance in the breeding program.

True resistance to blast

There are two types of resistance to blast: true resistance and field resistance. True resistance is characterized by specific reaction of a pathodeme-pathotype. The resistance or susceptibility of varieties that have resistance of this kind can be determined by their reactions to specific races of the pathogen. In Japan, genotypes of varieties resistant to blast were estimated by the reactions to the injection testing method (Kuribayashi and Terasawa, 1953) using seven standard fungus isolates devised by Yamasaki and Kiyosawa (1966). By the injection method, the varieties can be classified into 12 reaction types: Shin 2 type, Aichi-asahi type, Kanto 51 type, Ishikari-shiroke type, Yashiro-mochi type, Pi 4 type, Fukunishiki type, Toride 1 type, To-to type, Shinsetsu type, Shimokita type, and Zenith type (Kiyosawa, 1967*a*; Yokoo and Kiyosawa, 1970).

To divide the reaction types into more detailed categories than the above system, additional fungus strains can be employed. Spraying fungus isolates belonging to race C-8 on rice plants can divide the varieties of Kanto 51 type and To-to type into two groups, one that possesses *Pi-i* gene and the other that does not (Yamada, 1969; Ezuka et al., 1969*a*).

By injection of two mutant fungus strains, Ina 168-a$^+$-k$^+$ and Ina 168-a$^+$-k$^+$-m$^+$, the varieties belonging to Kanto 51 type and To-to type can be classified into two groups, one with *Pi-m* and the other without it (Kiyosawa, 1968*a*; Ezuka et al., 1969*a*).

Furthermore, by spraying C-6 isolates, the varieties belonging to Shin 2 type, Aichi-asahi type, Ishikari-shiroke type, and Shinsetsu type can be divided into two groups, one with a hypersensitive reaction and the other without it (Nakanishi and Nishioka, 1967). This reaction may be controlled by major gene or genes because all the varieties showing the reaction are descendants of the upland variety Sensho. The varieties classified by these testing methods are listed in Table 1.

The linkage relationships of resistance genes have been studied by the genic analysis method with marker genes (Nagao and Takahashi, 1963) and by the chromosome reciprocal translocation method (Nishimura, 1961). The results indicate that four linkage groups were involved (see the paper by S. Kiyosawa elsewhere in this book).

The gene *Pi-s*, one of the multi-racial resistance genes (Yunoki et al., 1970*b*), was found in the variety 65A15 by selecting among individuals of variety Asahi seeded in the blast nursery by Sekiguchi and Furuta (1967). It is not yet certain whether resistance of this variety was caused by natural crossing or by spontaneous mutation. By the reciprocal translocation method close linkage was observed between *Pi-s* and RT 7.8 and RT 8.12 probably on Chromosome 8 (H. Shinoda, *personal communication*).

Field resistance to blast

In blast nursery tests, resistance to blast differs among varieties that have the same genotype for true resistance genes (fig. 3). These differences within the same genotypes for true resistance may be caused by the differences in the

Table 1. Japanese paddy rice varieties classified by the genotype for blast resistance.

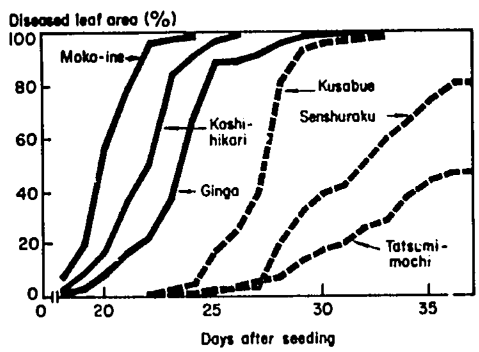
Reaction type	Genotype estimated	Varieties
Shin 2	+	Akibae, Chidori, Chikuma, Chiyo-hikari, Chiyo-sakae*, Choo-kai, Dewa-minori, Ginga*, Harima, Hatsu-nishiki, Honen-wase, Iburi-wase, Kameji 1, Kame-no-o, Kinki 33, Kogane-maru, Kogane-nishiki*, Koshiji-wase, Koshi-hikari, Koshi-sakae, Manryo, Nan-ei, Nihonkai, Norin 1, Norin 6, Norin 8, Norin 12, Norin 20, Norin 22, Norin 23, Norin 25, Norin 29, Norin 37, Norin 48, Omachi, Ooita-mii 120, Rikuu 132, Sachi-midori, Sachi-watari, Sen-ichi, Seto-honami, Shin 2, Shinju*, Shinriki, Shin-yamabuki, St 1, Takenari, Tone-wase, Tosan 38, Toyosato, Ukon-nishiki*, Wakaba*, Wase-aikoku 3, Yachikogane, Yaeho,

Continued on next page.

Table 1. *Continued.*

Reaction type	Genotype estimated	Varieties
		Yamaji-wase*, Yamase-nishiki, Iwai-mochi, Saigoku-mochi Shimehari-mochi, Shin-tsuru-mochi, Suzuhara-mochi, Yama-fuku-mochi
Aichi-asahi	*Pi-a*	Aichi-asahi, Akage, Akebono, Akibare, Ariake, Asahi, Ayan-ishiki*, Chukyo-asahi, Chusei-shin-senbon, Eiko, Fujiminori*, Futaba, Hakkoda, Hasiri-bozu, Hatsushimo, Homare-nishiki*, Hoyoku, Jukkoku, Kinmaze, Kinpa, Kochikaze, Kyoto-asahi, Nagiho, Norin 17, Norin 18, Norin 21, Norin 27, Norin 41, Obanazawa 6, Oirase, Sasahonami, Sasa-nishiki, Sasa-shigure, Sawa-nishiki, Senbon-asahi, Sendai, Shin 5, Shiranui, Shuho*, Tachikara, Takara, Tokai-senbon, Towada, Toyo-chikara, Tsukuba-nishiki, Wase-wakaba*, Yamabiko, Zensho 26, Zuiho, Aratama-mochi, Kogane-mochi, Kotobuki-mochi, Norin-mochi 5, Niji-mochi, Nishiki-mochi, Otome-mochi, Shinano-mochi 3, Tancho-mochi, Yuki-mochi
Ishikari-shiroke	*Pi-i*	Asashio, Fujisaka 5*, Fukuyuki, Gohyakumangoku, Hama-minori, Ishikari-shirokem, Kitaminori, Koshi-homare, Miya-zaki 7, Norin 34, Obanazawa 3, Sekiyama 2, Shinano-hikari, Todoroki-wase, Toyama-wase, Yoneshiro, Akishino-mochi, Isao-mochi.
Shinsetsu	*Pi-a, Pi-i*	Kiho*, Miyoshi, Naruho, Sawa-minori, Shinsetsu, Shuurei*, Takane-nishiki, Yamahibiki.
Kanto 51	*Pi-k*	Koshi-minori, Kusabue, Matsumae, Senshuraku, Tachi-hona-mi, Yachiho, Dewa-no-mochi, Mangetsu-mochi
	Pi-i, Pi-k	Hida-mochi
	Pi-k, Pi-m	Tsuyu-ake
To-to	*Pi-a, Pi-k*	Koshi-hibiki, Ooyodo, Teine, Yuukara, Hatsune-mochi, Sak-aki-mochi, Tsukimi-mochi
	Pi-a, Pi-i Pi-k	Hokkai 219
	Pi-a, Pi-k Pi-m	Hokushin 1, Kongo, Mine-hikari, Sanpuku, Suzukaze, Takara-senbon
Yashiro-mochi	*Pi-ta*	Tosa-senbon, Yashiro-mochi
Shimokita	*Pi-a, Pi-ta*	Pi 1, Pi 2, Shimokita
Pi 4	*Pi-ta*^{2}	Akiji, Asa-hikari, Pi 3, Pi 4, Pi 5, Satominori
	Pi-a, Pi-ta^2	Kansai 13
Fukunishiki	*Pi-z*	Fukunishiki, Ouu 244, 54BC 68
Zenith	*Pi-a, Pi-z*	Fukei 67
Toride 1	*Pi-z*^{t}	Toride 1
	Pi-a, Pi-z^t	Toride 2
Others		BL 1, BL 2, BL 3, BL 4, BL 5, BL 6, BL 7

*Estimated to possess another resistance gene for C-6 and N-6 races.



3. Cumulative daily change in diseased leaf area on seedlings in the blast nursery (solid line: Shin 2 type; broken line: Kanto 51 type).

field resistance of some varieties (Hirano et al., 1967; Hirano and Matsumoto, 1971; Asaga and Yoshimura, 1969). If varieties lack field resistance, they are severely affected by the fungus races virulent to true resistance genes. The field resistance of the varieties is estimated by the degree of damage in the field where the virulent races are prevalant.

In general, the composition of fungus races is not constant. It varies with year, location, and season (Japan Ministry of Agriculture and Forestry, 1964; Yamada and Iwano, 1970). For example in Fukuyama, the strains belonging to N race propagate in the early part of the rice growth, then the strains belonging to the C race follow (Matsumoto and Okamoto, 1963; Okamoto and Matsumoto, 1964; Ezuka et al., 1969*b*). This phenomenon of race change is repeated every year. Major fungus strains of the N race collected in Fukuyama fields probably belonged to N-2 race because they showed virulence to the *Pi-a* gene of Aichi-asahi type but did not attack the *Pi-i* gene of Ishikari-shiroke type. The strains of the C race which followed the N race were estimated to belong to C-8 race, because they were virulent to *Pi-k* and *Pi-a* and were avirulent to *Pi-i* (Ezuka et al., 1969*b*). In Fukushima, the fungus situation was different. Gene *Pi-k* did not express a resistant reaction in the early stages of rice growth. In contrast, gene *Pi-a* showed moderate resistance because the major fungus strains in Fukushima were virulent to *Pi-k* and avirulent to *Pi-a*. Reactions in the field, therefore, did not directly indicate field resistance itself because of the complex reaction against races.

The degree of resistance in field should be evaluated only within varieties that have the same true resistance genes. Evaluation of resistance is unreliable when the comparison is done between varieties with different genotypes for true resistance. If the field resistance of varieties is directly evaluated only by the observed value in the testing field, the field resistance of the varieties that possess the *Pi-i* gene may be ranked as high, and the field resistance of the varieties that possess the *Pi-k* gene may be classified as high when observed in the early stages of rice growth in Fukuyama as shown in figure 3. For the same reason, the field resistance of the varieties with the *Pi-a* gene may be graded as higher than that of Shin 2 type and Kanto 51 type in Fukushima.

To compare field resistance between varieties of genotypes differing in true resistance, a disease rating index was proposed by Sakurai and Toriyama (1967).

The disease rating index is calculated from the ratio of susceptibility of a given variety to that of a standard variety that is the most susceptible variety chosen from the varieties of the same resistant genotype. The disease rating index for field resistance allows comparison between varieties that have different true resistance genes in different locations, years, and seasons. The other way to determine varietal difference of field resistance is repeated tests by the spray inoculation method with various virulent fungus strains. Varieties that show few lesions and small lesions in the spray inoculation test may be considered to have field resistance (Niizeki, 1967).

By either the spray or injection testing method, the true resistance (equal to vertical resistance in this case) of given varieties is distinguished by its hypersensitive reaction to the fungus pathogen. The varieties that have susceptible lesions, therefore, are classified as susceptible, and as lacking the true resistance gene against fungus strain inoculated, regardless of the number of lesions produced. In this way, Sakurai and Toriyama (1967) found that the variety St 1 had high field resistance controlled by a major gene, although it is generally considered that field resistance is controlled by a polygenic system. St 1 showed the susceptible reaction to all the seven standard fungus strains when injected, but it produced only a few lesions of susceptible type when inoculated by the spray method. St 1, therefore, was determined to have an extremely high degree of field resistance. Chugoku 31 which is a sister line of St 1 had also high field resistance in addition to the gene *Pi-k* (Toriyama et al., 1966; Toriyama, Sakurai, Yunoki, and Ezuka, 1967). By gene analysis, it was found that the extremely high field resistance of St 1 and Chugoku 31 was controlled by a major gene, *Pi-f*, which is linked to the *Pi-k* gene with a recombination value of 20 percent (Toriyama, Yunoki, and Shinoda, 1968). Recently, it was reported by Yunoki et al. (1970), that some fungus strains could severely attack the varieties possessing *Pi-f* and produce many susceptible lesions. This means that the field resistance due to *Pi-f* gene is specific resistance, not horizontal resistance.

Another example showing that the major gene plays an important role in field resistance of rice was found in Ohu 244. Ohu 244 is a sister line of Fuku-nishiki. They were developed from a cross with Zenith and possess the true resistance gene *Pi-z*. Both varieties, however, showed susceptible reaction when virulent fungus isolates such as FS 66-59, TH 65-105, and Chu 66-45 were inoculated by the injection method. When these two varieties were instead inoculated by the spray method with the same fungus isolates, Fuku-nishiki still produced many susceptible lesions, but Ohu 244 had only a few lesions, most of which were moderately resistant type lesions. The resistant parent, Zenith, showed the same reaction as Ohu 244 in these tests (Yunoki et al., 1970*a*). The high field resistance of Ohu 244 and Zenith is specific resistance, however, because Zenith has a susceptible reaction at some locations in the world (International uniform blast nurseries, 1964-1965 results, 1966).

Some Japanese upland rice varieties, such as Kuroka and Fukuton, also have high field resistance like Zenith. In the injection test, Kuroka was found to have only the true resistance gene *Pi-a*. Fukuton had none of true resistance genes. Nevertheless, when inoculated by the spray method with fungus strains virulent to *Pi-a*, these varieties developed only a few lesions of the moderately resistant type and were recognized to have high field resistance (Ezuka et al., 1969*b*). Inheritance of high field resistance in Kuroka was investigated by the chromosome reciprocal translocation method, and it was found that high resistance was controlled by two or three major genes one of which may be located on Chromosome 4 and the other on Chromosome 11 (Shinoda et al., 1970).

Recently, the high field resistance of these upland rice varieties was found to be specifiic because some fungus isolates could produce many susceptible lesions on these upland varieties (Y. Sekiguchi, *personal communication*). In these examples the high field resistance apparently is controlled by a major gene (or genes) and is specific.

The other type of field resistance governed by major genes may be the simultaneous effect of genes for true resistance to other fungus isolates. Some varieties that are descended from Sensho have a hypersensitive reaction controlled by a true resistance gene when inoculated with fungus isolates of C-6 race by the spray method. They also show a moderate degree of field resistance as compared with the varieties susceptible to C-6 race in the blast nursery (Nakanishi and Nishioka, 1967).

Conversely, it had been considered that the existence of the true resistance gene *Pi-k* caused inferior field resistance against fungus races virulent to *Pi-k* (Suzuki and Yoshimura, 1966; Iwano, Yamada, and Yoshimura, 1969). But it was found that the *Pi-k* gene and degree of field resistance were independent (Asaga and Yoshimura, 1970).

Since field resistance includes the resistant reaction controlled by a major gene (or genes), field resistance is specific and is not the same as horizontal resistance. Specific resistance should include both true resistance and field resistance. Any difference between true resistance and field resistance is only due to the testing methods. Some resistance genes that are found to be true resistance genes by the spray method are sometimes not recognized to be true resistance genes in the injection method employing the same fungus strains. For example, the gene for true resistance to C-6 race in Homare-nishiki showed a hypersensitive reaction when inoculated by the spray method. Conversely, this resistance gene could not express its hypersensitivity against C-6 race in the injection test.

The sheath inoculation method for evaluating resistance to blast was proposed by Takahashi (1951). He recommended the highest degree of hyphal growth in host cells as a basis for measuring susceptibility or resistance (Takahashi, 1967). The value of resistance evaluated by this method, therefore, was more complex than that of the spray or injection method because the hyphal growth of pathogens in host cells was affected by both the true resistance and the field resistance of the varieties tested. The degree of field resistance evaluated by the sheath inoculation method coincides well with the disease rating index proposed by Sakurai and Toriyama (1967). This coincidence may mean that there is some possibility that horizontal resistance to all virulent fungus races exists.

These phenomena lead to the conclusion that non-specific field resistance, i.e. horizontal resistance in a strict sense, to blast disease will be difficult to find in rice varieties in Japan although some possibilities remain.

New directions in breeding for resistance to blast

Breeding work for blast resistance in Japan is progressing step by step. The first step was the use of variability within domestic varieties. The second step, incorporation of true resistance genes, was severely affected by prevalence of fungus races virulent to newly introduced resistance genes. This unexpected breakdown of resistance was a turning point in the Japanese breeding program for blast resistance.

Several breeding programs to cope with this situation have been proposed: 1) making new combinations of three or more true resistance genes in one variety, 2) using high field resistance genes in place of true resistance genes (Ito, 1967), 3) combining true resistance genes with field resistance, 4) developing multilineal varieties—mechanical mixtures of many phenotypically similar lines that differ genotypically for blast resistance (Okabe, 1967), and 5) changing to varieties that have different genotypes for blast resistance every year (Kiyosawa, 1965).

Some practical problems in the above proposals are unsolved. One is whether the occurrence of fungus strains virulent to true resistance gene varies with the genes (Niizeki, 1967), and stabilizing selection among fungus strains. If there are any differences among true resistance genes in the mutation ratio of fungus strains from avirulent to virulent, breeders will be able to combine the genes that are less often attacked by virulent races. And if stabilizing selection is practiced on blast fungus, it may be worthwhile to try combining more true resistance genes to lower fungus activity.

Combining several true resistance genes and field resistance in one variety would be an acceptable program to most breeders. But the degree of field resistance must be evaluated with the fungus strains that have virulence to all true resistance genes employed. A testing method that uses such widely virulent races has not been developed yet, so the third proposal may be more difficult to achieve than the first and second ones.

Multilineal varieties and changing varieties are being investigated on a fundamental basis.

BACTERIAL LEAF BLIGHT

Breeding progress

The history of breeding for resistance to bacterial leaf blight in Japan has been reviewed by Mizukami (1966), Fujii and Okada (1967), and Mizukami and Wakimoto (1969). Breeding for resistance to this disease started in the 1920's. The first technique used was the selection of resistant individuals or lines from farmers' fields where bacterial leaf blight was prevalent.

Kano 35 was selected as the resistant individual from a field planted with Shinriki in 1926. Shiga-sekitori 11 and Shobei were recognized to be resistant up to 1924 (Fujii and Okada, 1967). From the cross Kano 35 x Ashi 1, Norin 27 was developed as the first recommended variety resistant to bacterial leaf blight. Then Asakaze, Hayatomo, and Nishikaze were released as the varieties possessing resistance through Norin 27 (Okada et al., 1958, 1968). The resistance of Shiga-sekitori 11 descended to Zensho 26, and through Zensho 26 to Hoyoku, Shiranui, Kokumasari, and Ooyodo, then through Hoyoku to Reiho and Toyotama (Soga et al., 1963; Okada et al., 1967). Shobei was also employed for breeding resistant varieties. Hagare-shirazu has the resistance gene from Shobei (Yamaoka et al., 1966).

No attempts were made to select for resistance to bacterial leaf blight from foreign varieties, but some resistance genes for bacterial leaf blight were unintentionally incorporated into the varieties that were developed from the crosses with foreign varieties for blast resistance. The resistance gene for bacterial leaf blight from the U.S. variety Zenith was incorporated into Ohu 244 together with the blast resistance gene *Pi-z*. The bacterial leaf blight resistance gene of Philippine variety Tadukan was joined into Pi 1 with the blast resistance gene *Pi-ta* (Sakaguchi, 1967).

Differentiation of pathogen

The pathogen of bacterial leaf blight is classified by two criteria, virulence and lysotype (Kuhara et al., 1965; Mizukami and Wakimoto, 1969). These criteria, however, are independent of each other. Only the classification by virulence is useful for breeding work. Several inoculation methods for testing resistance have been devised. These are single-needleprick or multi-needleprick inoculation and spray inoculation for seedlings or adult plants, and dip inoculation for seedlings (Mukoo and Yoshida, 1951; Yoshida and Mukoo, 1961; Kurita et al., 1960; Yoshimura and Iwata, 1965; Yoshimura and Yamamoto, 1966). Of these methods, the needleprick method is now widely employed by breeders in evaluating the resistance of varieties.

The variety-pathogen relationship shown in Table 2 was determined by the multi-prick inoculation method at the flagleaf stage. The varieties tested were classified into four groups: Wase-aikoku 3 group, Rantajemas group, Kogyoku

Table 2. Variety-pathogen relationship for bacterial leaf blight.

Varietal group	Pathogen group I	II	III	Varieties belonging to each group
Wase-aikoku 3	0	0	0	Nakashin 120, TKM-6
Rantaj-emas	0	0	+	Maratelli (A), Nep Vai, Nigeria 5, Tadukan, Tetep
Kogyoku	0	+	+	Akashinriki, Asakaze, Hagareshirazu, Hamakaze, Hayatomo, Houyoku, Kanto 60, Kogyoku, Kinko-asahi, Koganemaru, Kokumasari, Nangoku-mochi, Nishikaze, Norin 27, Ooyodo, Pi 1, Shiranui, Taiyo, Zensho 26
Kinmaze[a]	+	+	+	Asahi, and others

[a]Most Japanese paddy varieties belong to Kinmaze group.

Table 3. Varietal resistance to lesion enlargement[a] expressed by three groups of *Xanthomonas oryzae*.

Varietal group	Variety	Isolate group I Giken 44	II Shinjo	III Beniya
Rantajemas	Nep Vai	0	0	5.2
Kogyoku	Sigadagabo	0	5.6	6.3
	Kogyoku	0	1.8	3.6
Kinmaze	Kinmaze	4.5	4.1	4.3
	Shimotsuki	2.7	2.1	3.1

[a] 0 = no symptoms; 7 = severely diseased.

group, and Kinmaze group. The pathogenic strains were classified into three groups: Group I, II, and III (Washio, Kariya, and Toriyama, 1966; Sakaguchi, Suwa, and Murata, 1968).

The varieties resistant to bacterial leaf blight which were developed hitherto belonged to Kogyoku group which possesses resistance to Group I. Therefore, they are affected when the pathogens belonging to Group II or III are prevalent. Actually, the resistant variety Asakaze of the Kogyoku group was severely affected by bacterial leaf blight in 1957. Asakaze had been widely planted in the Kyushu District not only because of its resistance to bacterial leaf blight but also because of its high yielding ability and stiffness of straw. The pathogen isolated from diseased tissue of Asakaze was found to belong to Group III which shows the widest range of virulence (Kuhara, Sekiya, and Tagami, 1957, 1958). The wide spread of the pathogen belonging to Group II was reported by Kusaba, Watanabe, and Tabei (1966).

By electron microscopy, the pathogen in the vessel of susceptible variety appeared to be filled with a homogeneous substance, but that in the vessel of resistant variety seemed to be melted with deformation of cell walls (Horino, Watanabe, and Ezuka, 1969).

Resistance to enlargement of lesion

When the varieties are inoculated with the virulent pathogen of bacterial leaf blight, varietal differences in the enlargement of the lesions are observed. The degree of enlargement of lesion correlates well with the degree of damage observed in the field where severe incidence of the disease develops. Therefore, enlargement could be used as an index for evaluating field resistance of varieties (Washio et al., 1956; Kariya and Washio, 1959). In general, the varieties of the indica type showed great enlargement of lesions, and kresek (Goto, 1965). Japanese lowland rice varieties had smaller lesions. There is however genetic variability in the enlargement of lesions among Japanese paddy varieties. As shown in Table 3, extreme enlargement of lesions was observed when Sigadogabo which belongs to the Kogyoku group was inoculated with the pathogens of Group II or III, and when Nep Vai of the Rantajemas group was inoculated with the pathogen of Group III. The degree of enlargement observed in these foreign varieties was much greater than that in the Japanese paddy variety Kinmaze which is one of the most susceptible varieties in Japan. Among the Japanese paddy varieties, Kogyoku of the Kogyoku group and Shimotsuki of Kinmaze group were found to have high field resistance as shown by the slight enlargement of their lesions (Washio et al., 1966).

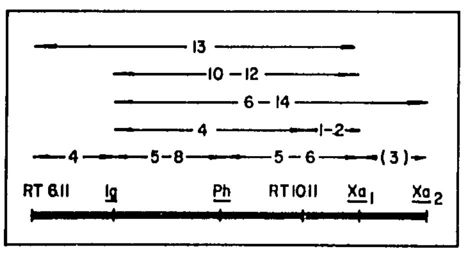
Inheritance of resistance to bacterial leaf blight

The mode of inheritance of resistance to bacterial leaf blight was investigated by two methods, gene analysis with marker genes and chromosome reciprocal translocation (Nishimura, 1961; Sakaguchi, 1967). Resistance in the varieties of the Kogyoku group against pathogens of Group I was found to be controlled by a dominant gene, *Xa-1*. The gene *Xa-1* was linked with the gene *lg* for ligulelessness by 6 to 14 percent of recombination value, and with the gene *Ph* for phenol staining reaction by 5 to 6 percent (Nishimura, 1961; Sakaguchi, 1967). These results indicated that the gene *Xa-1* belongs to the *Pl* linkage group (Group II) corresponding with Chromosome 11 (Iwata and Omura, 1971). The chromosome reciprocal translocation method indicated the same relation.

Resistance in the Rantajemas group was found to be controlled by two resistance genes, *Xa-1* and *Xa-2*. The gene *Xa-1* is the same gene as that of the Kogyoku group and expresses resistance against the pathogen of Group I. The gene *Xa-2* governs resistance against the pathogen of Group II. These two genes express their resistance against pathogens throughout the plant's growth, and are closely linked to each other with a 3 percent recombination value. The order and distances of these genes and the points of chromosome reciprocal translocation are diagrammatically indicated in figure 4 (Sakaguchi, 1967).

The variety Pi 1 which is a descendant of Tadukan belonging to the Rantajemas group showed resistance against the pathogen of Group I but not to the pathogen of Group II. This might be due to the lack of the *Xa-2* gene.

The nature of resistance gene of Wase-aikoku 3 is different from that of resistance genes, *Xa-1* and *Xa-2*. Wase-aikoku 3 did not express its resistance against the pathogen at the seedling stage, therefore, it was sometimes classified as susceptible when tested at the seedling stage. This variety, however, shows a wide range of resistance to this disease in older plants. The resistance of this variety may be a kind of adult resistance (Ezuka, Watanabe, and Horino, 1970).



4. Linkage relationship among genes for bacterial leaf blight resistance and some other traits belonging to the *Pl* linkage group (Sakaguchi, 1967). *lg* = liguleless, *Ph* = phenol staining; *Pl* = purple leaf; *Xa-1*, *Xa-2* = bacterial leaf blight resistance, RT 6.11 = reciprocal translocation point between Chromosome 6 and 11; RT 10.11 = reciprocal translocation point between Chromosome 10 and 11.

At the flag leaf stage, the resistance of Wase-aikoku 3 was found to be controlled by a dominant gene *Xa-w* (A. Ezuka, *personal communication*).

In the injection test with the pathogen of Group I at the seedling stage, the F_2 population of the cross between Wase-aikoku 3 and Kogyoku segregated in a ratio of 3 R : 1 S with the *Xa-1* gene coming from Kogyoku. When plants of the same F_2 population were inoculated with the pathogen of Group I and Group III at the flag leaf stage, the segregation of resistance against two strains became 12 RR : 3 RS : 1 SS by the respective reaction of the *Xa-w* and *Xa-1* genes. The combination of reaction types against the pathogens at the seedling and adult stages showed a digenic segregation ratio of 9 R.RR : 3 R.RS : 3 S.RR : 1 S.SS representative of each genotype for resistance to the pathogen relationship. Of course, the inoculation test at the flag leaf stage with the pathogen of Group I showed a ratio of 15 R : 1 S. These segregation ratios indicated that the gene *Xa-1* and *Xa-w* were independent of each other (A. Ezuka, *personal communication*). To combine the genes *Xa-1* and *Xa-w* in one variety, the breeding materials must be selected on the basis of resistance by the inoculation test with the pathogen of Group I at the seedling stage and with the pathogen of Group II or III at the flag-leaf stage. Ideal varieties will result from the selections showing resistance at both testing stages.

The resistance to enlargement of lesions was also heritable. By the biometrical analysis for this trait, resistance to enlargement of lesions was found to be controlled by a polygenic system and was independent of the gene *Xa-1*. Heritability estimates of this trait varied with crosses from 35 to 68 percent (Washio et al., 1966).

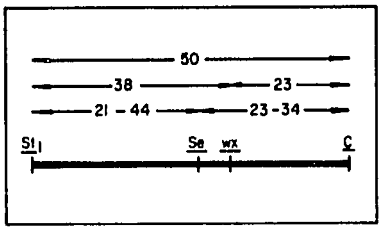
Recent breeding for resistance to bacterial leaf blight

To prevent pathogens that have a wide range of virulence from propagating, breeding for resistance to all strains should be emphasized. As shown in Table 2, varieties such as Wase-aikoku 3, Nakashin 120, "Lead rice," and TKM-6 show a wide range of resistance to different strains. Of these varieties, Wase-aikoku 3 was employed as a resistant parent, and Chugoku 45 was developed for practical use. "Lead rice" which is an indica type from Burma was used as a donor and was backcrossed three times with Japanese paddy varieties. X 38 and X 43 were developed at the National Institute of Agricultural Science. They possess the bacterial leaf blight resistance of "Lead rice."

STRIPE DISEASE

Inheritance of resistance to stripe disease

Stripe virus has become a major rice disease in Japan as the result of recent trends toward early planting and direct seeding. To identify resistant varieties in the field, early planting is favorable for disease development (Suzuki et al., 1960). The seedling inoculation method, in which seedlings are inoculated at any time by using viruliferous vectors reared artificially, was devised by Sakurai, Ezuka, and Okamoto (1963). This method, requires only 1 month, and allows the screening of many varieties and strains in a greenhouse.



5. Linkage relationship among genes for stripe resistance and some other traits belonging to the *wx* linkage group. *St-1* = stripe disease resistance, Se = photoperiod-sensitivity; *wx* = waxy endosperm, C = chromogen for anthocyanin color.

Extensive screening for resistance to stripe disease has been made by Sakurai and Ezuka (1964); Yamaguchi, Yasuo, and Ishii (1965); Washio et al. (1967); and Sonku and Sakurai (1967*a*). Japanese lowland varieties, ponlai varieties, and foreign varieties of japonica type were all susceptible; Japanese upland rice varieties and foreign varieties of the indica type were mostly resistant, and foreign varieties of intermediate type varied from resistant to susceptible. Since no varieties suitable for resistant parents were found among existing Japanese lowland varieties, Japanese upland varieties or foreign varieties of indica or intermediate type should be employed as sources of resistance to stripe disease in crosses with Japanese lowland varieties.

By serological investigation, it was found that susceptible varieties had a high concentration of the virus in the growing point; conversely resistant varieties had a low concentration in the growing point (Sonku and Sakurai, 1965, 1967*b*).

From the segregation ratio for resistance in the F_1, B_1, F_2, and F_3 generations of crosses between resistant Japanese upland rice and susceptible Japanese lowland rice varieties, it was found that the resistance of Japanese upland varieties is controlled by two complementary dominant genes *St-1* and *St-2*. This was proven by the appearance of resistant individuals in the F_1 generation of crosses between the susceptible F_4 lines. One of the stripe resistance genes, *St-1*, showed linkage to gene *wx* for waxy endosperm and the gene *Se* for photosensitivity. The *St-1* gene, therefore, belongs to the *wx* linkage group (Group I) corresponding with Chromosome 6 (Washio, Ezuka, Toriyama, and Sakurai, 1968; Washio et al., 1968*a*; Toriyama, 1969) (fig. 5).

The varieties of the indica type and of the Indonesian bulu type were found to be controlled by an incompletely dominant gene $St\text{-}2^i$, which is an allele of *St-2*. The gene action of $St\text{-}2^i$ differed with the variety tested. The gene for high levels of resistance showed nearly complete dominance over the gene for low levels. The expression of the resistance gene $St\text{-}2^i$ in the F_1 generation and backcrossed F_1 individuals was slightly influenced by the cytoplasm of the female parent. The gene *St-1* showed a complementary gene action not only with *St-2* but also with $St\text{-}2^i$. Modifying genes have some influence on the degree of resistance that might be present (Washio, Ezuka, Toriyama, and Sakurai, 1968; Washio et al., 1968*b*; Toriyama, 1969).

Culm length, panicle length, number of grains per panicle, grain length, grain width, and the ratio of grain length to width were not correlated with resistance to stripe disease, but seed dormancy was correlated with $St\text{-}2^i$ (Washio, Ezuka, Toriyama, and Sakurai, 1968; Toriyama 1969).

From analysis employing chromosome reciprocal translocation, it was found that the *St-1* gene was located on Chromosome 6 corresponding with the *wx* linkage group (Group I) and that the *St-2* (*St-2ⁱ*) gene was located on Chromosome 12 corresponding with the *I-Bf* linkage group (Group 5) (Washio, Ezuka, Toriyama, and Sakurai, 1968).

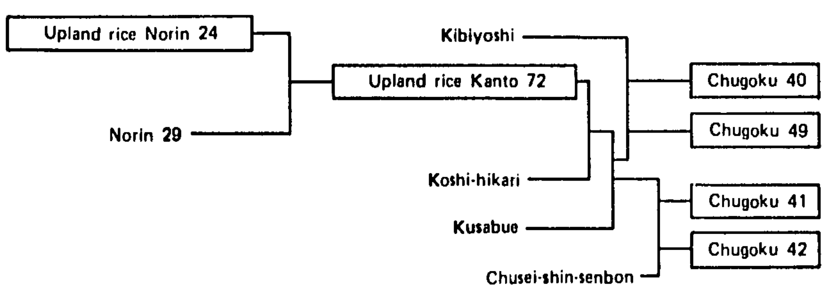
Breeding for resistance to stripe disease

For rapid development of stripe-resistant commercial varieties, a parental upland variety was chosen from the upland strains derived from crosses between Japanese upland and lowland rice varieties. The upland variety Kanto 72 which is one of the upland-lowland hybrids was crossed with Koshihikari. The F_1 plants were three-way-crossed with a lowland variety Kusabue. Then the three-way F_1 plants were examined for reaction to stripe by the seedling inoculation method. The resistant plants were selected as the parental materials and were crossed again with paddy varieties such as Chuseishin-senbon and Kibiyoshi.

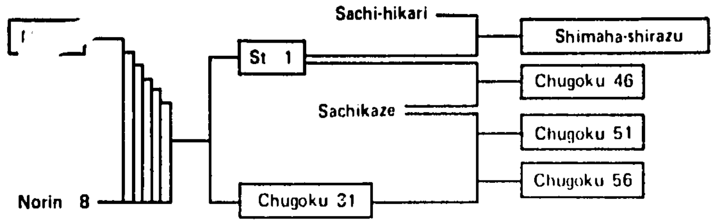
After repeating the seedling test and the field selection for general traits, the F_1, F_3, and F_5 generations were shortened in a greenhouse during the winter season for early fixation. Four varieties, Chugoku 40, Chugoku 41, Chugoku 42, and Chugoku 49 were developed (fig. 6). They possess resistance and are equal to the check variety in yielding ability (Toriyama, 1969).

The monogenic inheritance of resistance in indica varieties as compared with resistance controlled by the complementary genes in Japanese upland rice, is advantageous for the selection of fixed lines in an early generation. The first effort, therefore, was made to select the lines carrying the resistance gene in indica varieties and the properties of Japanese paddy rice from existing indica-japonica hybrids. Of 570 lines, St 1 and Chugoku 31 were resistant to stripe disease. Both varieties were developed from the fifth backcross involving Norin 8 as a recurrent parent and the Pakistani variety Modan as a donor (Toriyama et al., 1966).

As a result of the second breeding step, using St 1 and Chugoku 31 to adapt to the shortened breeding cycle in segregating generations by the bulk method, some resistant varieties available to commercial use were developed. These are



6. Lineage of varieties possessing stripe resistance derived from Japanese upland rice varieties.



7. Lineage of varieties possessing stripe disease resistance derived from Modan.

Shimaha-shirazu, Chugoku 46, Chugoku 51, and Chugoku 56 (fig. 7). They have superior resistance to stripe disease in the regions where stripe disease is severe (Toriyama, 1969).

SHEATH BLIGHT

Sheath blight is common throughout the country. It is favored by high temperatures and humidity and has often caused serious damage especially in southern Japan.

Varietal differences have been found in the proportion of healthy leaf sheaths in field experiments. Late maturing varieties had more resistance than the early ones. Heading date had a correlation coefficient of 0.746 with the proportion of healthy leaf sheaths (Ezuka, Sakurai, and Okamoto, 1971). By the inoculation test, which was free from secondary influences such as heading date or plant type, no remarkable differences in resistance to sheath blight evaluated by lesion length were observed among Japanese lowland varieties (Ezuka, Sakurai, and Okamoto, 1971). These results indicated that resistance to sheath blight in late varieties might be the result of late growth under cool weather which is unfavorable for the causal fungus.

Breeding for resistance to sheath blight has not been started because no resistant varieties have been found.

DWARF DISEASE

Varietal differences for resistance to dwarf disease have been observed in paddy fields where this disease is severe. Varieties were classified into five grades according to the proportion of diseased plants. Most Japanese lowland rice varieties were graded as susceptible or highly susceptible. Late varieties showed higher susceptibility than early ones. All Japanese upland rice varieties tested were highly susceptible. Some foreign varieties showed high resistance. They belonged to the indica type such as Tetep, the intermediate type such as Loktjan, and the japonica type such as Hyakunichi-to. Resistance in the foreign varieties was also found by the seedling inoculation test (Ishii, Yasuo, and Yamaguchi, 1969).

Highly resistant foreign varieties caused a low population of hatched insects, the death of young nymphs, and lightweight insects. The quantity of juice absorbed by insect from highly resistant varieties was comparatively less than that from susceptible Japanese varieties. Conversely, on Japanese varieties, large numbers of insects hatched, and the insects gained weight fast. Thus insect resistance of foreign varieties could play an important role in breeding for resistance to dwarf disease (Ishii et al., 1969).

Breeding for resistance to dwarf is just beginning, and the testing method for insect preference is proposed for selecting for resistance to dwarf disease.

BLACK-STREAKED DWARF

Varietal differences in resistance to black-streaked dwarf were found by the seedling inoculation method. All Japanese lowland rice varieties tested were susceptible. Japanese upland rice varieties were susceptible or moderately susceptible. Of 178 foreign varieties tested, eight indica-type varieties and four intermediate-type varieties were resistant. The other foreign varieties were moderately susceptible. The resistant varieties were from China, Indonesia, Indochina, the Philippines, and India (Morinaka and Sakurai, 1967, 1968; Sakurai, 1969).

The mode of inheritance of resistance to this disease was studied with the seedling inoculation method. F_1, B_1, F_2, and F_3 generations of two crosses between a resistant variety, Tetep, and two susceptible Japanese paddy varieties were tested in one season. In both crosses, the F_1 and B_1 progeny showed that resistance was dominant to susceptibility, and the F_2 and F_3 data indicated that resistance was controlled by a dominant gene, *Bs*. Other modifying genes for resistance might be present, too (Morinaka, Toriyama, and Sakurai, 1969*a*, *b*).

The resistant indica variety Tetep has been employed as a donor in back-crosses and polycrosses with Japanese lowland varieties.

YELLOW DWARF DISEASE

Varietal differences to yellow dwarf disease were observed in a paddy field in southern Japan that had a severe attack of yellow dwarf. All Japanese non-glutinous lowland varieties tested were susceptible. Three glutinous varieties of Japanese paddy rice were resistant: Saitama-mochi 10, Naozane-mochi, and Kagura-mochi. Foreign varieties were ranged from susceptible to resistant. The resistant foreign varieties belonged to indica type and intermediate type (Komori and Takano, 1964; Morinaka and Sakurai, 1970).

Sixty-six varieties were tested by the seedling inoculation method to evaluate varietal resistance. Saitama-mochi 10, Kagura-mochi, Shinano-mochi 3, Mangetsu-mochi, and Tetep were classified as resistant.

The percentage of diseased plants in the paddy field and the percentage of diseased plants in the seedling inoculation test had a correlation coefficient of 0.618, showing some discordance within foreign varieties. Some resistant foreign varieties in the field test showed a high percentage of diseased plants in the seedling inoculation test. These conflicting results might be due to insect preference for some varieties (Morinaka and Sakurai, 1970).

The mode of inheritance to yellow dwarf disease was investigated using the seedling inoculation method and the F_1, F_2, and F_3 generations of the crosses between the resistant glutinous variety Saitama-mochi 10 and two susceptible non-glutinous varieties. The data on the F_1 seedlings suggested that resistance to this disease was dominant to susceptibility, but the d[illegible]n the symptoms of the ratoon crop of the same F_1 individuals showed incomplete dominance of resistance. F_2 and F_3 data indicated that resistance to yellow dwarf was controlled by a dominant or incompletely dominant gene (Morinaka, Toriyama, and Sakurai, 1970).

Breeding for resistance to this disease has not started.

NECROTIC MOSAIC DISEASE

Necrotic mosaic disease is of limited importance in Japan. Japanese paddy rice varieties are susceptible or moderately susceptible, but most Japanese upland rice varieties are highly resistant. A wide range of variation from susceptibility to resistance has been observed in foreign varieties. Chugoku 42, one of the derivatives from Japanese paddy-upland rice hybrids, was found to be resistant, and was selected as the parental material in a breeding program for resistance to necrotic mosaic disease (K. Fujii and X. Idei, *personal communication*).

BROWN SPOT DISEASE

Brown spot disease is widely observed in Japan, but recently the losses by this disease have been decreasing due to the improvement of paddy soil. Varietal differences have been observed in the size and number of lesions and degree of leaf-wilting. Correlations between these three traits are low (Kondo and Sugiura, 1954). Desirable resistant varieties which show small spot type, few lesions, and a low degree of leaf-wilting will be developed soon. By field observation, Hainan Island 217 and Chiu Tzu Chiu were selected as resistant varieties (Asada, Akai, and Fukutomi, 1954). Some varieties belonging to the indica type were found to be resistant, too, by the spray inoculation method at the three-leaf to four-leaf stage (Hashioka, 1952).

Resistance to brown spot is not yet considered a major objective in rice breeding.

WHITE-TIP DISEASE

White-tip disease caused by the nematode, *Aphelenchoides besseyi* Christie, is widely distributed in Japan. Although no special attention has been given to development of resistant varieties, they are easily found in widely planted Japanese rice varieties (Kiryu, Nishizawa, and Yamamoto, 1950; Nishizawa, 1953; Goto and Fukatsu, 1956). According to the lineage of these resistant varieties, resistance to white tip disease is heritable and may be descended from Asahi.

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Discussion: Breeding for resistance to major rice diseases in Japan

N. E. BORLAUG: What is the longest time that an extensively cultivated commercial variety has retained its resistance to blast in Japan or elsewhere? Are those that have retained their resistance longest known to have had a combination of "true resistance" and field resistance, or only true resistance?

K. Toriyama: We introduced three true-resistance genes from foreign varieties into Japanese commercial varieties. But the resistance of these three genes was broken within 3 to 5 years after release. If we can combine the two or three true-resistance genes and field-resistance genes in one variety, such a variety might show high resistance for a longer time. We expect to have such a combination in the future.

N. E BORLAUG: I still would like to come back to this question of "elsewhere," because I think this question is of real significance to the orientation of a breeding program. I also wish to hear from plant pathologists who are working on rice diseases outside Japan. I hope you don't have to re-learn our sad experiences in wheat.

P. R. JENNINGS: I can only speak on the general area of Latin America, and in reference to blast. I don't think that there is a resistant variety today in the hemisphere. We have seen originally resistant varieties come down with blast and become completely susceptible in one crop. Others might last for 2 [illegible] years, but none of the commercial varieties that I know of, are resistant today. And I suppose many of them were originally resistant.

L. M. ROBERTS: Was either "true" (or monogenic) resistance or horizontal-polygenic type of resistance found in those varieties?

P. R. JENNINGS: I do not wish to speculate on the genetics of horizontal resistance. I am not absolutely convinced that the so-called horizontal resistance is polygenic. It might not be. But taking the question in its generalities, I don't think that any Latin American variety has ever had the so-called field (or general or horizontal) resistance.

N. E. BORLAUG: I'll try to explain our predicament. From observations in different countries, certain wheat varieties had field resistance or the so-called general resistance to one or a combination of the two rusts that have persisted. These varieties have remained resistant, carrying the same general level of resistance. For instance, the Colombian variety Bonza has remained resistant to both stripe rust or yellow rust for about 17 years. In the case of stem rust, we also have Selkirk which is still grown commercially. So is Bonza, which has retained its resistance to stem rust for about 19 years, although it is less widely cultivated than formerly because of its suceptibility to leaf rust. Nevertheless, it has retained its resistance after it has been known that the specific or "true resistance" genes have broken down against some of the new races. Field resistance is still protecting Selkirk, but not the higher specific *Sr* genes. We also have Yaqui-50, one of the first varieties we developed in the 1940's, that apparently carried no specific *Sr* genes for resistance and is still as resistant today in experimental plots as it was when first developed. So I think that with the few exceptions, all of the others have broken down sooner or later and all too often too soon. And I am sure the same is evident in leaf rust, in stripe rust, and in stem rust. I caution you all not to work just with the specific type of genes where you will be sadly disappointed by the lack of permanence of resistance. Perhaps Virgil Johnson and Jim Wilson could tell us about their experience.

J. A. Wilson: In our wheat breeding program, we are pursuing both objectives, the field resistance and the immunity-type factors.

V. A. Johnson: We have too many bad cases of reliance upon specific resistance that has failed almost before the variety got off the ground. In our own program, we rely almost entirely upon field resistance over a broad spectrum of environments as we can measure it in the international uniform rust nurseries. Seedling tests or reaction to specific races are done only as a supplement to what we see and read in the field.

N. E. Borlaug: The comments of Dr. Johnson are particularly appropriate. The only way you can determine when you have found field resistance in a short period of time is by international testing: subjecting lines to a broad spectrum of disease organisms under a wide range of ecological conditions. You cannot do it in a greenhouse in one location, or in the field in one location, without taking about 20 years to do it. But when you work internationally, you have a good possibility of getting data to support the choice of varieties in that short time.

S. Okabe: In Japanese rice varieties, Norin 22 is just like the varieties described by Dr. Borlaug. Norin 22 has remained highly resistant to blast in Japan for a long period and I feel that it has field or horizontal resistance. It could be a good source for stable resistance to blast.

L. M. Roberts: Potato researchers have shifted over almost entirely to the horizontal type of field resistance in dealing with late blight. It will probably be more difficult to bring together the genes needed, but once you get it, you can count on it for a longer period of time.

B. B. Shahi: Besides breeding resistant varieties for bacterial leaf blight, do you think some chemicals that are now produced in Japan like Agrimycine, Sankel, and New-Sankel can control this disease? Results in Nepal showed negative response.

K. Toriyama: It was reported that some chemicals are very effective in controlling bacterial leaf blight in Japan. I cannot give a reason for the negative response in Nepal. But, I think genetic control is more economical, if available.

S. H. Ou: There is only one systemic bactericide that is effective. It is called TF130. But the bacteria develop resistance to the chemical very quickly. So, at present, I do not think any chemical is really effective against bacterial leaf blight.

Resistance to bacterial leaf blight — India

Harold E. Kauffman, P. S. Rao

The development of resistant or tolerant varieties offers the most promise for reducing the incidence of bacterial leaf blight in dwarf varieties. The task of breeding resistant dwarf varieties in India is formidable, however, because the causal bacterium, *Xanthomonas oryzae*, is quite variable in virulence and no highly resistant variety has been found for use as a donor parent for resistance. Available varieties which possess a moderate degree of resistance are being used in breeding programs aimed at reducing the disease to acceptable levels. Reliable screening and disease evaluation methods have been developed and standardized so that new donor parents can be identified and progeny material evaluated faster.

In India, as in other countries of tropical Asia, bacterial leaf blight has become a major disease of rice in recent years. Although applying less nitrogen fertilizer significantly reduces disease incidence, it lowers yield potential, too (Have and Kauffman, 1972). Since chemical control of bacterial leaf blight has not been proven effective in the tropics, the identification and development of high yielding, disease resistant varieties is extremely important.

Bacterial leaf blight is a complex disease which is greatly affected by a number of environmental factors, so simultaneously with beginning a breeding program for disease resistance in India, attempts have been made to determine the variation in virulence of the pathogen and the range of resistance to the pathogen in the host, and to identify the environmental influences on the interaction between host and pathogen. Only when these factors are known can results from screening programs aimed at identifying resistant varieties be valid and useful for breeding programs.

Relative humidity, temperature, rainfall, wind, and sunlight play important roles in disease ecology. In addition, the nitrogen status and the age of the plant affect disease infection, development, and expression. For screening trials to be reliable, these conditions must be standardized to the maximum extent possible so that all varieties within a trial are exposed to uniform disease pressure every season. Spraying bacterial cultures on the crop during the early growth stages to start disease development and using an overhead sprinkler irrigation system to simulate rainfall have successfully created uniform epiphytotic conditions in screening trials at Hyderabad during both the monsoon

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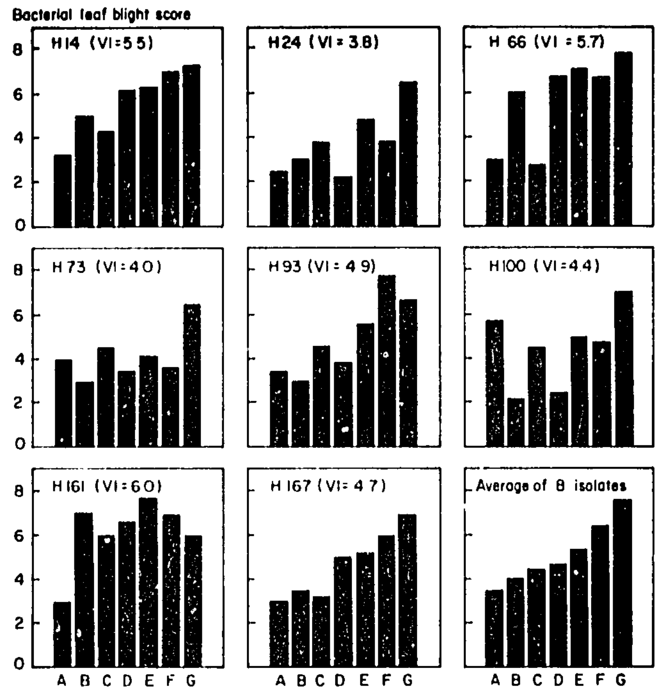


1. Virulence patterns of eight representative Indian *X. oryzae* isolates on seven differential varieties: A) BJ1; B) Malagkit Sungsong; C) Sigadis; D) Wase Aikoku; E) Lacrosse x Zenith-Nira; F) Semora Mangga; G) Taichung Native 1. (VI = virulence index).

season and the dry season. A mixed population of "susceptible feeder" plants of different growth durations helps spread the disease uniformly by supplying a relatively uniform inoculum load to the test plants. All test varieties are exposed to a heavy inoculum load after the booting stage when the disease is most serious under field conditions.

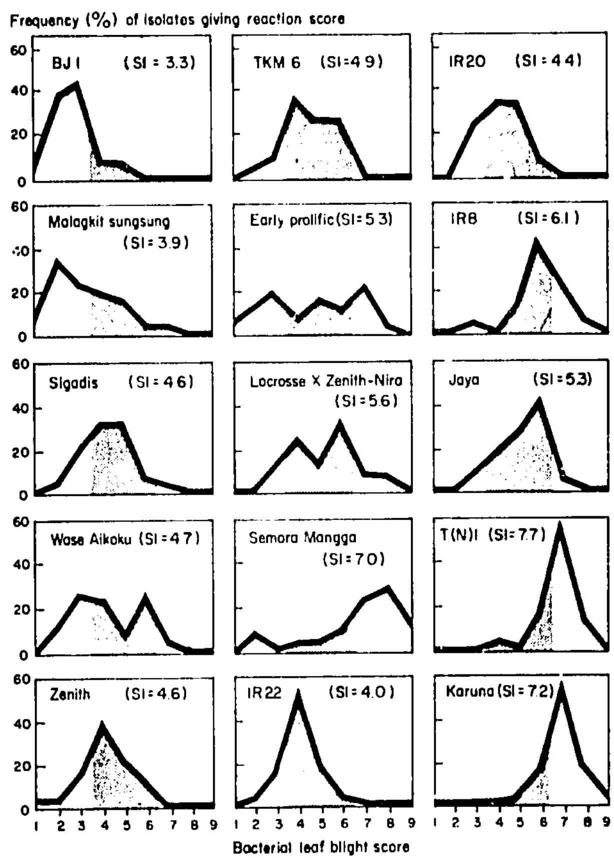
Virulence studies of 161 isolates of *X. oryzae* from 37 locations in major rice-growing areas of India have indicated that the Indian isolates of *X. oryzae* differ greatly in virulence when tested on four differential varieties (Kauffman and Pantulu, 1971). Subsequent selections of 25 representative isolates from this group were repeatedly tested on seven varieties and the variation in virulence was confirmed. Although the differences between some isolates were clearcut, indicating the presence of strains, most differences in virulence were relatively small (fig. 1).

A distinct characteristic of some isolates, exemplified by H 24 and H 73, is the generally low virulence on all varieties, except Taichung Native 1. H 14 and H 161, on the other hand, are generally highly virulent on all varieties except BJ 1.

No isolates were highly virulent on all varieties. H 100 the most virulent isolate on the most resistant variety, BJ 1 (with a score of 5.8), was weakly virulent on Malagkit Sungsong (with a score of 2.2), while H 161 was highly virulent on Malagkit Sungsong (6.8) but weakly virulent on BJ 1 (2.7). Similar reactions occurred on other variety-isolate combinations. Wase Aikoku and Lacrosse x Zenith-Nira showed an especially wide range of reactions: they were highly susceptible to some isolates but highly resistant to others.

Generally, similar patterns of variation in virulence were noticed in the isolates from most locations where a large number of strains were collected and tested. But a few areas, such as two locations in the state of Madhya Pradesh, had a limited number of strains, all of which were very weakly virulent. This type of variation probably indicates that *X. oryzae* has been present in India for many years during which time numerous strains have developed, some of which are common to many areas and others of which are distinct to certain localities.

Differences in varietal susceptibility to the Indian isolates are pronounced (fig. 2). Varieties BJ 1 and Malagkit Sungsong possess the broadest spectrum of resistance to the representative isolates tested. They appear to be the best



2. Spectrum of resistance of 15 varieties to 25 representative Indian isolates of *X. oryzae*. (SI = susceptibility index; bacterial leaf blight score: 1 to 3 = resistant, 4 to 6 = moderately susceptible, 7 to 9 = susceptible).

varieties for use as donor parents in a resistance breeding program for India. Other varieties, like Sigadis, Wase Aikoku, Zenith, TKM-6, Early Prolific, and Lacrosse x Zenith-Nira, are resistant to some isolates but moderately susceptible or susceptible to others. They can best be used as donor parents to contribute resistance to specific isolates of the bacterium, but most of them cannot be expected to have broad field resistance.

Among the semidwarf varieties, IR22 and IR20 have considerably more resistance to bacterial leaf blight than IR8 or Jaya. IR8 and Jaya, however, genetically possess more tolerance to the disease than Taichung Native 1 or Karuna, a semidwarf variety recently released in India.

With the development of high yielding varieties with adequate field resistance to bacterial leaf blight as the ultimate objective, the primary emphasis in screening should be placed on results from field testing against the natural population of bacterial strains. Too much reliance on artificial inoculation tests in the greenhouse may be misleading since not enough representative strains of the bacterium may be available for testing. On the other hand, if many isolates are used the work is extremely time consuming.

At Hyderabad, a combination of field and greenhouse screening is used. All available breeding trial material, released varieties, and germ plasm from the Assam Rice Collection are first field-tested under heavy disease pressure. Detailed and frequent observations are made throughout the growing season to identify and accurately assess minor degrees of difference in tolerance to the disease. Varieties that have moderate field resistance are subsequently rescreened in both the field and the greenhouse to determine the spectrum of their resistance. Varieties with broad-based resistance are then used as donor parents.

From 1968 to 1971, about 6,700 varieties and selections were field screened. Of these, less than 100 were classified as moderately resistant in their initial screening trial. In subsequent field screening less than 40 were consistently moderately resistant. None were highly resistant.

BJ 1 and Malagkit Sungsong, the two varieties that showed the broadest spectrum of resistance when inoculated with individual isolates, have generally shown moderate to good field resistance. BJ 1, however, has been planted in the same field at Hyderabad every month for the past 2 years and it is currently becoming moderately susceptible to the prevailing strains of the bacterium. IR22, the semidwarf variety that has the broadest spectrum of resistance, has also recently shown moderate to high susceptibility at Hyderabad and at several locations in Tamil Nadu. Thus resistance to this disease may apply only to limited areas and the development of new strains of the bacterium probably will limit the life of resistant varieties in the tropics as it has in Japan (Fujii and Okada, 1967). For this reason, field tests must be made in many endemic areas. The results of artificial inoculation with only a few of the Indian isolates can not be heavily relied on.

With this information in mind, the AICRIP breeding program for resistance to bacterial leaf blight has emphasized the use of BJ 1, Malagkit Sungsong, and Sigadis as resistant donor parents. Since BJ 1 has both poor combining ability and poor agronomic type, numerous backcrosses are being made to combine the resistance of BJ 1 with the semidwarf plant type. Some semidwarfs that have resistance equal to that of BJ 1 have been identified in the F_4 generation. Numerous crosses are also being made with other varieties resistant to a few isolates in an effort to combine genes from various sources. Semidwarf plants with Malagkit Sungsong, Wase Aikoku, Zenith, and Sigadis as parents have moderate field resistance as well as high resistance to some isolates when artificially inoculated. Although the resistance of Sigadis generally is not high, it is moderately broad and many of the progeny have high yield potential.

Breeding varieties for resistance to bacterial leaf blight in India will be a long-term project. More sources of resistance must be identified and incorporated into semidwarf types to improve tolerance to existing isolates as well as to counteract the new bacterial strains that can be expected to arise.

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The host, the environment, Xanthomonas oryzae, and the researcher

I. W. Buddenhagen, A. P. K. Reddy

Work in Hawaii and observations in many tropical Asian countries indicate that *X. oryzae* populations in India, East Pakistan, Ceylon, and Indonesia are generally more virulent than in other countries. But no clear-cut "races" were found with the possible exception of Australian isolates. A better understanding of field epidemiological requirements for blight and better methods of field screening based on epidemiological knowledge are needed. Application of improved methods to larger rice collections from blight endemic areas and to large F_2 populations to assess for resistance should markedly improve chances of obtaining greater field resistance.

In breeding for resistance to a pathogen, the breeder and pathologist alike would like to believe the pathogen is indeed what its name implies, a fixed entity, always defined within narrow genetic and phenotypic limits by its Linnaean binomial. It is difficult to conceive of the single "species" name, *Xanthomonas oryzae*, as representing pathogenic populations of many billions of individuals scattered across a million square miles, not even genetically linked by sexual recombination. It is also hard to realize that none of the individual bacteria present today existed in last year's breeding plots nor will they be present in next years' screening experiments. The probability of variability and of potential pathogen plasticity seems great indeed as environment, host variety, and cropping practices are changed.

Thus, questions of fundamental importance to a resistance breeding program arise and efforts should be made from time to time to answer them:

1. How different are the existing populations of *Xanthomonas oryzae* in various countries and parts of countries where they occur, in terms of virulence and of range of host variety "attackability?"
2. How variable are these populations potentially in their virulence and their range of host variety adaptability?
3. How quickly can any new, more virulent strains or clones become widespread, both locally and regionally, either by frequent mutation-selection or by true "spread?"
4. How accurately do existing screening programs represent bacterial pathogens and rice in farmers' fields?

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5. How valid are existing screening programs in assessing genetic resistance to maximum pathogen pressure?

6. How restricted are screening methods by minor fluctuations of environmental conditions which are difficult to measure or prevent, thus limiting duplication in different locations and seasons?

7. How meaningful are the existing screening methods in assessing varietal resistance to the bacterial population's step-by-step epidemiological requirements?

8. How thoroughly and logically has the search for resistant donors been carried out?

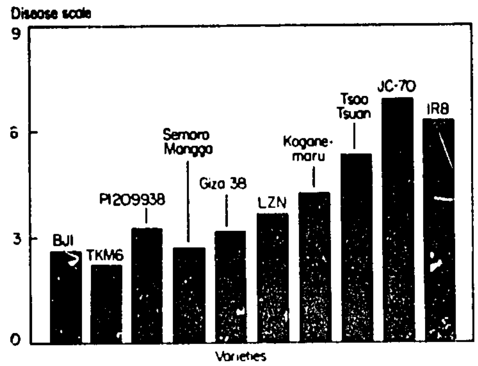
9. How much of the potential resistance in a cross is found by existing breeding-selection methods?

We will not try to answer most of the questions here. Some have fair answers, others are not now answerable and require research. But two common misconceptions that relate to several of the questions should be removed.

One is that change to increased virulence, if potentially possible, is automatically going to occur. This is not necessarily so. It is an easy anthropomorphism to equate greater virulence with greater success. Most pathogens obviously could be much more virulent than they are, but they are not. Why? The answer is complex and could be the subject for several profound papers. To simplify greatly here, it is a logical deduction that higher virulence must have negative survival value in nature. The reasons relate to the complex epidemiological requirements of a disease and to the differing forces that are applied to pathogenic populations as seasons change. Bacterial blight pathogens, for example, are reacting to at least two worlds – a pathogenic and a saprophytic one. Those that survive the off-season to initiate disease must be an extremely small part of the total population which attacked the previous crop. They are the pathogens that are best adapted to an off-season saprophytic survival and probably are not those most potentially virulent (Buddenhagen, 1965). During the short period of a disease epidemic those bacteria that can best enter, grow, and be released from the host will replace the median bacterium in the population and thus selection for "virulence" will then occur, but only within the genetic potential of the total population.

The second common misconception is that races or strains exist if isolates of different virulence can be shown to exist. If isolates do not act differentially with varieties of the host, they are in fact isolates of differing virulence, not races or pathotypes in the true sense, with differing potential for replacement as varieties are shifted. We are not following Van der Plank's (1968) terminology and only partly his concept in this regard. For definitions, see Robinson (1969, 1971).

In Hawaii, during the past $2\frac{1}{2}$ years, in cooperation with IRRI and with support from The Rockefeller Foundation, we have attempted to answer some of the questions relating to *Xanthomonas oryzae* populations and virulence (Silva, Buddenhagen, and Ou, 1970; Buddenhagen, Reddy, and Silva, 1971). More than 200 bacterial blight isolates were collected from 11 countries of Asia and tested for virulence on a set of rice varieties. The pin-prick method of

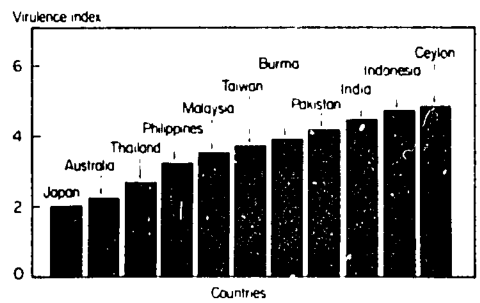


1. Average susceptibility index of 10 rice varieties to *Xanthomonas oryzae* isolates from 11 countries.

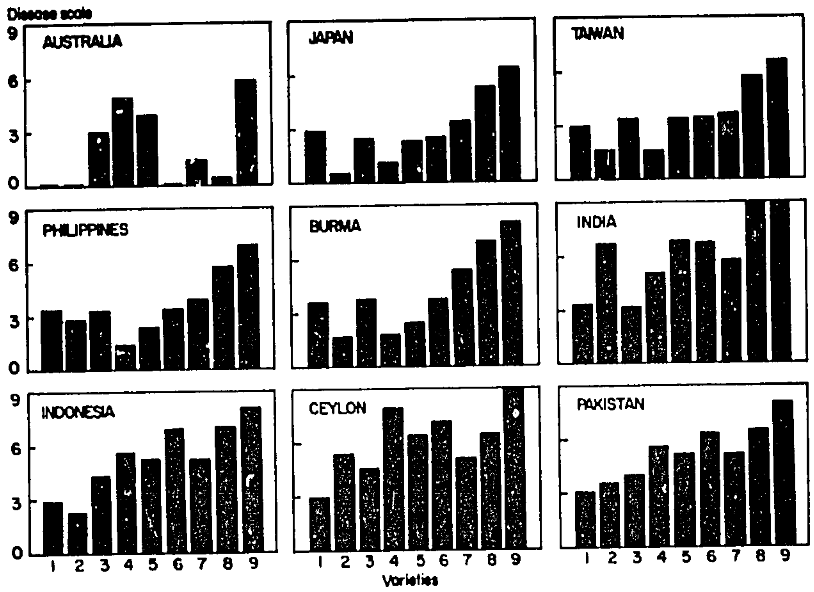
inoculation was used on a set of 27 varieties initially which was later reduced to nine varieties. Disease ratings were taken 21 days after inoculation, according to a scale developed at IRRI based on lesion size. Susceptibility indices for varieties and virulence indices for bacterial isolates were developed from lesion data.

The results of many thousands of inoculations are radically summarized below. First, testing the nine rice varieties finally selected as the differential set with 150 isolates, plus IR8 tested with a smaller number an average susceptibility index has been obtained (fig. 1). The varieties differ markedly in their overall average susceptibility, ranging from 2.2 for TKM-6 through 6.3 for IR8 and 7.0 for JC 70 (maximum susceptibility is 9). Although variation in isolate-variety interaction is not shown, analysis of the raw data reveals that a given susceptibility index is meaningful across the majority of isolates, i.e. if a variety's susceptibility goes up with a given isolate it also goes up on a variety standing higher in the susceptibility index when tested with the same isolate.

Second, a virulence index of bacterial isolates by countries (fig. 2) shows that the *average* virulence of isolates gathered (hopefully at random) from different countries differs among countries. The lowest average virulence was obtained from Japan and Australia and the highest from East Pakistan, India, Indonesia, and Ceylon. Although these are facts, their value is questionable because there was wide variation in virulence among isolates from each country, and because the small sample size cannot be representative of each country as a whole. In spite of these reservations, perhaps they do mean something, i.e.



2. Average virulence index of *Xanthomonas oryzae* isolates from 11 countries on nine rice varieties.



3. Comparison of virulence of representative isolates from nine countries on nine rice varieties: 1) BJ1, 2) TKM-6, 3) PI209938, 4) Semora Mangga, 5) Giza 38, 6) LZN, 7) Kogane-maru, 8) Tsao Tsuan, and 9) J.C.70.

breeding for a given level of blight resistance in country A may be easier than and different from doing so in country B. Other evidence indicates that this is so.

Third, grouping isolates from Asia into true races that clearly differ in reaction on a set of differential varieties has not proven possible. Although isolates differ in virulence and also differ slightly in virulence patterns across a set of differential varieties (fig. 3), I consider these continuum differences to be just that—an expression of slight genetic differences, isolate by isolate, across an unending continuum of gradations. I do not believe that such isolate variability represents races in any meaningful sense. This is strong and heartening evidence that the interaction of rice varieties with *X. oryzae* is an expression of a "horizontal" relationship. This means that increasing the resistance of rice varieties to *X. oryzae* will probably not result in the ready appearance of new aggressive races that have a high capacity to exert a vertical relationship and "break down" the new variety's resistance. Except for a few Indian isolates, the major exception to this non-race idea is represented by the Australian group.

Fourth, in contrast to the absence of discrete races in Asia, eight isolates from tropical Australia reacted consistently and differently from all other isolates on the set of nine differentials (fig. 3). We consider these isolates, obtained from wild rice species and IR8 in northern Australia to represent a genetic break from all other isolates tested. Presumably their evolution has been associated with *Oryza rufipogon* and *O. australiensis*, unlike all other isolates tested which have been evolving in recent millennia with *O. sativa* varieties.

Table 1. Pathogenicity groupings of *X. oryzae* isolates based on reaction of six differential rice varieties.

Variety	Pathogenicity group							
	A	B	C	D	E	X	Y	Z
BJ 1	R	R	R	R	R	R	S	R
TKM-6	R	R	R	R	S	R	R	S
Semora Mangga	R	R	R	S	S	S	R	R
LZN	R	R	S	S	S	R	R	R
Tsao tsuan	R	S	S	S	S	R	S	S
JC 70	S	S	S	S	S	S	S	S

Fifth, an attempt has been made to group isolates, albeit not races, into pathogenicity groups based on reaction to the six best differentials and to see where isolates from different countries would fall in relation to these groups (Table 1). Groups A through E represent isolates of increasing overall virulence on varieties ranked in order of decreasing resistance from top to bottom in the table. Groups X, Y, and Z are of different patterns representing possible differential reactions of isolates that could be fit into "races" if such preliminary sampling were confirmed on a much larger scale. When pathogenicity groups are considered in relation to countries (Table 2), it can be seen that most isolates from most countries fit into group B—a not very virulent group. Seven of the eight groupings are present in India and only one in Australia. These points seem interesting, but otherwise these tables may not mean too much; however others may wish to build on these or construct other models.

Now we should like to make some general comments relating resistance breeding to population variability and epidemiology.

Table 2. Pathogenicity groupings of isolates of *X.oryzae* from various countries.

Country	Pathogenicity group							
	A	B	C	D	E	X	Y	Z
Australia	–	–	–	–	–	6	–	–
Japan	7	1	–	–	–	–	–	–
Thailand	9	6	1	–	–	–	–	–
Philippines	3	20	2	–	–	–	–	–
Malaysia	–	3	–	–	–	–	–	–
Taiwan	–	5	3	–	–	–	–	–
Burma	–	13	7	–	–	–	–	–
Pakistan	–	6	2	8	–	–	3	–
India	1	7	6	1	3	–	1	1
Indonesia	–	–	3	9	–	–	–	–
Ceylon	1	–	–	–	5	–	–	1
Total	21	61	24	18	8	6	4	2

A pin-prick inoculation screening method measures two things: the growth and the spread (near the pin prick) of the particular bacterium introduced into the leaf at a specific moment of environmental and nutritional state. It does not measure how a rice variety would react in the field to the step-by-step epidemiological requirements of a bacterial pathogen's population. The pin-prick method is valid in this regard only to the extent that it may be correlated with complex epidemiological characters.

It seems logical that the way to obtain a field resistant line is to apply maximum pathogen pressure in the field to a segregating F_2 or bulked F_3 population of maximum size from a specifically selected cross. Only in this way can the variability of both the pathogen population and the host population be assessed. This is seldom done. Instead, usually a hundred or so lines are established, largely on other criteria, from thousands of segregating F_2 plants. In the F_4 or F_5 generation, the pathologist is asked to determine which ones are resistant (if any). Meanwhile, the breeder has hoped that his plots contained the pathogen and that weather and nutrient levels were conducive to disease development. It is surprising this method works as well as it does. We can thank mainly the mediocrity of the pathogens and the antiquity of natural selection and primitive man's natural field selection.

Phytobacteriologists think in terms of 50 to 100 genes to make a bacterial pathogen work. A breeder thinks in terms of one or a few genes for resistance in his crop and can usually prove it. To prove this readily he must also ignore pathogen variability as much as possible. There are good reasons why the pathologist and the breeder hold these differing views. The two disparate positions must be reconciled to come up with an improved approach. If the pathogen in its epidemiological phase has anywhere near 50 to 100 genes making it work, and if even only 10 of these are interacting physiologically with the host, and if all 10 host reactions differ in kind or degree between two parents, about 59,000 genotypes could be present in the F_2 that differ in disease response levels. (We emphasize that these host differences are not "disease resistance genes" *per se*, rather they may be genes governing normal host processes that in some way affect the host's field population reaction to the epidemiological requirements of the disease). In fact, however, breeders who have a good pathogen-environment system working for them in their F_2 plots are already three-fourths home. The difficulty comes when epidemic conditions are precise and unknown, when breeders' plots do not represent farmers' fields, and when artificial inoculation is equally unrepresentative of both epidemiological requirements and pathogen variability.

We believe an improved approach combining the best ideas from the epidemiologist and the breeder is both straightforward and simple. 1) A better search for resistant donors in areas of greatest disease antiquity (areas of greatest pathogen variability) and of host variability (hopefully the same region). 2) A field testing system that will exaggerate the severity of the disease, based on improved knowledge of epidemiological requirements. 3) Application of the testing system to large populations of early segregating material from specifically selected crosses. 4) Insuring the presence in this testing system of a variable pathogen population which is representative of the pathogens present in all areas of the country or region where the new variety is to be "adapted." 5) Combining resistances from different sources.

Recent work in India has stepped well forward along these lines of realistic assessment. Systematic screening of the large collection at IRRI has been very useful as an essential initial step. With further improvement of the field approach in India, and then adoption of this approach on an international basis in countries that are most environmentally suitable for bacterial blight, we believe that bacterial blight will become an unimportant disease within 10 to 15 years.

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Varietal resistance and variability of Xanthomonas oryzae

S. H. Ou

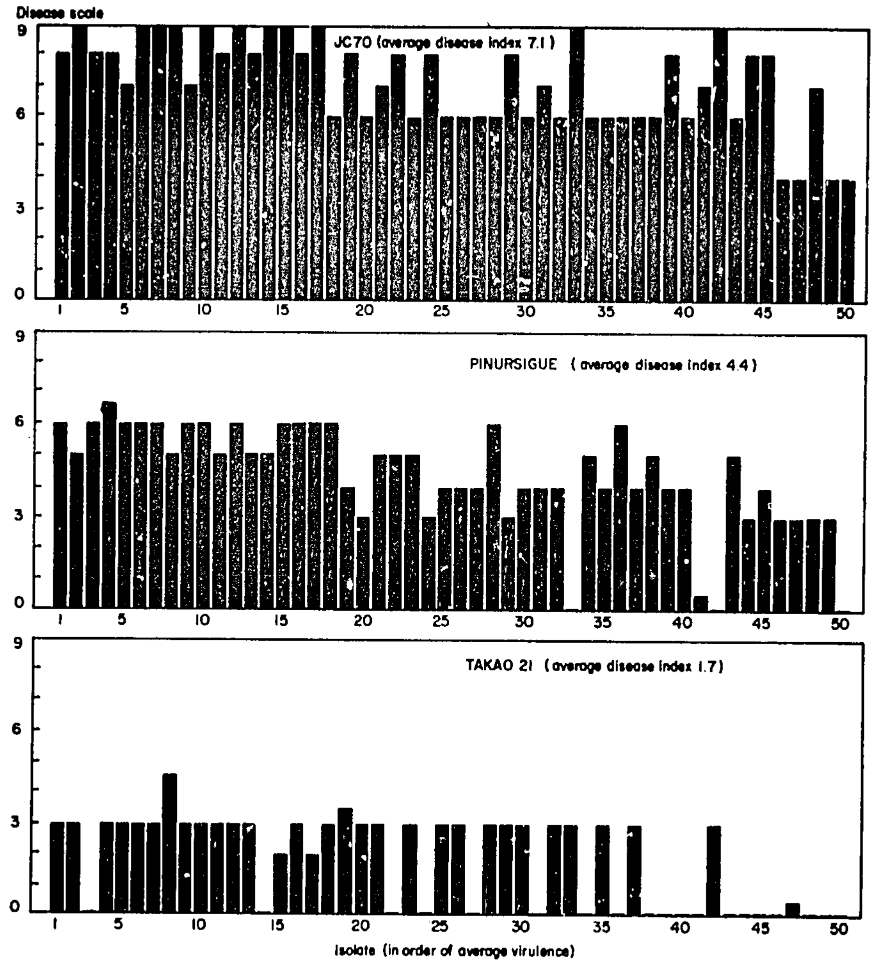
Varietal resistance to bacterial leaf blight would have wider and more lasting use if it had a broader spectrum. Studies show that certain varieties have a non-differential reaction to bacterial isolates. These varieties promise a more stable resistance. Continuous selection within isolates of the more virulent single colonies of the causal organism of bacterial leaf blight resulted in still greater virulence in the subcultures. The virulent subcultures may be used, in addition to field isolates, for testing varietal resistance.

BROAD-SPECTRUM RESISTANCE AND NON-DIFFERENTIAL INTERACTIONS

Our study of the reaction of 24 rice varieties to 50 strains of *Xanthomonas oryzae* (Ou, Nuque, and Silva, 1971*a*) showed that some varieties are generally resistant to all strains, some are intermediate, and others are generally more susceptible to all strains. Figure 1 shows three representative varieties: JC-70 is susceptible, Pinursigue is intermediate, and Takao-21 (Kaohsiung 21) is resistant. On this basis a group of varieties with a high degree of resistance to the Philippine strains was selected (Ou, Nuque, and Silva, 1971*b*). These varieties, however, become moderately susceptible or susceptible when tested with different virulent strains from India, Ceylon, Burma, and other countries. Some are susceptible to several of the virulent strains while others are susceptible to a few. Only varieties such as BJ 1 remained resistant against all isolates so far tested in Hawaii. Varieties that have a broad spectrum of resistance should be resistant to most strains in various countries. An international cooperative program is therefore necessary for testing resistance.

"Differential" and "non-differential" reactions were observed among varieties. "Non-differential" varieties are those that react similarly to all isolates, while "differential" varieties react differently to different isolates. These types of reaction are shown by three varieties in figure 2. Variety 221/BCIV/1/45/5/1 is, on the average, more resistant. It has a susceptibility index (to all 50 strains) of 2.9 but its reaction is differential, i.e. it is very susceptible to two strains while it is resistant to all others. Variety DJ 31 has a susceptibility index of 3.2 but its reaction is more or less non-differential, i.e. its reactions to all strains are similar. Variety BPI-76 has a susceptibility index of 5.1 and is generally susceptible and also differential.

S. H. Ou. International Rice Research Institute.

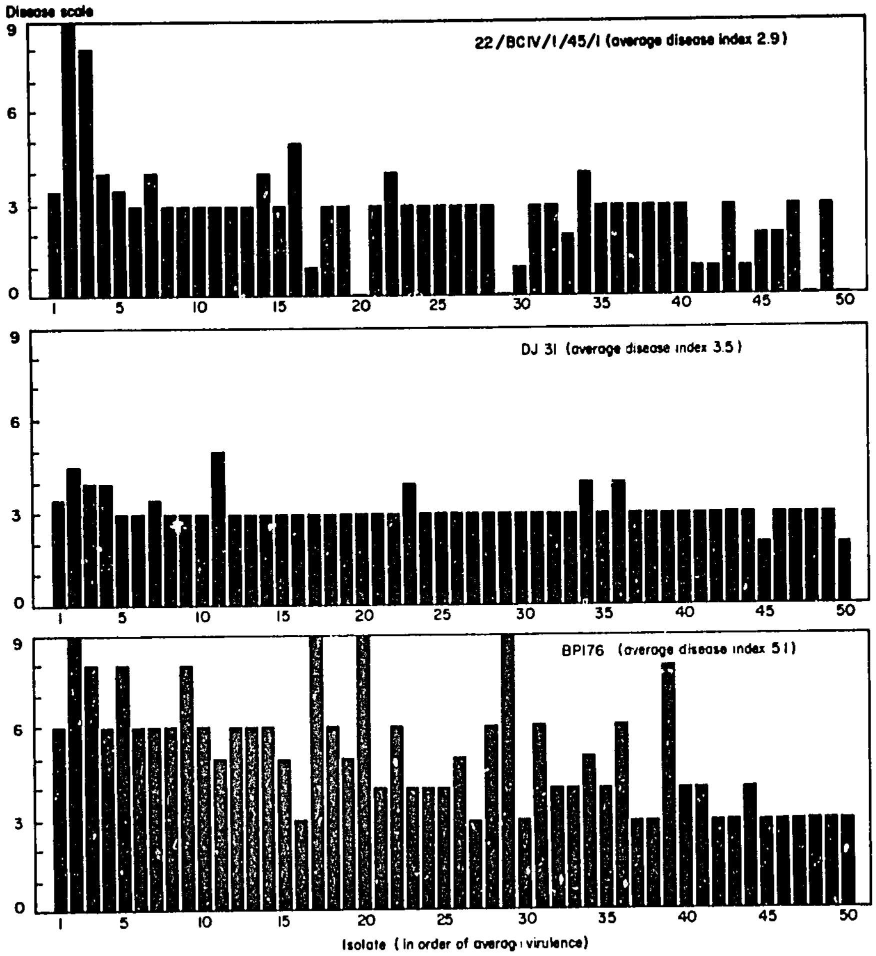


1. Reactions of three representative rice varieties to bacterial isolates on a disease scale of 0 to 9: susceptible (top), intermediate (middle), and resistant (bottom).

It is practically impossible, whether by artificial inoculation or by natural infection in the field, to test all existing strains of the bacterium, as it is impossible to test new strains that might develop in the future. A variety may have high resistance to the test strains, but if it has a variable reaction, it may not be as resistant to new virulent strains. A variety with a non-differential reaction promises a more stable resistance, even against new virulent strains, if it has a relatively high resistance. A search for varieties with such non-differential resistance should be undertaken.

PATHOGENIC VARIABILITY OF *XANTHOMONAS ORYZAE*

As mentioned, it is difficult to obtain all the virulent strains of the bacterium for testing varietal resistance. Is it possible to select more virulent strains in

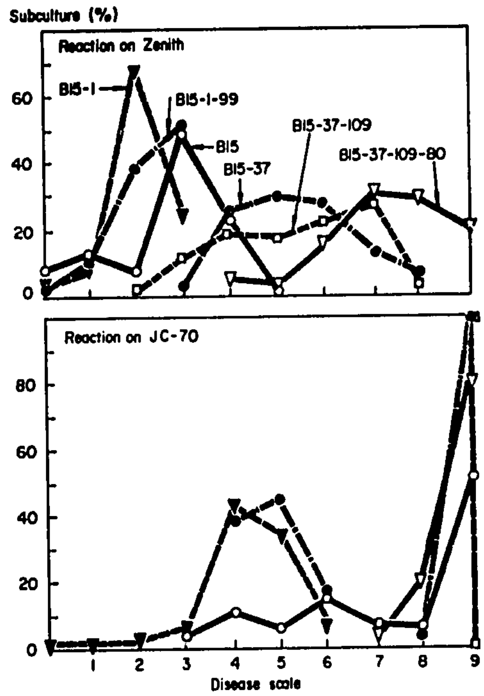


2. Reactions of three representative rice varieties to 50 bacterial isolates on a disease scale of 0 to 9: wide-spread or differential (top and bottom) and narrow-ranged or non-differential (middle).

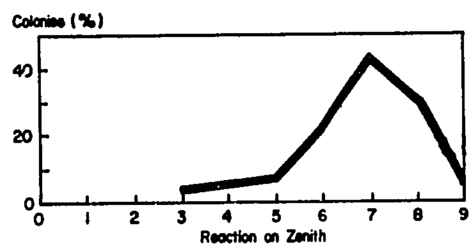
the laboratory and greenhouse from the virulent strains already in culture? It may (IRRI, 1970).

Strain B15, a virulent strain, originally had a reaction of 3 (on a pathogenicity scale of 0 to 9) on Zenith, a resistant variety, and caused 50 percent kresek symptoms (a reaction of 9) on JC-70, a susceptible variety. Continuous selection toward more virulent colonies increased the virulence of subcultures (fig. 3). Fifty percent of single colonies of B15-37-109, a further selection of B15, produced reactions of 6 to 8 and a peak of 7 on Zenith, and 20 percent of single colonies of a further selection, B15-37-109-80, produced kresek symptoms on Zenith. Zenith therefore became very susceptible. B15-37-109 also completely killed variety JC-70. Continuous selection of weakly virulent single colonies, however, tended to reduce the virulence of subcultures.

The isolation of single colonies of the organism from a diseased leaf for pure



3. Variation in pathogenicity among single-colony subcultures of strain B15 (*Xanthomonas oryzae*) by repeated selection.



4. Pathogenicity of single-colony isolates from a single infected leaf lesion on variety Zenith.

culture should also be considered. A mixture of colonies with low and high virulence seems to result when colonies are plated out in a medium from diseased leaves (fig. 4). When one colony is isolated for pure culture it may be either weakly or highly virulent, and it does not represent the specimen. Variation in pathogenicity of *X. oryzae* therefore deserves further study.

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Studies on the inheritance of resistance to bacterial leaf blight in rice varieties

V. V. S. Murty, Gurdev S. Khush

Breeding for resistance to bacterial leaf blight is an important objective of the IRRI breeding program. Several resistant varieties from different geographical areas have been used in the hybridization program. The inheritance of resistance and the allelic relationships of the resistance genes of these varieties using B15-37 of *Xanthomonas oryzae* are under investigation. The resistance may be either dominant, incompletely dominant, or recessive, depending upon the variety. The resistance of BJ1 appears to be controlled by one gene while the resistance of DZ 192 seems to be conditioned by two recessive genes.

Bacterial leaf blight of rice, which is caused by *Xanthomonas oryzae*, was first reported in Japan in 1890 (Ishiyama, 1928; Tagami and Mizukami, 1962). Since then it has been reported from almost all important rice-growing countries of Asia. With the introduction of high yielding and photoperiod-insensitive varieties, farmers have started using intensive agronomic practices, such as application of high rates of nitrogen fertilizers, closer spacing, weed control, and better water management. In several tropical and subtropical countries the area under continous cropping with rice is increasing. All these practices favor the development of the disease. To combat the losses caused by bacterial leaf blight, resistant varieties with high yield potential are being developed at IRRI and elsewhere.

Several resistant varieties from different rice-growing countries have been used in IRRI's hybridization program as sources of resistance. Some of these varieties, such as Sigadis, BJ 1, and TKM-6, are indicas, while Wase Aikoku 3 and PI 215936 are japonicas. Zenith and B589A4-18-1 are the products of indica-japonica hybridizations. The inheritance of resistance in most of these varieties has not been studied. Moreover it is not known whether these varieties have the same or different genes for resistance. Efforts are being made to identify varieties with a broad spectrum of resistance. Investigations aimed at determining the inheritance of resistance and the allelic relationships of the resistance genes are under way.

Some resistant varieties have been tested at a few locations in other countries. For example Sigadis has shown resistance in Ceylon, Indonesia, India, and Thailand. Zenith is resistant in Ceylon, Philippines, and Thailand but is susceptible in India. TKM-6 and Tadukan have been found to be resistant at all

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Table 1. Varieties used in the study of inheritance of resistance to isolate B15-37 of *Xanthomonas oryzae*.

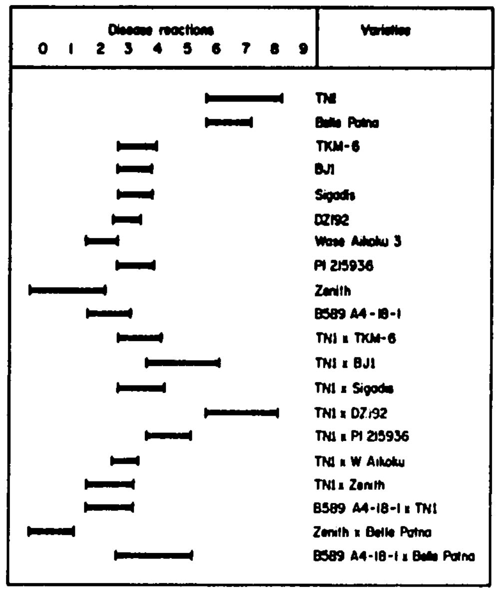
Variety	Origin	Classification	Height	Reaction to isolate
Taichung Native 1	Taiwan	Indica	Short	Susceptible
Belle Patna	U.S.A.	Indica-japonica	Intermediate	Susceptible
TKM-6	India	Indica	Tall	Resistant
BJ 1	India	Indica	Tall	Resistant
Sigadis	Indonesia	Indica	Tall	Resistant
DZ 192	Pakistan	Indica	Tall	Resistant
Wase Aikoku 3	Japan	Japonica	Short	Resistant
PI 215936 (Tainan iku 487)	Taiwan	Japonica	Intermediate	Resistant
Zenith	U.S.A.	Indica-japonica	Intermediate	Resistant
B589A4-18-1	U.S.A.	Indica-japonica	Intermediate	Resistant

test locations. In the laboratory BJ 1, appears to have a broader spectrum of resistance than other varieties (S. H. Ou, *personal communication*).

A few workers investigating the inheritance of resistance in several cross combinations between resistant and susceptible varieties in the Philippines found the resistance to be dominant in some varieties and recessive in others (IRRI, 1967). Sakaguchi (1967) reported two linked genes for resistance, *Xa-1* and *Xa-2*. The varieties of Kidama group carry *Xa-1* which conveys resistance to group I of the bacterial isolates. The Rantajemas group of varieties carry *Xa-1* and *Xa-2*; *Xa-2* conveys resistance to group II of the bacterial isolates. According to Washio, Kariya, and Toriyama (1966), resistance to bacterial group A in variety Kidama is controlled by two complementary dominant genes, *Xa-1* and *Xa-2*. Resistance to bacterial group A in Norin 274 and Kanto 60 is conditioned by a dominant gene. In crosses between Norin 27 and Asahi I and between Norin 27 and Norin 18 the resistance of Norin 27 is governed by a single dominant gene. The resistance of Sigadis to Philippine isolate 72 of the bacterium was conditioned by a pair of alleles and resistance was reported to be incompletely dominant (Heu, Chang, and Beachell, 1968). The resistance of Lacrosse x Zenith-Nira selection to an Indian isolate was governed by a single recessive gene (All-India Coordinated Rice Improvement Project, 1969).

We have been investigating the inheritance of resistance in selected varieties. Table 1 lists the resistant and susceptible varieties used in the study, their taxonomic classification, and their countries of origin. A highly virulent strain of the bacterium B15-37 from the Philippines was inoculated to the varieties by the pinprick method (Muko and Yoshida, 1951; Ou, Nuque, and Silva, 1971). At least three flag leaves were inoculated per plant. Disease reactions were scored 20 days after inoculation on a scale of 0 to 9 (0, highly resistant; 9, highly susceptible). Plants with reaction scores of 0 to 3 were classified as resistant while those with 4 to 9 were classified as susceptible.

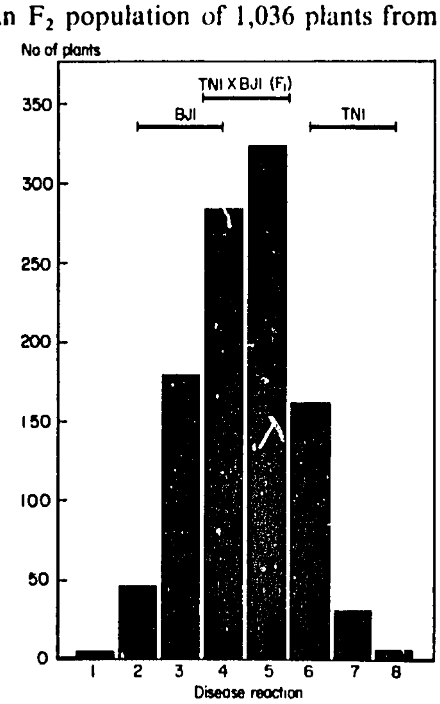
The reactions of the parents and F_1 hybrids to isolate B15-37 of the bacterium are given in figure 1. The resistant parents differ in their level of resistance.



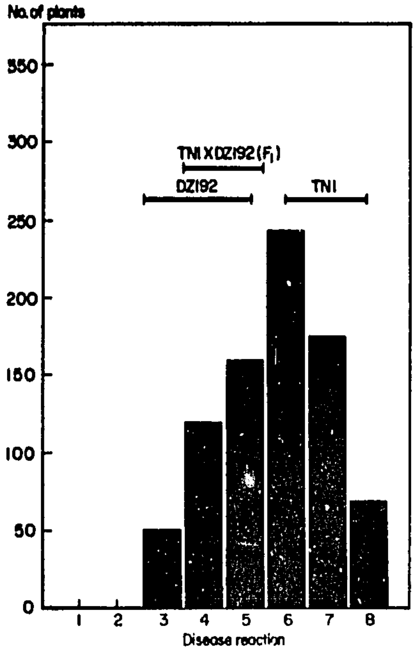
1. Disease reactions of parents and F_1 hybrids to isolate B15-37 of *Xanthomonas oryzae* (0 to 3 = resistant; 4 to 9 = susceptible).

Zenith and Wase Aikoku 3 are the most resistant among the resistant group. The reactions of the F_1 hybrids indicate that resistance is dominant in TKM-6, Sigadis, Wase Aikoku 3, Zenith, and B589A4-18-1; incompletely dominant in BJ 1 and PI 215936; and recessive in DZ 192.

The F_2 and F_3 populations are being studied to determine the inheritance of resistance in different varieties. In an F_2 population of 1,036 plants from



2. Disease reactions of parents, F_1 and F_2 populations of Taichung Native 1 x BJ 1 to isolate B15-37 of *X. oryzae*.



3. Disease reactions of parents, F_1 and F_2 populations of Taichung Native 1 x DZ 192 to isolate B15-37 of *X. oryzae*.

the Taichung Native 1 x BJ 1 cross, 229 plants were resistant and 807 were susceptible, indicating monogenic control of resistance (fig. 2). The F_2 population of 792 plants from Taichung Native 1 x DZ 192 segregated into 51 resistant and 741 susceptible plants (fig. 3), giving a ratio of 1 resistant to 15 susceptible. It appears that recessive alleles at two loci condition resistance in DZ 192. Segregating populations from other crosses are being studied. F_2 populations from crosses between resistant varieties are also being studied.

Previous work as well as the preliminary results of the present study indicate that the mode of inheritance of resistance to bacterial leaf blight in different varieties may be under monogenic or digenic control. The resistance may be dominant, incompletely dominant, or recessive. It thus appears that different resistant varieties may have different genes for resistance. We expect results from crosses between different resistant varieties to yield critical information. If different genes for resistance are identified resistant varieties could be bred with diverse genes for resistance. Thus if new races of the pathogen are able to attack a resistant variety, a second resistant variety with a different gene would serve as protection.

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Discussion of papers on bacterial leaf blight

T. T. CHANG: For rice breeders who might depend on natural infections to score varietal reactions to the bacterial leaf blight pathogen, it is important to score and compare disease readings at the same stage of plant growth because leaf reactions become more severe as leaf senescence begins.

H. D. Kauffman: Yes, varieties of all durations should be scored during the 2 to 3 weeks from flowering to maturity. Each variety should be scored at least three to four times during this period.

R. FEUER: Is the incidence and severity of bacterial leaf blight as serious on farmers' fields, where only one-third to perhaps two-thirds of the nitrogen levels of experimental fields, or of recommendations are used?

H. D. Kauffman: The amount of disease depends on the nitrogen fertility level of the soil. Crops grown on fertile soils show more disease at lower rates of applied nitrogen than in unfertile soils.

T. H. JOHNSTON: From a practical standpoint, will splitting the nitrogen application and topdressing according to plant development help to hold down the level of damage from bacterial blight in the farmer's field as it has with blast disease?

H. D. Kauffman: Yes, from preliminary experiments it looks like the split levels of nitrogen application can reduce the disease to some extent.

P. R. JENNINGS: How long do the bacterial blight pathogen remain viable on infected seeds?

S. H. Ou: No bacteria were recovered from seeds at 30 days following harvest under Los Baños conditions.

H. D. Kauffman: We have isolated bacteria from seeds later than 30 days after harvest. But there is no transmission through seed.

H. I. OKA: Isn't it too early to estimate the number of genes controlling the blight reaction from the pattern of F_2 segregation?

G. S. Khush: I mentioned that this is only a preliminary report and we are trying to verify the results from the study of F_3 families.

Breeding for disease and insect resistance at IRRI

Gurdev S. Khush, H. M. Beachell

Six diseases, blast, sheath blight, bacterial leaf blight, bacterial leaf streak, tungro, and grassy stunt, and four insect species, stem borers, green leafhoppers, brown planthoppers, and gall midge, attack the rice crop in most rice-growing countries of tropical Asia. To prevent the losses caused by these diseases and insects, resistant varieties are being developed at IRRI. Several sources of resistance to each disease and insect have been identified in the IRRI collection of rice varieties. These varieties were crossed with semidwarf, high yielding varieties or selections, and resistant lines with improved plant type were obtained. These lines were intercrossed to combine the sources of resistance to different diseases and insects. Selections from these crosses are resistant to several diseases and insects. In a new series of crosses, diverse sources of resistance are being combined to provide the new varieties with a defense mechanism against any new strains or races of the diseases or insects that may develop. Nothing is known about the relative stability of major gene resistance as compared with polygenic resistance in rice. The major gene for resistance to green leafhopper in Indonesian varieties has been effective for the last 30 years. However, polygenic variation for resistance to brown planthopper and stem borer is being exploited in the breeding program.

INTRODUCTION

The tropical climate is ideal for rice growing and for proliferation of disease organisms and insect populations throughout the year. Consequently diseases and insects take a heavy toll on rice production. Rice has traditionally been grown in the tropics without protection against pests and diseases. A small number of the tall, traditional varieties of Asia are resistant to one or more diseases or insect pests, but most of them are susceptible to several diseases and insects. Little research has been done on the chemical control of rice diseases in the tropics. It is difficult to control high populations of pathogens with chemicals for prolonged periods under the monsoon climate. Moreover, the economic and social conditions of the tropics present serious obstacles to chemical control of rice diseases and pests. Since rice varieties resistant to major diseases and insects would suppress the build-up of insect and plant pathogen populations and thus minimize yield losses, breeding for disease and insect resistance is a major objective of the IRRI breeding program.

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DISEASES OF RICE IN THE TROPICS

The important fungus diseases of rice are blast (caused by *Piricularia oryzae*), sheath blight (caused by *Corticium sasakii*), stem rot (caused by *Helminthosporium sigmoideum*), and brown leaf spot (caused by *Helminthosporium oryzae*). Blast occurs throughout the world and is probably the most serious disease of rice. The pathogen is highly variable and many different races occur in the rice-growing areas. The fungus can attack the rice plant at all stages of growth, from seedling to flowering. It causes serious yield losses and even total crop failures. Sheath blight and stem rot cause some damage in certain seasons. Besides causing direct yield reduction, they reduce the straw strength and make the crop more likely to lodge. Brown leaf spot is a minor disease in the tropics. The Bengal famine of 1942, caused by large-scale crop failure, has been attributed to the attack of *Helminthosporium oryzae*. Rice pathologists believe, however, that *Helminthosporium* by itself does not cause serious damage to the crop. Rather, serious damage is generally associated with other primary problems, such as nutritional and physiological disorders (Baba, 1958; Abeygunawardena, 1967; S. H. Ou, *personal communication*). With the introduction of high yielding varieties, management practices have improved. Thus the danger of large-scale attacks of the disease should be much reduced.

Two bacterial diseases of rice in tropical Asia, bacterial leaf blight (caused by *Xanthomonas oryzae*) and bacterial leaf streak (caused by *Xanthomonas translucens* f. sp. *oryzicola*), occur widely. Bacterial leaf blight is more destructive. It can attack the rice crop at all stages of growth. When a serious attack at seedling stage kills the entire crop, the disease is referred to as kresek. Such attacks have caused heavy losses in Indonesia (Siwi and Oka, 1967). The better known symptoms of the disease are blighting of the leaves of the adult plant. These symptoms appear more often after the panicle-emergence stage and yield losses are serious. Bacterial leaf streak is not a very serious disease. Its attack occurs in the rainy season, generally after typhoons and heavy rains which cause leaf injury and disseminate the bacterial cells.

Four virus diseases, tungro, grassy stunt, yellow dwarf, and orange leaf, occur widely in tropical Asia. Of these tungro (also known as "yellow-orange leaf" in Thailand, "penyakit merah" in Malaysia, "mentek" in Indonesia and "yellowing" in India) is by far the most important. This virus, transmitted by the green leafhopper, *Nephotettix impicticeps*, has been reported in most major rice-growing countries of tropical Asia (Ou and Jennings, 1969). Serious outbreaks of the disease have occurred in Indonesia (Siwi and Oka, 1967), Malaysia (Van, 1967), India (All-India Coordinated Rice Improvement Project, 1969), Thailand (Wathanakul and Weerapat, 1969), and East Pakistan (Alim, 1967). Several thousand hectares of the crop were badly affected in the Philippines in 1970 and 1971.

Grassy stunt disease is not as widespread as tungro but it is potentially destructive. Besides the Philippines, it occurs in India (Raychaudhuri, Mishra, and Ghosh, 1969), Ceylon (Abeygunawardena, 1969), Malaysia (Ou and Rivera, 1969), Thailand (Wathanakul and Weerapat, 1969), and East Pakistan

(P. C. Lippold, *unpublished*). In 1970 serious outbreaks occurred in Bacolod and Cotabato, two widely separated areas of the Philippines. With the development of irrigation facilities and the introduction of continuous rice cropping, the incidence of this disease is likely to increase. The virus is transmitted by the brown planthopper, *Nilaparvata lugens* (Rivera, Ou, and Iida, 1966).

Yellow-dwarf and orange-leaf viruses are of minor importance and it is unlikely that they would ever become serious diseases in the tropics. The incubation period for yellow dwarf in the vectors and the plant is more than a month. But this disease could become a serious problem on the ratoon crop, if large-scale ratooning is introduced in Asia. Orange-leaf may be termed a self-eliminating disease. The infected plants do not live long, thus limiting the source of inoculum.

Hoja blanca has been a devastating virus disease of rice in parts of Latin America. It does not occur in Asia, however. Sources of resistance to the virus and its vector, *Sogatodes orizicola*, are available and are being used in the breeding program of Centro Internacional de Agricultura Tropical (Jennings and Pineda, 1970).

INSECT PESTS OF RICE IN THE TROPICS

The insect species which cause severe yield losses in rice are the stem borer, the green leafhopper, the brown planthopper, and the gall midge.

Stem borers cause severe losses at the vegetative as well as at the reproductive stage of the plant. When the vegetative tillers attacked by the stem borer larvae die, a condition known as "dead heart" results. If the attack occurs after the panicle emergence stage, the entire panicle dies without producing any grain. This condition is referred to as "white head." Several stem borer species are present in different rice-growing countries of Asia (Pathak et al., 1971). The striped borer (*Chilo suppressalis*), the yellow borer (*Tryporyza incertula*), the white borer (*Tryporyza innotata*), the dark-headed borer (*Chilotraea polychrysa*), and the pink borer (*Sesamia inferens*) are the most important species.

Light infestations of green leafhoppers and brown planthoppers reduce the overall vigor of the crop and cause a decrease in the number of productive tillers per plant and an increase in the percentage of unfilled grains. Heavy infestations cause a complete drying of plants, a condition commonly known as "hopperburn." In addition to causing physical damage to the rice plant, the leafhopper and planthopper species are vectors of virus diseases.

The rice gall midge is a serious pest in some parts of India, Ceylon, East Pakistan, Thailand, Vietnam, and Indonesia. The typical damage is a tubular gall, resembling an onion leaf. The tillers that have galls do not produce panicles because the larvae of the gall midge feed on the growing point and destroy it. Heavy infestations of the insect can wipe out entire rice fields.

Based on the extent of the damage they cause and their distribution, five diseases and four insect species are considered of major importance: blast, bacterial leaf blight, bacterial leaf streak, tungro, grassy stunt, stem borers, green leafhoppers, brown planthoppers, and gall midge (Beachell and Khush, 1969). Efforts are under way to develop varieties resistant to these insects and diseases.

SOURCES OF RESISTANCE

Before a program for resistance breeding can be launched, sources of resistance must be identified and techniques for rapid screening of hybrid populations must be developed. IRRI pathologists and entomologists have developed such techniques, they have screened varieties in the world collection of rice, and they have identified a number of outstanding sources of resistance to the major diseases and insects.

Several blast-resistant varieties have been identified through the International Blast Nursery Program (Ou, 1965; Ou, Nuque, and Ebron, 1970). The varieties used in the breeding program as sources of blast resistance are listed in Table 1. Recent studies at IRRI (Ou, Nuque, Ebron, and Awoderu, 1971) indicate that Tetep and Carreon have a broader spectrum of resistance than other varieties. The emphasis of the breeding program for blast resistance has shifted to these varieties, especially Tetep.

Several dozen varieties with resistance to bacterial leaf blight have been identified (Ou, Nuque, and Silva, 1971). Some, like BJ 1, appear to have a broad spectrum of resistance. Table 1 lists the varieties resistant to bacterial leaf blight being used in the IRRI breeding program. The resistant varieties come from different geographical areas and probably have different genes for resistance.

Several varieties are resistant to bacterial leaf streak (Goto, 1965; Ou, Franck, and Merca, 1970). Zenith, CP-SLO, DZ 192, Malagkit Sungsong, and IR127-80-1, a breeding line from a cross of CP-SLO and Sigadis, are excellent sources of resistance (Table 1).

Many tungro-resistant varieties have been identified (Ling, 1969). The important ones are listed in Table 1. Pankhari 203 from India has the highest level of resistance and consequently has been used as a parent in several crosses. Several related varieties from Indonesia which were specifically bred for tungro resistance in the late 1930's such as Peta, Mas, Bengawan, and Intan are good sources of resistance.

Over 6,700 varieties in the world collection were screened for resistance to grassy stunt but none were resistant. Available collections of several wild species of *Oryza* were then screened and one accession of *O. nivara* from central India was found to be highly resistant (Ling, Aguiero, and Lee, 1970). The resistance to grassy stunt in this species is governed by a single dominant gene (G. S. Khush, *unpublished*).

A large number of varieties resistant to the green leafhopper have been isolated from the world collection (Pathak, Cheng, and Fortuno, 1969; Cheng and Pathak, 1971). The ones being used as sources of resistance in the breeding program are listed in Table 1. This group includes varieties with different genes for resistance. Thus Pankhari 203 has the *Glh-1* gene, ASD 7 has *Glh-2* and IR8 has *Glh-3* (Athwal et al., 1971).

The varieties resistant to brown planthopper that are used as sources of resistance in the breeding program (Table 1) were identified by Pathak et al., (1969). Several other varieties from India and Ceylon are resistant to this pest (IRRI, 1971). The resistance of Mudgo, CO 22, and MTU 15 is governed by a single dominant gene, *Bph-1*, and that of ASD 7, by a single recessive gene, *bph-2* (Athwal et al., 1971). Recently two dwarf selections IR747B2-6 and IR1154-243, were found to be resistant to the brown planthopper (IRRI, 1970) and are now being used in the breeding program. The origin of the resistance in these two selections, whose parents are susceptible, is being studied. The dominant gene for resistance of IR747B2-6 is allelic to that of Mudgo while the recessive gene of IR1154-243 is allelic to that of ASD 7. Moreover H-105 has the same recessive gene for resistance as ASD 7 (C. R. Martinez, *unpublished*).

Several sources of resistance to stem borer are being used (Table 1). TKM-6, EK 1263, Ptb 18, and Ptb 21 which have good levels of resistance to stem borers are also resistant to several other insect pests. The varieties resistant to the gall midge mainly come from the Indian subcontinent. EK 1263, which inherited its resistance from Eswarakora, and Ptb 18 have been used in the crossing program.

Table 1. Disease and insect resistance of parental varieties used as sources of resistance in the breeding program.

IRRI acc. no.	Variety	Disease and insect resistance[a]								
		BL	BLB	BLS	TG	GS	GLH	BPH	GM	SB
11115	Tetep	R	S	MR	S	S	S	S	—	—
5993	Carreon	R	S	S	S	S	S	S	—	—
131	Zenith	R	R	R	S	S	S	S	—	S
9804	Tadukan	R	R	R	MR	S	S	S	—	—
256	BJ 1	S	R	S	S	S	S	S	—	—
9797	B589A4-18-1	R	R	R	S	S	S	S	—	S
237	TKM-6	S	R	MR	MR	MS	MS	MS	—	R
611	Sigadis	R	R	MR	R	S	R	S	—	—
4066	CP 231 x SLO-17	S	R	R	S	S	S	S	—	S
8518	DZ 192	S	R	R	S	S	S	S	—	—
599	Malagkit Sungsong	S	R	R	S	S	S	S	—	—
5999	Pankhari 203	S	S	S	R	S	R	S	—	—
3634	Peta	MR	S	S	R	S	R	S	—	MR
3612	Mas	S	S	S	R	S	R	S	—	—
633	HR 21	S	S	S	R	S	S	S	—	—
101508	*Oryza nivara*	S	S	MR	S	R	S	S	—	—
6663	Mudgo	S	S	S	S	S	S	R	—	MR
158	H-105	R	S	S	S	S	MS	R	—	—
6303	ASD 7	S	S	S	S	S	R	R	—	MR
11057	EK 1263	S	MS	MR	R	MS	R	R	R	R
11052	Ptb 18	S	S	S	R	MS	R	R	R	R

[a]BL = blast, BLB = bacterial leaf blight, BLS = bacterial leaf streak, TG = tungro, GS = grassy stunt, GLH = green leafhopper, BPH = brown planthopper, GM = gall midge, SB = stem borers, R = resistant, S = susceptible, MR = moderately resistant, MS = moderately susceptible.

BREEDING FOR RESISTANCE

Most varieties that have been identified as sources of disease and insect resistance have poor plant type and low yield potential. As a first step in the IRRI breeding program, we cross these varieties with a variety that has improved plant type, such as Taichung Native 1 or IR8, or a breeding line, such as IR262-43-8. Dwarf lines with improved plant type are screened for the resistance traits of the tall parents in these crosses. The pedigree method is being used in handling the segregating generations. We use part of the seed from the plant selections for planting the pedigree rows and the rest for disease and insect screening.

Sometimes it is difficult to recover lines that have good plant type from single crosses. One or two backcrosses to the improved plant-type parent are therefore made in certain combinations. Occasionally the F_1 is crossed to a third improved plant-type parent to obtain a three-way cross.

Most of the important sources of resistance to major diseases and pests have been incorporated into lines that have improved plant type. Some lines were considered promising enough to be named as varieties, while others have proved to be good parents in the new crosses. Data on disease and insect resistance of the named varieties and of the promising selections are given in Table 2.

Some of the newer crosses made to combine the factors for disease and insect resistance are reviewed below.

Blast

The varieties Tetep and Carreon which have broad spectrum of resistance to blast have been crossed with high yielding dwarf selections. Tetep was crossed with IR400-28-4 and with IR24 while Carreon was crossed with IR24. Several selections from these crosses have resistance to blast, tungro, bacterial leaf streak, and green leafhopper (Table 3). Many of them have long, slender, and translucent grains. Tetep has combined very well with the semidwarf plant type but most of the lines from the Carreon cross have poor plant type. Some of the blast-resistant lines from this cross have been crossed again to a selection with desirable plant type. Selections from Tetep crosses identified as resistant to blast at Los Baños are being tested in other countries to identify those with a broad spectrum of resistance. Blast-resistant semidwarf lines from Dawn, Zenith, and Kataktara are parents of several new crosses.

Sheath blight

A lack of sources of resistance has delayed the breeding program on sheath blight. S. H. Ou, IRRI plant pathologist, recently identified some varieties that appear to have a good level of resistance and we have begun a crossing program with these varieties.

Bacterial leaf blight

Lines from crosses of Sigadis (IR127-80-1), Zenith (IR498-1-88), B589A4-18-1 (IR790-28-1), Tadukan (IR22), BJ 1, and Wase Aikoku 3 that have improved plant type and are resistant to bacterial leaf blight have been crossed with other

Table 2. Data on disease and insect resistance of named varieties and promising breeding lines.

Selection or variety	Parents	Disease and insect resistance						
		BL	BLB	BLS	TG	GS	GLH	BPH
IR5	Peta x Tangkai Rotan	MR	S	S	S	S	R	S
IR8	Peta x Dee-geo-woo-gen	MR	S	S	S	S	R	S
IR20	(Peta/3 x TN1) x TKM-6	MR	R	MR	R	MS	R/S	S
IR22	IR8 x Tadukan	S	R	S	S	S	S	S
IR24	(CP-SLO x Sigadis) x IR8	MR	S	MR	R	S	R	MS
IR4-93	H 105 x Dee-geo-woo-gen	R	S	S	S	S	S	R
IR127-80-1	CP-SLO x Sigadis	MR	R	R	R	S	R	S
IR140-136	CP-SLO x Mas	S	S	R	R	S	R	S
IR305-3-17	Sigadis/2 x TN1	R	R	MR	MR	S	R	MS
IR262-43-8	Peta/3 x TN1	MR	S	S	R	S	R	S
IR400-5-12	Peta/4 x TN1	MR	S	S	MR	S	R	S
IR503-1-104	(Peta/3 x TN1) x (B589A4-18-1 x TN1)	R	S	MR	S	S	R	S
IR579-48-1	IR8 x Tadukan	S	R	S	S	S	S	S
IR665-40	IR8 x (Peta/5 x Belle Patna)	MR	S	MR	S	S	R	S
IR751-595	IR8/2 x (Peta/5 x Belle Patna)	MR	MR	S	S	S	R	S
IR878B4-220-3	IR8/2 x (CP-SLO x Nahng Mon S-4)	R	MS	S	S	S	R	S
IR841-67-1	(Peta/3 x TN1) x Khao Dawk Mali	MR	S	S	S	S	R	S
IR790-28-1	IR400 x {IR8 x [IR4-253-3 x (B589A4-18-1/2 x TN1)]}	R	R	R	S	S	S	S
IR825-28-4	(IR8 x Pankhari 203) x (Peta/6 x TN1)	S	S	S	R	S	R	S
IR747B2-6	TKM-6/2 x TN1	MR	R	MR	R	S	S	R
IR1154-243	IR8/2 x Zenith	S	MR	S	S	S	S	R
IR833-6-2	(Peta/3 x TN1) x Gam Pai 15	R	S	S	MR	S	R	S
IR759-86-3	IR8 x (Peta/3 x Dawn)	R	MR	MR	S	S	R	S

disease- and insect-resistant lines. Selections from IR1480 (IR790-28-1 x IR825-28-4) and IR1487 (IR127-80-1 x IR442-2-50) combine sources of resistance to bacterial leaf blight, blast, bacterial leaf streak, tungro, and green leafhoppers. The resistance of IR22 to bacterial leaf blight has been combined with resistance to green leafhoppers and brown planthoppers in IR1614 lines (Table 3). All the lines from these crosses have excellent grain quality and high yield potential.

Bacterial leaf streak

Several parent lines resistant to bacterial leaf blight are also resistant to bacterial leaf streak. Thus several lines resistant to bacterial leaf blight from the crosses IR1480, IR1487, and IR1529 are also resistant to bacterial leaf streak. DZ 192, a highly resistant variety, was crossed with IR24 and many lines from this cross (IR1545) combine resistance to bacterial leaf streak, bacterial leaf blight, tungro, and green leafhopper (Table 3) and have excellent grain quality.

Table 3. Various disease and insect resistance traits which have been combined into the selections of some recent crosses.

Cross	Parents	Disease and insect resistance								
		BL	BLB	BLS	TG	GS	GLH	BPH	GM	SB
IR1330	(IR8 x Leuang Tawng) x EK 1263	S	MR	MR	R	MS	R	R	R	R
IR1480	IR790-28-1 x IR825-28-4	R	R	MR	R	S	R	S	S	S
IR1487	(CP-SLO x Sigadis x [(Peta/2 x TN1) x Leb Muc Nahng]	MR	R	R	R	S	R	S	S	S
IR1529	(Sigadis/2 x TN1) x IR24	R	R	R	R	S	R	MS	S	S
IR1539	IR24 x (Mudgo x IR8)	MR	MR	R	R	S	R	R	S	S
IR1541	IR24 x TKM-6	MR	R	R	R	S	R	R	S	R
IR1542	IR24 x Carreon	R	S	S	R	S	R	S	S	S
IR1544	IR24 x Tetep	R	MR	MR	R	S	R	S	S	S
IR1545	IR24 x DZ 192	MR	R	R	R	S	R	S	S	S
IR1561	(IR8 x Tadukan) x (TKM-6/2 x TN1)	MR	R	MS	R	S	S	R	S	R
IR1614	IR22 x (Mudgo x IR8)	S	R	MR	S	S	R	R	S	S
IR1721	IR24/3 x *Oryza nivara*	S	S	R	R	R	R	S	S	S

Tungro

Tungro-resistant lines with improved plant type from crosses of Pankhari, Sigadis, and HR 21 are sources of resistance to tungro in new crosses. Thus selections of IR1480 inherit their resistance from IR825-28-4, a selection from a triple cross (IR8 x Pankhari 203) x (Peta/6 x TN1). Similarly, the tungro resistance of IR1487 lines comes from IR127-80-1 which inherited its resistance from Sigadis. IR1364-37-3 (HR 21 x Peta/3 x TN1) is highly resistant to tungro and is the parent of several new crosses. Many selections from IR24 crosses (Table 3), such as IR1529, IR1539, IR1544, and IR1545 have a good level of tungro resistance.

Grassy stunt

Oryza nivara is the only known source of resistance to grassy stunt. This species has many undesirable agronomic traits, such as a fragile rachis (shattering), weak stems, droopy leaves, squatty and spreading growth habit, long awns, red pericarp, and a high level of sterility. Its desirable traits, besides resistance to grassy stunt, include a high tillering capacity, grain dormancy, and resistance to bacterial leaf streak. To incorporate these desirable traits into the genetic background of high yielding varieties, *O. nivara* was crossed with IR24. IR24 is resistant to tungro virus and its vector, but it has weak grain dormancy, it tillers moderately, and it is highly susceptible to grassy stunt. We have started a backcrossing program with IR24 as the recurrent parent. The backcross F_1 plants are artificially inoculated and only those with desirable traits are used for the next backcross.

Most of the F_1 plants of IR24/3 x *O. nivara* were dwarf, high tillering, awnless, and non-shattering. Most had normal fertility, excellent, long, slender grains, and some had good levels of dormancy. F_2 and F_3 populations of this cross (IR1721) have been evaluated. Many lines with excellent grain appearance and plant type have been identified that have the same level of resistance to grassy stunt as *O. nivara*. In addition they are resistant to bacterial leaf streak and some should have the tungro resistance of IR24. All are resistant to green leafhoppers (Table 3).

Green leafhoppers

Since many varieties resistant to the green leafhopper, such as Peta, IR8, Intan, Pankhari 203, Sigadis, and FB 24, were used in many earlier IRRI crosses, most of our breeding lines are resistant to this insect. Consequently, most of the parental lines of the new crosses are resistant. Resistance to green leafhopper has been combined in all the crosses listed in Table 3 except one.

Brown planthoppers

Although varietal differences in resistance to brown planthoppers were not discovered until 1967 (IRRI, 1968; Pathak et al., 1969), one of the earliest crosses made at IRRI, H-105 x Dee-geo-woo-gen, resulted in selections resistant to brown planthopper such as IR4-93 and IR4-67. These selections inherited the resistance to brown planthoppers as well as to blast from H-105. We started work on combining resistance to brown planthopper with resistance to other diseases and insects in 1969. The *Bph-1* gene of Mudgo has been combined with improved plant type in several crosses. The most promising crosses appear to be IR1539 [IR24 x (Mudgo x IR8)] and IR1614 [IR22 x (IR8 x Mudgo)]. Selections from IR1539 are also resistant to the green leafhopper and tungro and moderately resistant to bacterial leaf streak and blast while those from IR1614 combine resistance to green leafhopper and resistance to bacterial leaf blight. The IR1561 selections combine planthopper and blast resistance of IR747B2-6 and resistance to bacterial leaf blight of IR579-48-1. Selections from this cross mature in 100 to 105 days and have excellent, long, slender grains. In 1970, 230 F_3 dwarf selections from IR1541 (IR24 x TKM-6) were grown in a pedigree nursery and evaluated for resistance to brown planthopper. Two selections were found to be resistant to brown planthopper. The two parents of this cross, IR24 and TKM-6 are susceptible to this pest. Therefore the occurrence of these two resistant lines was unexpected. In addition these lines are resistant to green leafhopper, tungro, bacterial leaf blight, and bacterial leaf streak (Table 3).

Stem borers

Several dwarf lines from TKM-6 crosses with good level of resistance to stem borer are available. Dwarf lines from the crosses of EK 1263 and Ptb 18 are being evaluated for resistance. Several other tall varieties with resistance to stem borer such as Middle Farmer from West Pakistan and Lakhaya from East Pakistan have been obtained and will be used in the hybridization program. Since resistance to stem borers appears to be under polygenic control it will probably take several years to combine a high level of such resistance with other desirable traits.

Gall midge

F_2 bulk seeds from (Leuang Tawng x IR8) x EK 1263 were obtained from Thai rice breeders in 1968. The F_2 bulk population was grown at IRRI in 1969 and plant selections were made for growing in the pedigree nursery. IR1330 was assigned to this cross. F_7 selections from this cross are resistant to tungro, green leafhoppers, and brown planthoppers. Forty selections were evaluated for resistance to gall midge in cooperation with Thai entomologists and breeders and 12 were found to be resistant.

OUTLOOK FOR NEW VARIETIES

Selections from the crosses enumerated in Table 3 are now in the observational yield trials. Most have excellent grains and appear to have good yield potential. Thorough yield testing will be carried out in the replicated trials during 1972. We hope that a few varieties with resistance to several diseases and insects will be named during the next 2 years. Resistance to all the diseases and insects has not been combined in any cross listed in Table 3. But intercrosses between the lines of these crosses have already been made and the F_1 or F_2 populations from such hybridizations are under study. It should be possible to incorporate resistance to all the major diseases and insects into a set of high yielding varieties differing in grain size and shape, cooking quality, and growth duration, during the next 5 to 7 years.

HORIZONTAL VERSUS VERTICAL RESISTANCE

Ou and Jennings (1969) have argued in favor of incorporating horizontal (polygenic or minor gene) resistance, instead of vertical (major gene) resistance, into future rice varieties. In their opinion the polygenic resistance is more stable than major gene or race-specific resistance.

Let us examine what kind of resistance we are dealing with in rice. Atkins and Johnston (1965), Kiyosawa (1967*a*, *b*), and Hsieh, Lin, and Liang (1967) have shown that major genes at several loci govern blast resistance in several varieties. Pathological evidence provided by S. H. Ou (*unpublished*) suggests that minor genes, in addition to major genes, may be conditioning blast resistance in Tetep. Genetic evidence is lacking however. Two complementary genes (IRRI, 1967) convey resistance to tungro and one dominant gene (G. S. Khush, *unpublished*) conveys resistance to grassy stunt. Similarly resistance to bacterial leaf blight is also controlled by one major gene (Sakaguchi, 1967; Heu, Chang, and Beachell, 1968; V. V. S. Murty and G. S. Khush, *unpublished*).

As discussed earlier, resistance to brown planthopper and to green leafhopper is conveyed by major genes (Athwal et al., 1971). Resistance to gall midge is also under major gene control (S. V. S. Shastry and D. V. Seshu, *unpublished*). Resistance to stem borers may be under polygenic control (Koshairy et al., 1957).

It is thus clear that, in rice, we are mainly dealing with major-gene or vertical resistance. While this type of resistance can be easily bred into new varieties, the disadvantage is that the resistant variety may have only a short life. The plant pathogens and insects may develop new races that can attack the resistant variety. Polygenic resistance, on the other hand, is assumed to be less vulnerable to pathogen variation.

Major-gene resistance is short-lived in other cereals such as wheat (Allard, 1960) and oats (Stevens and Scott, 1950). But nothing is known about the relative stability of the polygenic and major-gene resistance in rice. Several varieties resistant to tungro were bred in the 1930's in Indonesia. These varieties, Peta, Mas, Bengawan, and Intan, inherited their resistance from the common parent, Latisail. Recently these varieties were found resistant to the green leafhopper, and they inherited the gene for resistance to green leafhopper from Latisail, too. These varieties have been grown on large areas in Indonesia and the Philippines for at least the last 30 years but their resistance has not broken down. Thus in rice there is at least one example of a single gene for resistance that has remained effective for a long time.

This does not imply that all the major genes for resistance in rice will be as stable as the gene for resistance to green leafhopper. We are trying to incorporate diverse sources of resistance into future varieties. For example, the present emphasis is on combining the resistance of Tetep to blast, the resistance of Sigadis to bacterial leaf blight, the resistance of IR8 to green leafhopper, and the resistance of Mudgo to brown planthopper. In a new series of crosses we will attempt to combine the resistance of Mamoriaka to blast, the resistance of BJ 1 to bacterial leaf blight, and the resistance of ASD 7 to green leafhopper and brown planthopper. This diversity should provide a safety factor if any of the diseases and insects develop new races.

We are always on the lookout for sources of polygenic variation in disease and insect resistance. Varieties like Sigadis, TKM-6, Leb Muc Nahng, and H 8 have some resistance to the brown planthopper, although they do not have the major gene for resistance. Several dwarf selections which lack the major gene for resistance but have some resistance to the insect have been isolated from crosses between Mudgo and other resistant varieties. It appears that modifiers segregate along with the major gene in the crosses between resistant and susceptible varieties. We have isolated from different sources a dozen selections with moderate resistance. We are now trying to combine the minor genes to get higher resistance without the major gene. A similar program is under way to exploit the polygenic variation for resistance to stem borer from TKM-6, EK 1263, Ptb 18, Middle Farmer, and Lakhaya.

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Discussion: Breeding for disease and insect resistance at IRRI

S. C. LITZENBERGER: To date most effort on insect and disease resistance has been concentrated on developing pure lines that incorporate or gradually accumulate resistance to the disease or insects. Do you have any plan for developing populations with multiple-resistance to disease and insects, incorporating the broadest possible known sources of resistance which exist throughout the world? As an international agency, IRRI perhaps should consider this method of improvement in helping developing nations, using the male-sterile technique in developing the populations.

G. S. Khush: We are planning to start breeding populations in the near future. We are particularly interested in starting a breeding population for developing high protein varieties of rice.

J. K. ROY: The incorporation of disease and insect resistance genes into IR8-type plants is to stabilize their yields. In what direction is IRRI working to create a breakthrough in the yield level of IR8?

G. S. Khush: We are trying to combine the high photosynthetic efficiency of variety T 141 with the improved and high yielding plant type, hoping thereby to increase the present yield level of the high yielding varieties.

S. D. SHARMA: How do you record the *O. nivara* collection (that showed resistance to grassy stunt) as highly sterile? Generally, *O. nivara* plants are highly fertile. What is the percentage of sterility of this particular collection?

G. S. Khush: The accession of *O. nivara* that is resistant to grassy stunt shows about 40 to 50 percent sterility under Los Baños conditions. It seems that environmental conditions at Los Baños are causing the sterility.

S. V. S. SHASTRY: Although the resistance to green leafhoppers held up for 30 years, don't you think that the pest pressures in the past have been low, relative to what we can expect in the future?

G. S. Khush: That remains to be seen.

H. L. CARNAHAN: Are tropical virus diseases transmitted by seed?

T. T. CHANG: K. C. Ling of IRRI has carried out some experiments on this matter. His negative findings are given in the 1968 IRRI Annual Report.

H. D. KAUFFMAN: The disease and insect reactions given refer to the varietal resistance to Philippine populations of the pathogens and pests. The promising selections should be tested in international screening trials in endemic areas of many countries to get an overall picture of the disease and pest reactions. Uniform rating scores for different diseases are needed.

Insect resistance

Resistance to insect pests in rice varieties

M. D. Pathak

At the International Rice Research Institute, 10,000 varieties have been evaluated for their resistance to stem borers and 30 varieties have been identified as resistant. On resistant varieties, stem borers laid fewer eggs; the larvae suffered high mortality, were smaller in size, had slower rate of growth; and more male than female moths developed. Factors of resistance to the striped borer were investigated. From breeding programs to combine borer resistance with other desirable plant characters, the variety IR20 was developed. It has resistance to stem borers, green leafhopper, tungro virus, bacterial leaf blight, bacterial leaf streak, and blast. The techniques of screening for varietal resistance to the leafhoppers and planthoppers are simpler than for the stem borers. Many varieties have been identified as highly resistant to the green leafhopper, the brown planthopper, and the white-backed planthopper in screening tests at IRRI. The varieties resistant to the brown planthopper appear to possess a feeding repellent or to lack a feeding stimulus for the insect while the varieties resistant to the green leafhopper are either toxic to or lack vital nutrients for the insect. Resistance to the brown planthopper has been combined with resistance to the green leafhopper in strains of high yield potential.

INTRODUCTION

The ecological conditions under which rice is grown, warm temperatures and high humidity, are also optimum for the proliferation of pests and pathogens. Consequently, the rice crop is under constant pressure from pests and diseases. Heavily fertilized, high-tillering plants, and the practice of growing rice throughout the year favor the build-up of pest populations. Thus in the tropics the rice fields grown with modern technology often end up with more severe pest infestations than conventionally grown and poorly managed fields. For these reasons the incorporation of natural resistance to insect pests into commercial rice varieties appears to be essential for raising rice production in the tropics.

Differences in host plant resistance to pest infestations have been known to exist for more than a century, but the first commercial varieties bred to be insect resistant started appearing only in the 1940's (Painter, 1951, 1958; Pathak, 1970). In recent years the use of resistant varieties, along with other biological methods of pest control, has received more attention because of the growing awareness of the shortcomings of chemical pesticides. The outstanding advantages of using resistant varieties as a method of insect control are that they cost no

M. D. Pathak. International Rice Research Institute.

money to the cultivators, they operate at all levels of pest infestation, and they cumulatively reduce pest populations.

Varietal resistance is defined as the "relative amount of heritable qualities possessed by the plant which influences the ultimate degree of damage done by the insect. In practical agriculture it represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population" (Painter, 1951). The word *relative* is important in this definition since host plant varieties immune to insect attack have seldom been recorded, and even highly resistant varieties suffer some damage under heavy insect infestations.

The nature of varietal resistance to insect pests is classified into three broad categories: Non-preference, antibiosis, and tolerance (Painter, 1951). A plant is non-preferred when it possesses factors that render it unattractive to insect pests for their oviposition, feeding, or shelter. It has antibiosis when it adversely affects the insects feeding on it. It is tolerant if in spite of supporting a population large enough to severely damage susceptible hosts it suffers little damage.

Some scientists consider varietal resistance and antibiosis as synonymous. Non-preference, however, is an important factor of resistance and it may be even more important than antibiosis where even brief infestations cause severe

Table 1. Rice varieties resistant to insect pests at IRRI.

Chilo suppressalis	*Hydrellia philippina*	*Nephotettix impicticeps*	*Nilaparvata lugens*	*Sogatella furcifera*
Bir-co 884	ARC 6089	ADT-14	ASD 7	ARC 5752
C-409	ARC 6231	ASD-7	Babawee	ARC 6248
Chiang-an-Tsao-Pai Ku	ARC 6588	ASD-8	Balamawee	ARC 6563
Choh-chang-san-hao	ARC 6607	ARC 5752	CO 3	ARC 6624
CO 13	ARC 10299	ARC 7059	CO 22	ARC 6650
CO 21	ARC 10301	ARC 7302	Dikwee	ARC 7251
DD 48	ARC 10696	ARC 10229	Gangala	ARC 7331
DNJ 97	ARC 10699	Baguamon 14	Hathiel	ARC 10595
DZ 41	ARC 11094	CO 9	H 105	ARC 10600
DV 88	ARC 11098	D-204-1	Kuruhondarawala	Balamawee
Ginmasari	ARC 11123	DK 1	MTU 15	C 5-17
HBJ Boro II	HR 106	DM 77	Mudgo	CI 5662-2
Kipusa	Ma-li-bin 2	DNJ 9	Murunga 307	Colombo
Lu-wan-hsien	MGL 2	DNJ 97	Murungakayan 3	Dahanala 2014
Patnai 6	RDR 2	DV 29	Murungakayan 101	HR 106
PI 160, 638	T 1145	DV 139	Murungakayan 104	JBS 34
Rusty Late		Hashikalmi	Murungakayan 302	Kaluheenati
Su-yai 20		Jingasail	Murungakayan 303	Miao-Tien-I-Li-Chan
Szu-miao		Kalimekri 391	Murungakayan 304	MTU 18
Taitung 16		Khama 49/8	Ptb 19	Mudgo
Ta-mao-shan		Palasithari 601	Seruvellai	Muthumanikam
Ta-poo-cho 2		Pankhari 203	SLO 12	Pankhari 203
Ti-Ho-Hung		Ptb 18	Sudurvi 305	Pu San 1
TKM-6		Ptb 21	Thirissa	Sudurvi 306
Yabami Montakhab 55		Su-yai 20	Vellailangayan	Tien-lie

damage such as severing growing parts of the plants or transmission of virus diseases. Field plantings of non-preferred varieties frequently escape infestation or develop low infestations, and when insects are caged on non-preferred hosts they lay fewer eggs and develop smaller populations. Thus both antibiosis and non-preference influence insect populations. Tolerant varieties, however, do not inhibit insect multiplication. Moreover, because they can support larger infestations with little plant damage they may be even more conducive to population build-up than susceptible varieties.

Significant progress has been made in the use of varietal resistance against stem borers, leafhoppers and planthoppers, stem maggot, and the rice whorl maggot, *Hydrellia philippina*. Some of the varieties showing high resistance to test insects at IRRI are listed in Table 1. General information about these insects has been extensively reviewed previously (IRRI, 1967; Pathak, 1970). Varietal resistance to the rice gall midge, *Pachydiplosis oryzae*, is discussed elsewhere in this book.

RICE STEM BORER

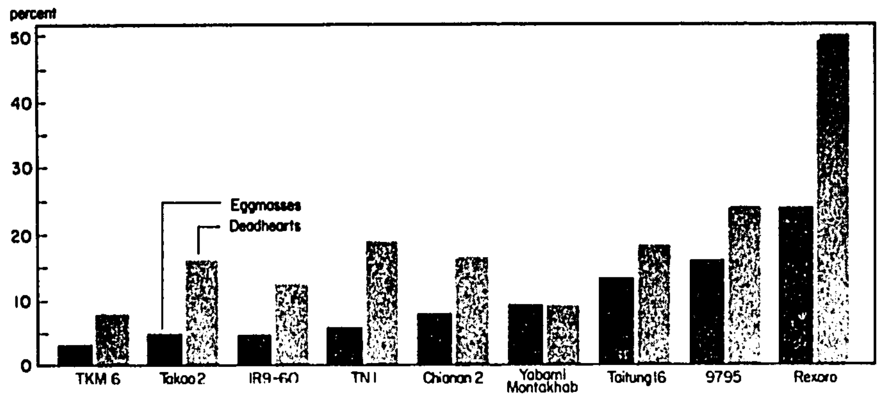
The stem borers have been conventionally considered the most serious insect pests of rice throughout Asia. About 20 species of borers damage the rice plant but four are of major significance in Asia: The striped borer, *Chilo suppressalis*; the yellow borer, *Tryporyza incertulas*; the white borer, *Tryporyza innotata*; and the pink borer, *Sesamia inferens*. Of these, *Chilo suppressalis* and *Tryporyza incertulas* have been widely investigated. Information on the resistance in rice plants to these two species has been reviewed by Israel (1967), Munakata and Okamoto (1967), Pathak (1967), and Pathak et al. (1971).

At IRRI, 10,000 varieties of rice were screened for resistance to the striped rice borer, *Chilo suppressalis*. They were tested over six crop seasons, 1,000 to 2,000 each season The planting of test varieties at a time when the neighboring crop was nearing maturity generally brought about heavy infestation of borers. The varieties that showed low borer incidence in these tests were re-evaluated in field and greenhouse experiments. In the latter tests, plants were infested artificially with a uniform borer population.

The test revealed distinct differences in the susceptibility of varieties to the borers. The larvae caged on resistant varieties suffered high mortality, grew slower, had smaller body size, and had a lower percentage of pupation than larvae caged on susceptible varieties. Similar results were obtained when the larvae were reared on stem pieces or seedlings of resistant and susceptible varieties.

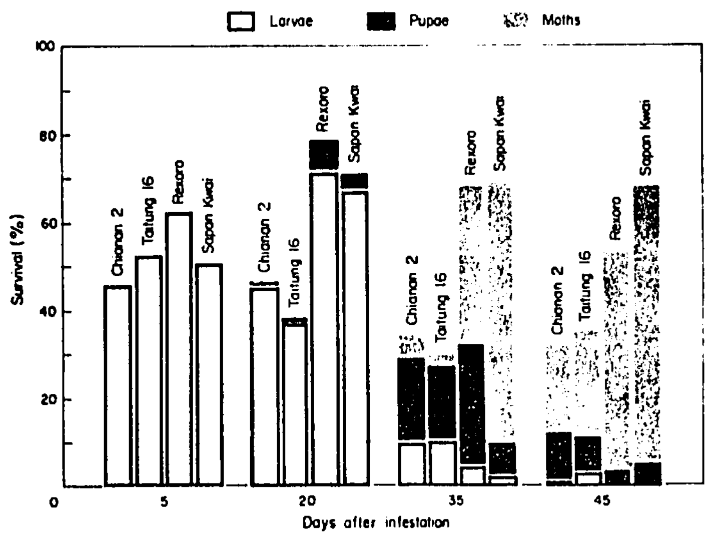
Causes of resistance to stem borers

Field experiments at IRRI indicated that the moths strongly preferred certain varieties for oviposition. Even under a low borer population, the moths oviposited heavily on certain varieties while other varieties remained virtually insect-free. Many varieties, however, had only a few egg masses, even under heavy infestations (fig. 1). For most varieties a larger number of eggs received

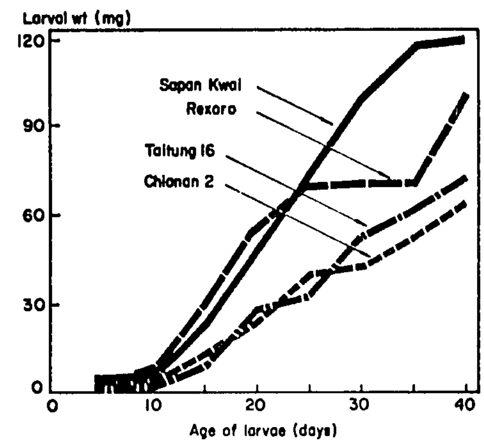


1. Ovipositional preference of stem borer moths (percentage of plants with egg masses) and percentage dead hearts on selected resistant and susceptible varieties.

corresponded with a higher percentage of dead hearts, indicating that preference for oviposition plays an important role in determining borer damage. The varieties, Chianan 2, Yabami Montakhab, and Taitung 16 however received comparatively large numbers of eggs but had rather low percentages of dead hearts. In subsequent experiments these varieties were observed to exert adverse effects on the borer larvae caged on them. Chianan 2 and Taitung 16 exhibited an interesting phenomenon: they were highly resistant during the vegetative phase but became susceptible after flowering when they developed high percentages of white heads.



2. Survival and development of 600 *C. suppressalis* larvae caged on each of four rice varieties (Because of their small size not all living larvae in the plant tissues could be recovered on the fifth day after infestation).



3. Average weight of individual *C. suppressalis* larvae reared on resistant and susceptible varieties of rice.

The adverse effect of resistant varieties on the survival and development of larvae appears to be another major factor of varietal resistance (fig. 2). On the resistant varieties, Chianan 2 and Taitung 16, only about half as many borer larvae survived as on the susceptible varieties, Rexoro and Sapan Kwai. The larvae also pupated earlier, and in greater numbers on the susceptible varieties. Furthermore, the larvae caged on the susceptible varieties weighed about twice as much as those caged on the resistant varieties (fig. 3).

We have also found a general association between several morphological and anatomical features of the rice plant and resistance to stem borer (Table 2). Although each of these characters appears to contribute to borer resistance, none by itself appears to be the real cause of such resistance. This relationship was evident in several varieties that reacted as susceptible to the borers even

Table 2. Correlations between rice plant characters and percentages of tillers infested with striped borer.

Plant character	Correlation coefficient
Elongated internodes, number	0.632**
Third elongated internode, length	0.715**
Flag leaf, length	0.798**
Flag leaf, width	0.836**
Culm height	0.796**
Culm, external diameter,	
at half its length	0.672**
at one-fourth its length from the base	0.785**
Culm, internal diameter	
at half its culm	0.671**
at one-fourth its length from the base	0.790**
Tillers per plant, number	−0.756**
Stem area occupied by	
vascular bundle sheaths (percentage)	−0.756**

when one of the characters they possessed was positively correlated with resistance.

Tall varieties, because of their height, might be more attractive to ovipositing moths. The number of internodes and the elongation of the third internode contribute to the height of the plants. The length and width of the flagleaf blade were positively correlated with borer susceptibility. In separately conducted ovipositional preference tests these characters were positively correlated (r = 0.743 and 0.924, respectively) with the number of egg masses laid.

A hairy leafblade surface might act as a physical repellent for the female moths during oviposition. Most eggs were laid on the smooth lower leaf surface or along the smooth midrib area or on the upper leaf surface. To determine the role of hairiness of the leafblade surface we shaved the hairs off the leafblade of the resistant variety TKM-6 and compared the number of eggs laid on the hairless leafblade with the number of eggs deposited on the leafblades of the susceptible variety Rexoro. Moths laid significantly fewer eggs on hairless TKM-6 leafblades than on those of Rexoro indicating that hairiness by itself may not be the major factor deterring the moths from ovipositing.

Generally within 48 hours after hatching the borer larvae migrate between the leafsheaths and the rice stem. There they feed on the leaf sheath tissues for about 6 days, and then bore into the rice stem. Thus, varieties whose internodes are completely covered by tight leaf sheaths offer more resistance to the first-instar larvae than varieties whose internodes are only partially covered by loose leafsheaths.

Several plant anatomical characters, such as heavily sclerotized stem tissues, closely spaced vascular bundle sheaths, ridged stem surface, and high silica content, are positively correlated with resistance to stem borer (Van and Guan, 1959; Israel, 1967; Djamin and Pathak, 1967; Patanakamjorn and Pathak, 1967). Each of these characters interferes with larval feeding. On rice varieties with high silica content, the larvae suffer high mortality and their mandibles tend to wear off (Sasamoto, 1961; Djamin and Pathak, 1967). Also, many of the larvae die without being able to bore inside the stems, which is not true of larvae on varieties with low silica content.

Striped borer population on resistant and susceptible varieties

To investigate the cumulative effects of varietal resistance on borer population we confined an identical number of borers for several generations on the resistant variety, Chianan 2, and on the susceptible variety, Sapan Kwai. The number and emergence of moths and the number of eggs laid on these varieties were recorded periodically. The plants in each cage were replaced with uninfested healthy plants of the same variety at 40-day intervals. At 120 days after infestation, we recovered 91 larvae and two egg masses from the resistant variety, while the susceptible variety had 1,583 larvae and 83 egg masses. Furthermore, the susceptible variety had 56.3 percent dead hearts while the resistant variety had only 1 percent. Besides the low survival of borer larvae and their slow rate of growth, the uneven emergence of moths appeared to be an important cause of the low number of eggs laid on resistant varieties.

Breeding for resistance to stem borers

About 30 varieties have been identified as resistant to striped borer through intensive field and greenhouse experiments. Although most of these varieties showed consistently low borer infestations in repeated field experiments, many were damaged by other insect pests or by some diseases. Only the variety, TKM-6, remained comparatively free of insects and disease in most field experiments. Other varieties were severely damaged. Subsequent experiments showed that TKM-6 is also resistant to bacterial blight and tungro virus. But it is a leafy, narrow-stemmed, tall, variety that often lodges even before flowering. Thus it has a low yield potential.

The resistant varieties have been used in a hybridization program, in collaboration with the rice breeders, to improve their level of borer resistance and to incorporate borer resistance in plants possessing better agronomic characters. The following crosses were studied.

Cross no.	*Parentage*	*Nature*	*Number of F_8 lines selected*
IR356	Taitung 16 x TKM-6	R x R	–[a]
IR357	Taitung 16 x Rexoro	R x S	–[a]
IR358	Chianan 2 x Rexoro	R x S	–[a]
IR359	TKM-6 x Rexoro	R x S	[a]
IR532	TKM-6 x (Peta/3 x Taichung Native 1)	R x MS	5
IR580	TKM-6 x IR8	R x MS	3

[a]Although many lines were highly resistant to the striped rice borer, they all were of poor plant type.

A large number of progenies of each of these crosses were intensively evaluated for borer resistance in field experiments. Tall and leafy plants or those susceptible to other common insects and diseases prevalent during this test were rejected. This procedure led to the identification of several lines that were resistant to borers and other common pests and pathogens and that had better plant type. TKM-6 and IR8 progeny generally produced higher yields than TKM-6 x (Peta/3 x Taichung Native 1) but they had poor quality grains. TKM-6 x (Peta/3 x Taichung Native 1) had good quality grains, good resistance to stem borers and some other common organisms, and good plant type except that it had narrow stems that tended to lodge at high fertility levels. One selection from this cross was named IR20.

At IRRI, IR20 is resistant to the striped rice borer, the green leafhopper, tungro virus, bacterial leaf blight, bacterial leaf streak, grassy stunt virus (seedlings 40 days old or older), and rice blast. Its performance is good even under severe insect infestations. It generally outyields other recommended varieties when grown without insect protection, but with adequate insect protection it usually produces yields identical to those of other varieties. These characteristics and its good quality grain have made IR20 an increasingly popular variety in several Southeast Asian countries.

The nature of the rather broad resistance of IR20 to several insects and diseases is not fully understood. Probably it either has genes for resistance to each of these organisms or it possesses a factor that imparts resistance to many pests and diseases. Although not a common phenomenon, an example of the latter is the compound 6-methoxybenzoxazolinone which imparts resistance to the European corn borer in corn and inhibits the growth of a variety of organisms, including bacteria, free-living and pathogenic fungi, and a number of insects on corn and on other crops (Virtanen and Hietala, 1955; Whitney and Mortimore, 1959, 1961; Beck and Smissman, 1961).

Cross-resistance to four species of stem borers

The tests we conducted were primarily on the resistance of varieties to the striped rice borer, the predominant borer species at IRRI. We also used this species in all re-evaluation tests in the greenhouse. The reaction of the selected varieties to other common species of stem borers was determined by field-testing the varieties in areas where other borer species were predominant and by infesting the plants with these species in greenhouse experiments.

Highly significant differences were found in the incidence of dead hearts among varieties at all three locations tested. Several varieties reacted as highly resistant, several others were highly susceptible to all the four borer species tested, and some varieties differed in their susceptibility to different species of the borers (Table 3).

Table 3. Cross-comparisons of resistance in rice varieties to four species of stem borers at three locations in the Philippines.

Variety	Dead hearts (%)				
	IRRI	Iloilo		Maligaya	
	C. suppressalis[a]	*T. innotata*[a]	*C. suppressalis*[b]	*T. incertulas*[a]	*S. inferens*[b]
Rexoro	81.0	7.3	51.3	7.0	15.2
Milfor-6(2)	71.2	6.6	40.5	6.0	16.5
Binolayangun	90.5	7.3	36.3	6.1	11.6
MN62M	75.7	6.4	38.6	4.1	10.5
Pankhari 203	89.7	4.2	40.6	3.8	9.0
Paimat	64.0	4.4	26.1	4.1	10.2
RDR 2	19.3	4.3	26.7	4.0	8.0
IR8	37.1	3.6	21.9	4.0	6.5
Chianan 2	22.4	4.4	20.7	3.0	8.1
MTU 19	26.0	5.2	15.5	3.3	6.3
Taitung 16	23.4	2.9	20.4	2.6	8.2
DV 139	14.4	3.3	24.7	1.0	8.4
Mudgo	11.5	3.5	22.7	1.9	6.2
Su Yai 20	16.5	3.2	16.2	1.0	5.0
Ptb 10	11.2	2.5	17.3	0.8	6.1
TKM-6	13.8	2.7	9.0	2.0	3.3

[a]Tested in wet season. [b]Tested in dry season.

Table 4. Survival, larval weight, and damage caused by four species of stem borers on eight selected rice varieties (averages for four borer species).[a]

Variety	Average larval wt (mg)	Insect survival (%)	Dead hearts[b] (%)	Index[c]
Rexoro	93.6	75.3	80.6	250
Pankhari 203	90.5	92.3	54.8	238
IR8	79.8	70.2	81.2	231
Mudgo	73.7	88.9	46.8	210
DV 139	66.7	84.8	52.0	204
Taitung 16	49.8	62.8	78.2	191
Chianan 2	47.5	55.4	83.4	187
TKM-6	50.9	67.8	53.5	172

[a]Figures represent relative values calculated separately for each species based on the most susceptible variety whose value is considered as 100. [b]Caused by 10 introduced borers. [c]Sum of values for average larval weight, insect survival, and dead hearts.

The four species of borers varied significantly in survival, larval weight, and damage on different varieties of rice (Table 4). These differences generally agreed with the differences in dead hearts caused by various borer species in field experiments. Several varieties resistant or susceptible to one species showed a similar response to other species of the borers. This cross resistance of the varieties has considerable practical importance in the use of varietal resistance as a method of borer control.

LEAFHOPPERS AND PLANTHOPPERS

Several species of leafhoppers and planthoppers damage the rice plant by feeding on it and by transmitting virus diseases. There appears to be a general increase in the populations of various leafhoppers and planthoppers in recent years. The exact cause of this increase is not known, but it is often attributed to the shift to short-statured and heavy tillering rice varieties, and to the use of greater quantitites of nitrogen fertilizers. Studies under way at IRRI have established that natural resistance to leafhoppers and planthoppers exists in rice varieties and such resistance is easily transferable to short-statured and heavy tillering strains.

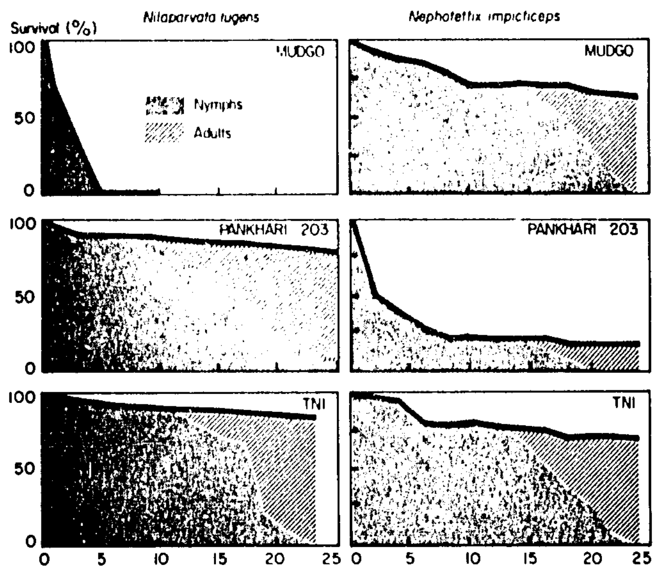
Screening for resistance

From the screening trials for borer resistance, we selected 1,400 varieties and evaluated them for resistance to the green leafhopper (*Nephotettix impicticeps*), the brown planthopper (*Nilaparvata lugens*), and the white-backed planthopper (*Sogatella furcifera*). Several varieties highly resistant to these pests were identified. Several hundred additional varieties have also been evaluated in a continuing screening program.

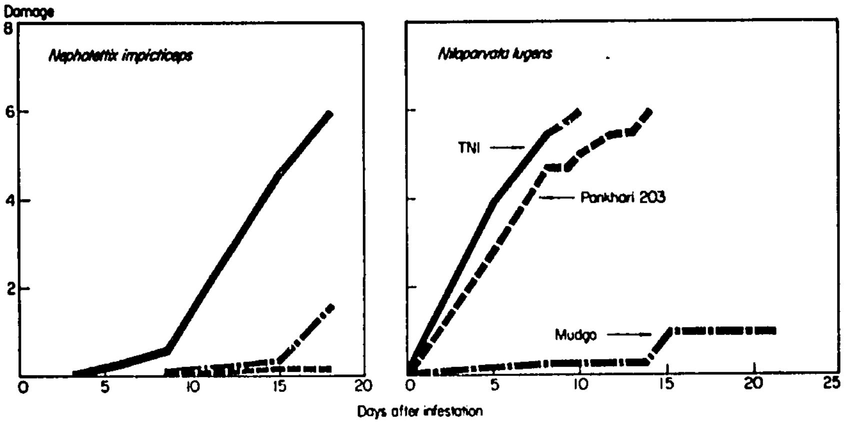
Table 5. Standards for rating damage by leafhoppers and planthoppers.

Grade	Damage to the seedlings caused by		
	Green leafhopper	Brown planthopper	White-backed planthopper
0	No visible damage	No visible damage	No visible damage
1	Yellowing of first leaf	Partial yellowing of first leaf	First leaf yellow-orange
2	50% to 75% of all leaves yellow	First and second leaves partially yellow	50% of the leaves, or at least their tips, yellow-orange; slight stunting
3	All leaves yellow; leaf sheaths and stem green	Pronounced yellowing and some stunting	Most of the leaves or their tips yellow-orange; stunting
4	Half the test plants dead	Wilting and severe stunting	Half the test plants dead; wilting and severe stunting
5	All test plants dead	All test plants dead	All test plants dead

Screening for varietal resistance to these insects is done by growing the test varieties in 60- x 45- x 10-cm seedboxes. Each variety is sown in a row 20-cm long. Each seedbox contains 10 rows, 10-cm apart. One row is planted to a susceptible check variety, another, to a resistant check. One week after seeding the seedboxes are transferred to a 5.2 x 1.3 x 0.1 m iron sheet tray inside a



4. Survival and development of first-instar nymphs of *N. lugens* and *N. impicticeps* on 60-day-old plants of resistant and susceptible varieties (Pathak, Cheng, and Fortuno, 1969).



5. Damage caused by caging 100 first-instar nymphs on resistant and susceptible varieties (Pathak et al., 1969).

large screen cage. Several thousand insects of a test species are uniformly scattered on the seedlings. This infestation is sufficient to kill susceptible varieties. Water, 4-cm to 5-cm deep in the tray irrigates the seedlings, helps keep humidity high, and keeps ants off the seedlings.

The number of insects on each variety and the damage they cause the seedlings are recorded at 5-day intervals according to the standards shown in Table 5.

The final grading is done after all susceptible check rows are killed. The varieties rated 0 to 2 are further evaluated for the consistency of their resistance. A uniform number of insects (either adults or nymphs) are caged on 20-day-old individual plants of the selected varieties. The varieties that allow low survival of the insects are classified as truly resistant and are used in future tests. The results of one such experiment are presented in figure 4.

Few nymphs of the brown planthopper survived on the variety Mudgo and they died within 10 days after caging; many survived on Taichung Native 1 and Pankhari 203. Survival of green leafhopper, however, was low on Pankhari 203, but high on Mudgo and Taichung Native 1. This pattern demonstrated that resistance to the brown planthopper is different from resistance to the green leafhopper. In repeated similar experiments, insects caged on resistant varieties had slower growth and suffered higher mortality than those caged on susceptible varieties. Furthermore, even a large population of the insects caged on resistant plants caused barely noticeable symptoms while the susceptible variety was killed (fig. 5).

Causes of resistance to leafhoppers and planthoppers

In the screening experiments, the insects exhibited a distinct non-preference for certain varieties. This reaction appeared to be gustatory rather than olfactory or visual since the insects did not show distinct differences in their alighting behavior on different varieties, but they did not stay on resistant plants for sustained feeding (Sogawa and Pathak, 1970; C. D. Pura, *unpublished*; C. H. Cheng, *unpublished*). The latter response was so strong for brown planthoppers caged on Mudgo that the insects starved to death rather than feed on the plants (M. B. Kalode, *unpublished*).

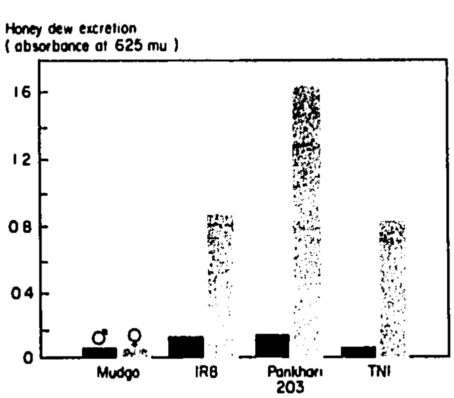
Ability of insects to feed on resistant plants

To determine whether the insects caged on resistant and on susceptible plants fed equally well, we measured the gain in their body weights and the amount of honeydew excreted by them. Insects caged on resistant plants lost weight while those caged on susceptible hosts gained weight. The loss of weight was much more pronounced with brown planthoppers than with green leafhoppers, and was illustrated more clearly by assessing the amounts of honeydew excreted by the insects on resistant and on susceptible plants (C. H. Cheng and M. D. Pathak, *unpublished*; Sogawa and Pathak, 1970).

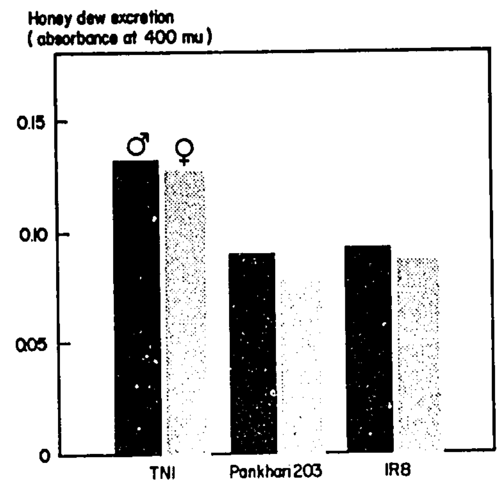
The brown planthopper fed less on the resistant variety, Mudgo, than on the susceptible varieties, IR8, Taichung Native 1, and Pankhari 203. Most feeding was done by females which exhibited marked differences in feeding on different varieties by excreting 30 to 50 times more honeydew on the susceptible varieties than Mudgo (fig. 6). The green leafhoppers excreted more honeydew on the susceptible variety Taichung Native 1 than on the resistant varieties Pankhari 203 and IR8. But the differences were not as distinct as for the brown planthopper (fig. 7). Furthermore, unlike the brown planthopper, male and female green leafhoppers excreted identical amounts of honeydew, suggesting that they do the same amount of feeding.

Accessibility of insects' stylet sheaths to feeding sites

The possibility that a mechanical barrier prevents the stylets of the insects from reaching proper feeding sites in resistant varieties was investigated by microtome sectioning of the insects' feeding sites. Adult brown planthoppers made two to three times more feeding punctures on the resistant variety Mudgo than on susceptible varieties, IR8 and Taichung Native 1 (Table 6). Furthermore, there were more stylet punctures through the fiber tissues (which are harder than the parenchyma cells) in Mudgo plants than in IR8 and



6. Qualitative assessment of the *N. lugens* honeydew excreted by five adults for 24 hours on different rice varieties by measuring their light interference in a spectrophotometer.



7. Quantitative assessments of the honeydew excreted by the five *N. impicticeps* adults feeding for 24 hours on different rice varieties by measuring their light interference in a spectrophotometer.

Taichung Native 1 plants. Thus, the hardness of the tissues was not a factor of planthopper resistance. Also a higher percentage of salivary sheaths terminated in the vascular bundles of Mudgo than in the vascular bundles of IR8 or Taichung Native 1 plants. Similar results were obtained for green leafhoppers caged on resistant and susceptible plants.

Thus no mechanical barrier to the insects' feeding was apparent in any of the resistant varieties tested. In fact, the insects made more feeding punctures on the resistant variety than on the susceptible varieties. These results suggest that the variety Mudgo either lacked feeding stimulus or possessed a feeding repellent for the brown planthopper. The green leafhopper however, did some feeding on resistant varieties, so resistance to it appears to be due to either a toxic factor for the leafhopper in the plants or the plants' lack of nutrients vital to the insect.

Further studies on the biochemical basis of resistance suggested that the resistance to brown planthopper in Mudgo could be attributed to the lower content of asparagine amino acid in this variety. The asparagine content of the

Table 6. Comparison of the feeding behavior of brown planthopper adults on different rice varieties.

Variety	Feeding marks per insect (no./day)		Insect feeding sites[a] (%)		Termination of salivary sheaths[a] (%)	
	Females	Males	Fiber layer	Parenchyma	Vascular bundles[b]	Non-vascular tissues
Mudgo	50.8	31.0	45	55	79	21
IR8	15.8	15.6	22	78	47	53
Taichung Native 1	15.4	17.2	10	90	60	40

[a]The number of salivary sheaths studied in Mudgo was 457, in IR8, 153, and in Taichung Native 1, 425. [b]Based on at least one branch of the salivary sheath entering the vascular bundles.

Table 7. Effect of different levels of nitrogen fertilizer on the reaction of Mudgo and Taichung Native 1 to the brown planthopper.

Nitrogen (kg/ha)	Insect survival[a] (%)		Male:female ratio[b]		Insect progeny produced[c] (no.)	
	Taichung Native 1	Mudgo	Taichung Native 1	Mudgo	Taichung Native 1	Mudgo
0	30	2	1:2.3	1:0.66	4775	11
50	38	0	1:1.4	1:0.71	5139	0
100	44	10	1:1.2	1:0.5	6835	19
150	54	22	1:1.4	1:1	8875	85
200	57	18	1:1.6	1:1.1	9363	70

[a]22 days after infestation with first-instar nymphs. [b]17 days after infestation with first-instar nymphs. [c]37 days after infestation with first-instar nymphs.

rice plant is believed to be greatly influenced by the amount of nitrogen fertilizers applied. In tests using various rates of nitrogen fertilizers, however, the relation of Mudgo to Taichung Native 1 in resistance to the brown planthopper remained the same at all fertility levels (Table 7). More information is required for an understanding of the biochemical basis of leafhopper and planthopper resistance in rice varieties.

Build-up of leafhopper and planthopper populations

The insects caged on resistant varieties grew slower, were smaller, and had underdeveloped ovaries, laid fewer eggs, and died more rapidly than insects caged on susceptible varieties. All these effects should cause cumulative reductions in the population of pests on resistant varieties. In greenhouse experiments, insects caged on resistant varieties generally died or reached low population levels within one to two generations while those caged on susceptible varieties increased several fold in each generation. Similarly, in field plots, few insects were found on resistant varieties while adjacent plots of susceptible varieties were heavily infested.

Breeding for resistance to green leafhoppers and brown planthoppers

Breeding for resistance to leafhoppers and planthoppers has gained wide popularity in recent years. It has become a main objective of the breeding program at IRRI and a large number of crosses have been made. The details of these are described in the paper by Khush and Beachell in this book. We are studying a few crosses that may combine resistances to leafhoppers, planthoppers, and other insects.

Mudgo x IR8 has produced progeny that are highly resistant to the green leafhopper and the brown planthopper and that possess the plant type of IR8 (Mudgo is a tall and lodging-susceptible variety with poor agronomic characters). The progeny of (Mudgo x IR8) x [(Peta/3 x Taichung Native 1) x Khao Dawk Mali] have, in addition, excellent grains. IR20 x (Mudgo x IR8) progeny appear to have resistance to stem borers, the green leafhopper, and the brown planthopper plus several other desirable qualities of IR20, but are highly susceptible to bacterial leaf blight and sheath blight.

So far we have found no japonica rice that is resistant to the brown planthopper, which is a major problem in many areas where japonica rice is grown. Kaneda (1971) investigated the feasibility of transferring resistance to brown planthopper from Mudgo to japonica rice. Several selections, now in the F_6 generation, from the Hoyoku x Mudgo cross are highly resistant to the brown planthopper and possess the japonica plant type and grains with low amylose content.

Jennings and Pineda T. (1970*a*, 1970*b*) evaluated 534 rice varieties for their resistance to *Sogatodes oryzicola* of which 28 varieties were highly resistant, 84 resistant, 213 intermediate, and 209 susceptible. All resistant varieties were indicas from Southeast Asia where this insect does not occur. All varieties from the western hemisphere were susceptible. The insects caged on resistant varieties suffered high mortality, had a slower rate of growth, and laid fewer eggs. The resistance was highly heritable and easily recombined with other agronomic traits. It was also independent of resistance to the hoja blanca virus which is transmitted by *Sogatodes oryzicola*. Significantly, the varieties Mudgo (resistant to the brown planthopper), IR8 (resistant to the green leafhopper), and TKM-6 (resistant to the striped borer), were all resistant to *Sogatodes oryzicola*.

T. Koshihara (*unpublished*) investigated the survival and development of newly hatched nymphs of *Nephotettix cincticeps* Uhler on 61 japonica and 27 indica varieties. All japonica varieties he tested were susceptible, but 14 indica varieties were resistant and three were moderately resistant. The remaining varieties were susceptible. The varieties Tadukan and Tetep were the most resistant. On resistant varieties, the nymphs had low survival and slower rate of growth, and the adults laid fewer eggs than on susceptible varieties. Hybridization of resistant indica varieties with susceptible japonica varieties, however, produced progenies that were all susceptible. No explanation is available for this rather unexpected reaction.

RICE STEM MAGGOT

The rice stem maggot, *Chlorops oryzae* Matsumura, is an important pest of rice in the northern and mountainous regions of Japan. The maggots feed within the plants, on the developing leaves, and on unemerged panicles. Such feeding causes broad, longitudinal stripes on the leaf blades and reduces the number of filled grains. The decrease in field grains generally reduces rice yields.

About 300 varieties of rice have been field-screened for their resistance to rice stem maggot (Fukuda and Inoue, 1962; Yushima and Tomizawa, 1967; Okamoto, 1970; T. Koyama and J. Hirao, *unpublished*). The selected varieties have been retested with controlled infestations in greenhouse experiments. A few varieties, such as Ou 188, Ou 230, Sakaikaneko, and Oha, have been identified as highly resistant. Although there were differences in the number of eggs laid

by the fly on different varieties, the high mortality of the maggots on resistant varieties was the chief factor of resistance. No effort seems to have been made to use this resistance in breeding commercial varieties.

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Discussion: Resistance to insect pests in rice varieties

N. PARTHASARATHY: Is CO 18 resistant to the stem borers?

M. D. Pathak: It has a moderate level of resistance.

B. R. JACKSON: Do IR20 and TKM-6 have the same level of borer resistance?

M. D. Pathak: Yes.

J. K. ROY: We plan to evaluate Ratna for borer resistance. Ratna was selected from the cross of TKM-6 x IR8.

H. M. BEACHELL: We do not know much about the nature of resistance to different insect pests or the stability of resistance. We have a long way to go in combining resistance to different insects and to develop field resistance.

N. E. BORLAUG: Resistance to insects can also be narrow in geographic range. Only continuous field testing will reveal the applicability.

Biology and laboratory culture of the rice gall midge and studies on varietal resistance

Henry E. Fernando

Studies on the life history and behavior of the gall midge, *Pachydiplosis oryzae*, show that reproduction is entirely sexual with an actual sex ratio of 2:1, females to males. The eggs, first-instar larvae, and adults are highly susceptible to changes in relative humidity. The eggs require a relative humidity of over 90 percent for normal development. The first-instar larvae require a relative humidity of over 95 percent associated with moist surfaces for successful infestation of rice plants. Adult gravid females require a relative humidity of over 70 percent for normal longevity and egg lay. These environmental factors must be provided for the successful large-scale culture of *P. oryzae* in the laboratory. *P. oryzae* larvae are attracted specifically to shoot apices where development proceeds at the normal rate only in active shoot apices. Galls form only at the base of the leaf sheath primordium and are the result of insect feeding and fluctuations in insect secretions and plant nutrients. *P. oryzae* can be cultured in the laboratory on a large scale using adults or eggs mass-produced in specially designed oviposition tubes. This technique has been adapted for the laboratory screening of rice varieties for resistance to gall midge. The varieties Ptb 21, Leuang 152, Ptb 18, and W 1263 have been found to be resistant to *P. oryzae*. In W 1263, resistance is the result of inhibition of the first-instar larval molt. A program of breeding for resistance to gall midge, using W 1263 as the resistance donor parent and a number of agronomically desirable high yielding varieties, has reached the second backcross generation.

INTRODUCTION

Reddy (1967) reviewed information on the rice gall midge, *Pachydiplosis oryzae*, and confirmed that many aspects of the biology and ecology of this important insect were poorly understood. Perera and Fernando (1969, 1970) developed techniques for the laboratory culture of this insect, investigated its biology and ecology, and studied resistance in rice varieties to its attack. Wickramasinghe (1969) studied the field ecology of this pest. High levels of resistance to gall midge based on field observations in India were reported for four Eswarakora crosses (W 1251, W 1253, W 1257, and W 1263) in India (AICRIP, 1967). But in Ceylon these varieties show a low level of resistance (about 25 %) to this pest (H. E. Fernando and N. Perera, *unpublished*).

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I. D. R. Pieris (*unpublished*) screened many rice varieties for resistance to gall midge while S. D. I. E. Gunawardena and I. Sumanasinghe (*personal communication*) carried out a program of breeding and backcrossing using a selected strain of W 1263 and high yielding varieties to incorporate resistance to gall midge into the latter. Modder and Alagoda (1971) have investigated the basis of gall midge resistance in W 1263.

GENERAL DESCRIPTION OF *P. ORYZAE* AND ITS DAMAGE

The rice gall midge, *P. oryzae*, is a minute mosquito-like insect. The females are orange to orange-brown. The males are considerably smaller and pale brown. Under natural conditions adults emerge from galls on the rice plant at night or at early dawn and copulate immediately after emerging. The male dies within 12 to 18 hours after emerging while the female lives for 3 days, under Ceylon conditions. The females start ovipositing on the rice plants the evening after emergence; eggs start hatching 72 hours later at dusk. First-instar larvae work their way under the leaf sheaths, without boring through them, to infest the terminal and axillary buds at the base of the young rice plants. The infestation of active buds by the larvae alters the buds' growth pattern and produces white tubular sheath-galls, terminating in small leaf laminae of varying lengths. These galls signal the end of the growth of the tiller. For this reason a midge infestation of rice plants before all productive tillers have formed can be highly damaging to crop yields.

OVIPOSITION, EMBRYONIC DEVELOPMENT, AND HATCHING

The gall midge lays most of its eggs singly or in small groups on the undersides of leaves of young rice seedlings. The eggs are elongate, reddish brown, 0.44 mm x 0.25 mm. Oviposition begins in the evening after emergence and the female lays most of her 175 to 200 eggs on the first night after emergence.

Studies on the pupal stage show that the sex ratio in the gall midge is two females to one male, but male emergence and survival drops when humidity is low and temperature is high. Temperatures of 20.5 to 27.0 C and humidity of 75 to 79 percent are optimal for male survival. Reproduction is invariably sexual; careful investigations have failed to demonstrate parthenogenesis in this insect.

Thirty-six hours after oviposition, the eggs show the outline of the larva inside the chorion with two kidney-shaped, reddish eyespots located anterodorsally. These two eyespots meet mid-dorsally in the third segments to form an X-shaped eyespot as hatching approaches. Hatching begins in the evening when the eggs are 72 hours old and is at a peak at about 10 P.M. The eggs are very susceptible to changes in relative humidity. Below a relative humidity of 84 percent the hatch drops steeply. Between 84 percent and 90 percent relative humidity, eggs collapse and crumple, but many eventually hatch. A relative humidity of over 90 percent is essential for normal hatch.

IMMATURE STAGES

The first-instar larva is minute (0.50 mm x 0.127 mm) and fusiform with a 13-segmented body. The head is reduced in size with a chitinized oral cone for a mouth and greatly reduced antennae. An X-shaped crimson eyespot is located mid-dorsally in the third segment. The last two segments bear spines on lateral tubercles and this larval instar is characterized by the presence of a pair of very long spines on the 13th segment. This stage lasts 3 to 4 days.

The second-instar larva is 1.5 mm x 0.4 mm. It resembles the first-instar larva but all the spines in the last two segments are greatly reduced in size. This stage lasts 3 to 4 days.

The third-instar larva is considerably larger than the first two instars, 3.2 mm x 0.8 mm. Like the second-instar larva, the spines on the last abdominal segment are greatly reduced. The third-instar larva, however, differs from the first two stages in that it possesses a heavily chitinized Y-shaped sternal spatula on the mid-ventral line between the first and second segment. This stage lasts 6 to 7 days.

As the third-instar larva finishes feeding it enters a resting prepupal stage. Its anterior end becomes rounded and filled with a translucent fluid. This stage lasts about 24 hours after which pupation occurs. The pupa is characterized by a series of heavily chitinized adaptive spines which help the insect to move up the gall cavity and to escape from the gall. The most important of adaptive spines are the cephalic horns with the cephalic spines, the subocular spines, and the fine heavy spination on the tergites of abdominal segments 2 to 8. The male pupa is much smaller than the female. Claspers can be seen at the end of the abdomen in the male pupa.

EFFECT OF HUMIDITY AND MOISTURE ON FIRST-INSTAR LARVA

High relative humidity is essential not only for the development of the eggs of the gall midge but, associated with moist surfaces, for the survival of first-instar larvae, too. At relative humidities below 94.8 percent, freshly hatched larvae are capable of only limited movement and they cannot reach the feeding site. Their bodies soon contract and the slimy surface secretion hardens. If the humidity rises and the larva is wetted with water, recovery is immediate. Moist surfaces and relative humidities over 95 percent are therefore essential for survival of first-instar larvae and their successful infestation of young rice.

NORMAL GALL FORMATION

First-instar larvae hatching on leaves and leaf sheaths work their way under consecutive leaf sheaths to reach the terminal and axillary shoot apices within 12 hours of hatching. They are attracted specifically to both the active and the inactive shoot apices; they congregate in numbers only at these structures within the rice plants.

The first-instar larvae feed between the base of the growth cone and the youngest leaf primordium. The gall primordium is initiated within about 4 to 6 days of infestation. A ridge of cell proliferation develops on the inner side of the youngest leaf primordium. The ridge is located at the level of the posterior end of the first-instar larva below the ligule primordium. This ridge of tissue grows and fuses to form a primordial gall below it. The midge larva is then located within the gall primordium and feeds at the base of the growth cone probably by irritating the base of the growth cone with its chitinized oral cone and lapping up the exuding fluid.

The second- and third-instar larvae feed like the first-instar larva. When ready to pupate, the third-instar larva reverses its position inside the gall cavity with the aid of its sternal spatula so that its head faces upwards and away from the growth cone. In this position pupation takes place.

When mature, the pupa works its way up the gall cavity with the aid of the adaptive spines on its body surface. It bores a hole with its cephalic and subocular spines at the top of the gall immediately below the plug of tissue formed by the cell proliferation. Through this hole it thrusts the greater part of its pupal body and adult emergence takes place in that position.

The primordial gall cavity at the beginning of the second instar is about 2 mm in length and during the larval period of about 15 days it may grow to 10 mm. When feeding ceases and pupation takes place the gall elongates spectacularly, from 10 mm to 180 mm in 3 to 5 days on young IR8 seedlings grown under laboratory conditions. This rapid growth occurs because the larva has stopped feeding. Consequently nutrients are suddenly available for growth. A growth-promoting substance released by the insect at pupation is also probably involved.

MULTIPLE INFESTATION AND STAGGERED LARVAL DEVELOPMENT

In laboratory experiments, numerous first-instar larvae have been frequently found at a single shoot apex but the maximum survival thereafter was three larvae to the second instar, two to the third instar, and one to pupation in a single gall (Perera and Fernando, 1970). The axillary shoot apices, as well as the terminal shoot, often become infested by first-instar larvae. In such cases only the larvae at the active terminal shoot apices develop normally while those first-instar larvae in the inactive axillary shoot apices remain retarded in this stage until the shoot apex begins active growth. Consequently, the offspring of a single female midge can develop in a rice plant at different rates and adult emergence on the crop is staggered over as much as 1 month or more (Perera and Fernando, 1970).

POPULATION FLUCTUATIONS IN THE FIELD

Gall midge attack in the field in Ceylon begins with a low infestation rate in nurseries or in broadcast seedlings. Gall incidence increases gradually up to 8 to 11 weeks later, which is the stage of maximum tillering in a 4½ month rice variety. Most of the productive tillers have formed by the 10th week and thereafter mainly tertiary unproductive tillers are produced. Gall midge attack after about the 10th week from sowing has no adverse effect upon yield (Wickramasinghe, 1969).

Gall midge attack increases the numbers of tillers. This effect is most marked if the primary tillers are attacked. The number of tillers and panicles increases after a low level of midge attack early in the season. But grain yield does not increase (Wickramasinghe, 1969).

LABORATORY CULTURE OF GALL MIDGE

Gall midge can be multiplied in the laboratory by infesting plants with adults or with eggs. For infestation with adults, cement pots, 2.5 cm thick, with internal dimensions of 20 x 20 x 20 cm, are filled with soil to 7 cm from the top. In each pot, plant 225 IR8 seedlings. To ensure regular planting, place a 20- x 20-cm piece of 1-cm square (0.5-inch square) welded mesh on the soil surface and plant a germinated rice seed (24 hours soaking in water, 24 hours moist) in each square. When the plants are 10 to 14 days old, place each pot in a nylon cage with 10 to 15 freshly emerged, gravid, female gall midges. These adults survive for about 3 days, although egg laying occurs mostly on the first night. Under Ceylon conditions, gall midge eggs hatch within 3 days.

On the third morning after the introduction of the adult midges, place the culture pots in a mist chamber so the eggs can hatch and the first-instar larvae can move into the plants. The mist is provided by a humidifier operated at regular intervals by a time switch. High humidity and moist leaf surfaces are essential for hatching of eggs and for larval movement from leaves and leaf sheaths into the growing point areas of the plants (Perera and Fernando, 1969). After 3 days inside the mist chamber, remove the pots and maintain them until the adults emerge.

For infestation with eggs, place freshly emerged, gravid female midges in oviposition tubes at the rate of four per tube. The oviposition tubes should be glass, 15-cm long and 2.5-cm in diameter, fitted with plastic caps at both ends. A hole, 0.5-cm in diameter, is bored in the center of each cap. Before placing the cap in position, line the inner face with a little cotton wool and use a piece of muslin cloth, 5-cm square, to hold the cotton wool in place. Moisten the muslin and cotton wool through the hole in the caps with a water extract of macerated rice leaves.

The females inside the oviposition tube lay their eggs on the pieces of muslin cloth on the first night. Remove the cloth the next morning and place it on moist filter paper in petri dishes to allow the eggs to develop. The filter paper should be kept barely moist during egg development.

Hatching occurs on the evening and night of the third day. By the third day, the crimson eye spots of the larva and larval movement inside the chorion are clearly visible in fully developed eggs. On the third morning place the pieces of muslin in water in petri dishes and brush off the mature eggs lightly with a camel's hair brush. Pour the suspension of eggs into a graduated tube and dilute or concentrate the suspension as required by reducing or increasing the volume of water. The concentration of eggs can be estimated by counting samples under a microscope.

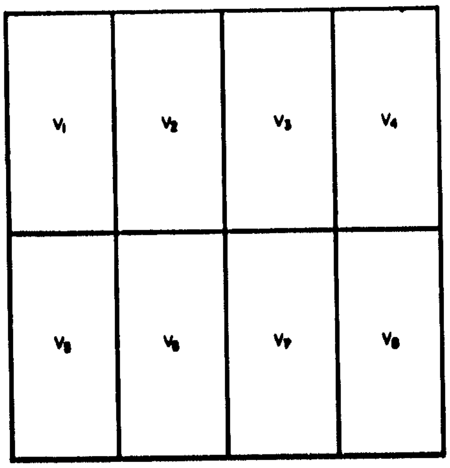
Plants are infested by applying 3,000 fertile mature eggs in 10 cc of water on the soil surface of previously drained pots. Use an eyedropper to place drops regularly between plant rows. Maintain the plants in the same way as described for infestation with adult midges.

Maintain the plants in a greenhouse until adults emerge, 20 to 25 days after infestation with adults or eggs. When the first signs of elongating galls appear, place the pots under large nylon film cages. Inspect the plants every morning thereafter and collect the adult midges in glass tubes for use either in maintaining cultures or in screening rice varieties for resistance.

Freshly collected adult females are adversely affected at relative humidities below 70 percent. The tubes containing the gravid females should be kept in trays containing a layer of moistened cotton wool and covered with polythene film until the insects are used for infestation.

Two important parasites of the gall midge can cause heavy parasitization in laboratory cultures. *Platygaster oryzae* oviposits in the eggs and in the exposed first-instar larvae before they enter the plant. The parasite pupates and emerges from the prepupal stage of the gall midge larvae at the time of gall elongation. These features of its life cycle can be used to effectively control this parasite, by maintaining the plants for infestation with adults and for incubation and hatching of eggs in an entirely separate location from the one where adult emergence is allowed to take place.

Norbanus sp. belonging to the family *Pteromalidae* is an external larval parasite. The adult parasite inserts its ovipositor through gall primordia at the base of rice seedlings, when water is low in the pots, and lays its eggs on a second- or third-instar larva. This parasite can be controlled by maintaining at least 2.5 cm of water in the infested pots until the gall elongates.



1. Planting system for screening rice varieties for resistance to gall midge.

SCREENING FOR GALL MIDGE RESISTANCE

I. D. R. Pieris (*unpublished*) evaluated eight planting systems involving eight to 16 varieties and seven to 105 test plants per variety per pot. Each test system was replicated 15 times. The adult method was used to infest the test pots. The planting system shown in figure 1 gave the most consistent and reproducible results for evaluating resistance to midge attack in rice varieties. In this system each test pot contains eight varieties with 21 plants per variety.

If only a few seeds are available, screening can be done in 20- x 20- x 20-cm pots with rows 2.5 cm apart and plants 1 cm apart with IR8 as the susceptible check and W 1263 as the resistant check. Resistance is evaluated about 1 month after midge infestation by a count of visible galls and dissection of the residue for undersized galls.

SELECTIVE BREEDING OF W 1263 FOR GALL MIDGE RESISTANCE

The four Eswarakora selections (W 1251, W 1253, W 1257, and W 1263), found to be highly resistant to gall midge in India (AICRIP, 1967), were screened in 1968 under intensive laboratory conditions in Ceylon. They all showed a small amount of resistance. Among them, W 1263 had the highest level of resistance, 25 percent. Selective screening and planting of W 1263 over four generations has raised the level of resistance to 73 percent. The marked difference in the resistance of W 1263 in India and in Ceylon may be due to the presence of biotypes of *P. oryzae* in Ceylon.

MECHANISM OF GALL MIDGE RESISTANCE IN W 1263

In W 1263 plants that were resistant to midge attack, development of first-instar larvae was retarded as was the development of first-instar larvae at inactive axillary buds of susceptible varieties (H. E. Fernando and N. Perera, *unpublished*). The larvae in resistant W 1263 plants eventually died without producing galls while larvae on inactive tiller buds of susceptible varieties developed normally after the buds became active.

Modder and Alagoda (1971) studied the basis for gall midge resistance in W 1263. They found that the gravid female midges had no more ovipositional preference for the susceptible IR8 than for W 1263 seedlings. They also found that first-instar larvae were equally successful in reaching the terminal shoot apices in IR8 and W 1263. There could therefore be no mechanical obstructions to larval movement on the surface or within the resistant W 1263 plants.

In a study on the rate of larval development in IR8 and W 1263, Modder and Alagoda (1971) found that by the 12th day after infestation 90 percent of the IR8 plants had second-instar larvae while only 35 percent of the W 1263 plants contained second instars and over 40 percent still contained first instars. Furthermore even after the number of first instars decreased no corresponding increase in the number of later instars occurred in W 1263, indicating that many of the first-instar larvae died in this variety. Modder and Alagoda (1970) concluded that the resistant W 1263 plants inhibited the transformation of first-instar larvae into second-instar larvae, resulting in eventual death of these larvae.

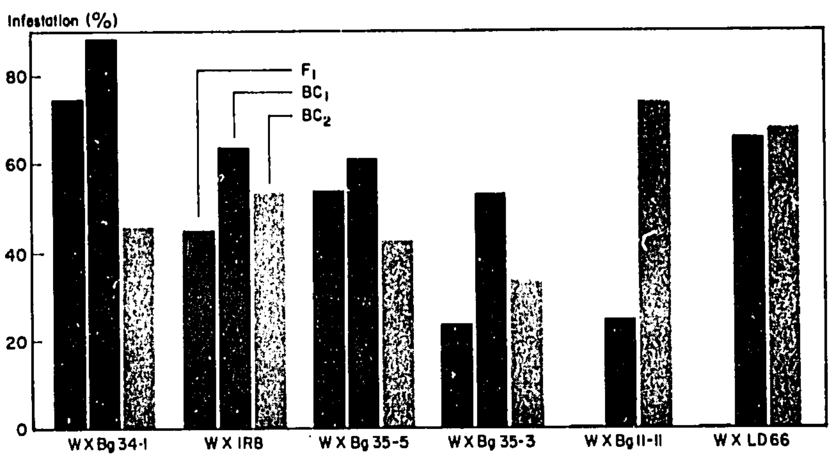
RESULTS OF SCREENING FOR RESISTANCE

A wide range of rice varieties and hybrids have been screened by techniques described by I. D. R. Pieris (*unpublished*). Other than the hybrids made in Ceylon and at the International Rice Research Institute with W 1263 as the resistant parent, few varieties have shown marked levels of resistance to the pest. Mudgo, which is resistant to the brown planthopper, is highly susceptible to gall midge. Ptb 21 and Leuang 152 are highly resistant while Ptb 18 and W 1263 (Cuttack Strain of the Central Rice Research Institute) are moderately susceptible. The reason for the large fluctuation in the infestation rate in the resistant varieties even though the infestation of the susceptible check IR8 remained uniformly high is not understood. The only possible explanation is the presence of several biotypes of *P. oryzae* in Ceylon.

BREEDING FOR GALL MIDGE RESISTANCE

S. D. I. E. Gunawardena and I. Sumanasinghe (*personal communication*) have crossed a selected strain of W 1263 (70 to 80% resistant) as the resistance donor and high yielding varieties that have desirable plant type. In the 4-month age group, the varieties used were IR8, LD 66, and Bg 11-11; in the $3\frac{1}{2}$-month age group, the varieties used were Bg 35-5 and Bg 35-3; and in the 3-month age group, Bg 34-1 was used. Ptb 21 and Leuang 152 are currently being used as resistance donors.

The F_1 plants were screened for resistance. The resistant lines were backcrossed to the recurrent high yielding parent. The progeny of the first backcross



2. Resistance to gall midge of F_1 crosses and two backcross generations.

were likewise screened and the resistant lines were backcrossed to the high yielding recurrent parent. The second backcross has been screened for midge resistance.

The results obtained in this program are presented in figure 2 (data are averages of percent infestation of the various lines). The high yielding parents were all highly susceptible (over 80% attack) while the W 1263 parent was moderately resistant (20 to 30% attack). These data cannot be interpreted until the possibility of biotypes of *P. oryzae* in Ceylon is fully resolved.

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Host-plant resistance to rice gall midge

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Pachydiplosis oryzae, commonly known as gall midge, is a major insect pest of rice in many areas of India. Only recently have excellent sources of resistance to the pest been identified and used in breeding programs. One resistant selection, W 1263, exhibits pronounced antibiosis to the first-instar larvae of gall midge. Some selections resistant to gall midge have multiple resistance to other pests, such as thrips, stem borers, leafhoppers, and planthoppers. Several dwarf selections combining resistance and plant type have been developed and evaluated for yield potential. The selection, RP 6-13 (IR8 x Siam 29), combines good yield potential with gall midge resistance, but it is susceptible to leafhoppers and planthoppers. While selections that are gall midge resistant remain resistant over wide areas of India and other Asian countries, some minor deviations have occurred. These deviations are attributed to the variation in the pest, which may have differentiated into biotypes. An admixture of biotypes occurs in most locations. The problem of biotypes in the pest may not become serious. If it does it could possibly be countered by relying upon diverse sources of resistance in breeding programs. Studies of inheritance in two crosses, IR8 x W 1263 and IR8 x Ptb 21, indicated that susceptibility results from the complementary action of three dominant genes, one of which is hypostatic to a nonallelic dominant inhibitory gene. While the same dominant inhibitor operates in Ptb 21, this variety possesses three recessive genes for resistance, while W 1263 has only one.

INTRODUCTION

Rice gall midge (*Pachydiplosis oryzae*) is a serious insect pest of rice that is prevalent in several southeast Asian countries. In India, the pest is endemic to parts of Mysore, Maharashtra, Andhra Pradesh, Orissa, and Bihar. The insect population becomes intense 6 to 8 weeks after the onset of the monsoon (Israel, 1959; AICRIP, 1968) and declines later in the growing season largely due to parasitization. The insect is virtually unnoticed in the dry season, when it probably survives on some grass hosts (Reddy, 1967; Israel et al., 1970). Like other internal feeders, chemical control is difficult except with costly insecticides.

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Most varieties now being grown are susceptible. The losses resulting from the pest range from 15 to 100 percent depending upon the location, season, variety, and time of planting (P. Israel and G. Veda Moorthy, *unpublished*).

The maggots of the insect invade the shoot apex and convert the apical leaves (Deoras, 1945) into tubular structures called silver shoots in which the larvae develop and pupate. The adult emerges from near the apex. Infestation is accompanied by accessory tillering which could cause crowding of the tillers in a hill and retard emergence of silver shoots. Under heavy infestation tillers become stunted. Stunted tillers are also the diagnostic symptoms of gall midge incidence. These typical symptoms appear only during the early vegetative tiller formation. For this reason farmers often grow seedbeds of photoperiod-sensitive varieties ahead of a heavy pest incidence and transplant over-aged (50- to 70-day-old) seedlings. The mother tillers, which escape infestation, produce panicles, although the later tillers may be infested (Israel and Veda Moorthy, 1958; Israel and Prakasa Rao, 1968). This practice prevents total crop failure which might occur if the young seedlings were planted at the peak of infestation.

All dwarf rice varieties thus far released and most popular tall varieties are highly susceptible to gall midge. The ecological factors governing insect distribution are not fully known, but the insect multiplies rapidly under hot and humid conditions that prevail through the major crop season in India.

Various aspects of host plant resistance have received the attention of the Central Rice Research Institute (CRRI), All-India Coordinated Rice Improvement Project (AICRIP), and the agricultural research station at Warangal in Andhra Pradesh.

VARIETAL RESISTANCE

Studies on varietal differences in resistance to gall midge were begun at CRRI in the early 1950's. The infestations were relatively low in scented, low-tillering varieties (CRRI, 1954). The collection of rice germ plasm composed of 3,600 indigenous types, 1,000 from the world catalog of genetic stocks, and 1,350 from the collections from Jeypore (Orissa) were screened under natural infestation during the kharif (monsoon) season. A numerical scoring scheme in which the resistant varieties received a score of 0 to 3, and susceptible ones, 7 to 9, was adopted. The data over several seasons were compared for confirmation since the pest population varied from season to season. The study identified 246 varieties from the FAO and CRRI genetic stocks and from Jeypore botanical survey collections that have various degrees of resistance (P. S. Prakasa Rao, *unpublished*). These varieties which originated from different sources had reaction scores of from 0 to 3 in tests during 4 years. Ptb 18 and Ptb 21, which were also moderately resistant to rice stem borers, had consistently low infestations of gall midge. An evaluation of wild rice collections revealed that *Oryza granulata* and related species are least susceptible to gall midge (Israel, Rao, and Prakasa Rao, 1963). The Thai variety Leaung 152 was also identified as highly resistant to gall midge (CRRI, 1970).

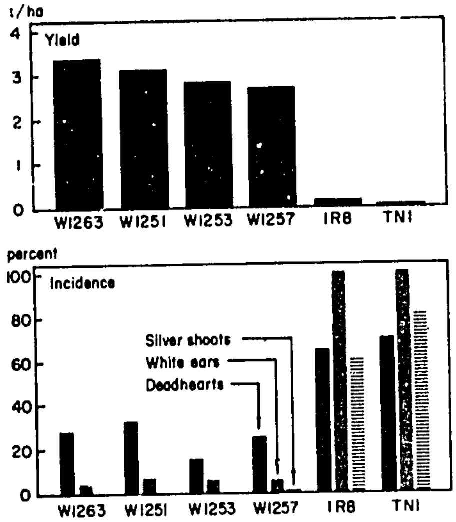
Field screening tests at the Warangal station between 1954 and 1964 confirmed the resistance of Eswarakora, HR 42, HR 63, Ptb 18, Ptb 21, and Siam 29. The varieties Eswarakora and Ptb 21 were the most consistently resistant. The consistent and heavy natural infestation by gall midge at Warangal has rendered the screening tests more dependable in differentiating between susceptible and resistant selections.

Local and exotic germ plasm were screened by AICRIP at Warangal between 1968 and 1970. The tests of kharif 1968 included 3,804 varieties from IRRI genetic stocks, 195 improved varieties from different Indian states, and 615 collections from the Jeypore botanical survey; while those of kharif 1969 included 96 varieties from IRRI genetic stocks, 491 from the Jeypore botanical survey, and 867 varieties from new collections made from northeast India. During the screening, the infestation of gall midge was fair in 1968 and negligible in 1970. The pest load was exceptionally heavy in 1969. The incidence of stem borer and leafhoppers was heavy during 1970, however. In the AICRIP screening tests at Warangal the criterion for classifying varieties as resistant was the absence of a single silver shoot in a hill with 20 to 30 tillers in a plot of 15 to 20 plants for each progeny or variety. Unlike the distribution pattern of stem borers, the pattern of the gall midge is more uniform, but as in all natural infestations some escapes are possible. Consequently rigorous criteria must be established for identifying resistance. For insects and diseases where differences are by degree and not qualitative, such criteria would not be possible.

The number of escapes in the AICRIP tests at Warangal in kharif 1969, when infestations were heavy, should be considered negligible. Studies of AICRIP confirmed the resistance of Ptb 18, Ptb 21, Eswarakora, Siam 29, JBS 446, and JBS 673. While 61 varieties in the Jeypore botanical survey collections were rated as moderately to highly resistant in CRRI screening tests, only two, JBS 446 (Desibayahunda) and JBS 673 (Ratnachudi), out of 615 varieties were rated resistant at Warangal in kharif 1969. In the same screening test at Warangal, 44 out of 867 ARC varieties proved resistant. Detailed description of the ARC varieties resistant to different pests and diseases will appear elsewhere (S. V. S. Shastry, S. D. Sharma, V. T. John, and K. Krishnaiah, *unpublished*).

BREEDING FOR RESISTANCE

Varieties, like GEB 24, which are highly susceptible to gall midge continue to be popular even in endemic areas mainly because of good grain type and photoperiod sensitivity which permits use of old seedlings so that some yield may be produced despite heavy gall midge populations. Because of other undesirable characteristics, varieties like Ptb 18 and Ptb 21 are not favored in spite of their high resistance to gall midge. To combine resistance to gall midge with other desirable characteristics, breeders at CRRI began in 1964 to cross Ptb 18 and Ptb 21 with GEB 24. Several selections from such crosses have resistance, tall-plant type, and good grain characteristics. Silver shoot incidence was below 3 percent in CR55-13 (Ptb 18 x Ptb 21) and in CR 56-1, CR 56-?, CR 56-12,



1. Yield and incidences of gall midge (silver shoots) and stem borers (dead hearts and white ears) in resistant tall selections compared with susceptible dwarf varieties — Taichung Native 1 and IR8, Warangal, India, Kharif 1967.

and CR 56-17 (all from Ptb 21 x GEB 24), while it was 20 to 30 percent in susceptible varieties like GEB 24. Most of these selections possess acceptable grain type, the best being CR 56-17, and resistance to gall midge, but because they have tall plant type, they do not offer as great a yield potential as the semidwarf varieties. Nevertheless, they have proved useful as breeding material.

At Warangal Eswarakora is used as a donor for resistance to gall midge and MTU 15 as the agronomic base. The choice of MTU 15 was fortuitous since both parents later proved to be resistant to green leafhopper as well. Consequently, the selections, W 1251, W 1253, W 1257, and W 1263, developed from the cross of MTU 15 x Eswarakora, proved resistant to gall midge and green leafhoppers. In the tests so far conducted at Warangal, not a single silver shoot has been recorded for W 1263. The reaction of this variety at other test locations was not consistent. At CRRI and Sambalpur (Orissa State), 6 to 12 percent silver shoots were observed on these varieties (Roy, Israel, and Panwar, 1969). At Mangalore, W 1263 had 17.6 percent silver shoots while the remaining three selections had 2 to 5 percent incidence. At Kanke, all the four selections were completely free of gall midge symptoms while the susceptible varieties had 30 to 40 percent silver shoots (AICRIP, 1968).

In a replicated trial of the four Warangal selections and the dwarf varieties under unprotected conditions, Taichung Native 1 and IR8, the high yielding dwarfs, gave negligible yields while W 1263, because of its resistance, produced 3.4 t/ha (fig. 1) (AICRIP, 1967). All four Warangal selections have multiple resistance to thrips, borers, gall midge, and leafhoppers. W 1263 appears even more resistant to stem borer than TKM-6 (AICRIP, 1970). In spite of these valuable resistance characters, W 1263, because of weak stem, poor nitrogen responsiveness, and only fair yield potential, was not released as a variety. These selections, however, became valuable sources of host plant resistance in the breeding programs, not only in India, but also in Ceylon, and Thailand, and at IRRI.

DWARF PLANT TYPES WITH RESISTANCE

The transfer of gall midge resistance into semidwarf plant types was started simultaneously at CRRI and Warangal. The program at CRRI involved eight crosses—Ptb 21 x TN1, IR8 x Ptb 21, CR 56-17 x IR8, CR 55-13 x IR8, CR 55-36 x IR8, Faya x TN1, IR8 x Leaung 152, and Leaung 152 x IR8—all made in 1966 (Roy et al., 1969). The program at Warangal was started with six crosses—IR8 x (Eswarakora x HR 35), IR8 x Siam 29, IR8 x Ptb 21, IR8 x W 1263, IR8 x W 1251, and IR8 x W 1257. The F_2 populations of all crosses made at CRRI and Warangal were subjected to natural infestation.

The program at AICRIP started relatively late (1968) and it relied initially on the F_1 stubbles obtained from Warangal. The breeding material developed at AICRIP has been screened under natural infestation at Warangal. While selection for resistance could be practiced only in the wet season of each year, the selection for plant type continued in rabi season.

Heavy natural infestation that prevailed all over the country in kharif 1969 permitted the rigorous selection of resistant progeny and the elimination of susceptible materials based upon a sizeable population in the early segregating stage (Table 1).

YIELD TESTING

Breeding material developed at each research center is intensely screened for reaction to the pest. Resistant selections from different centers are pooled into

Table 1. Efforts for incorporating gall midge resistance into dwarf plant types at Warangal and AICRIP.

Cross	F_2 population (no.)	Progenies (no.)			Selections (no.) nominated for yield test	
		F_3	F_4	F_5	1970	1971
			Warangal			
IR8 x (E. kora x HR 35)	10000	2841	2125	95		
IR8 x Siam 29	4500	108	102	135	4	1
IR8 x Ptb 21	2000	183	55	42	3	2
IR8 x W 1251	4000	337	37	27		
IR8 x W 1257	4000	235	73	55		2
IR8 x W 1263	2500	213	130	124	49	20
			AICRIP			
Eswarakora x IR8	1900	68	18	3		
IR8 x Siam 29	4000	104	35		3	7
IR8 x Ptb 21	20100	265	50	9		
IR8 x (E. kora x HR 35)	2800	57				6
IR8 x W 1251	5200	277	144			9
IR8 x W 1256	2900	47	28			
IR8 x W 1257	4800	128	147		6	8
IR8 x W 1263	6700	287	73			4

Table 2. Grain yield and gall midge incidence of some selections in the AICRIP variety trials, kharif 1968 and kharif 1969.

		1968					1969						
		Yield (t/ha)		Silver shoots (%)			Yield (t/ha)			Silver shoots (no./sq m)			
Variety	Cross	CRRI	Mangalore	CRRI	Mangalore	Kanke	CRRI	Sambalpur	Warangal	CRRI	Sambalpur	Warangal[a]	Overall rating[b]
Tall varieties													
W 1251	MTU 15 x E. kora	1.67	0.6	6.7	3.7	0.0	2.01	2.16	2.00	49	82	0	R
W 1253	MTU 15 x E. kora	1.94	0.2	8.9	2.7	0.0	1.62	2.01	1.94	29	33	1	R
W 1257	MTU 15 x E. kora	2.05	0.6	6.5	5.3	0.0	1.77	2.40	1.77	64	63	0	R
W 1263	MTU 15 x E. kora	2.37	1.1	7.8	17.6	0.0	2.54	2.70	1.94	49	22	0	R
CR 55-13	GEB 24 x Ptb 21	—	—	0.6	0.0	0.0	2.06	1.87	1.07	32	16	30	R
CR 56-12	GEB 24 x Ptb 18	—	—	1.9	—	—	1.60	1.83	1.28	23	71	165	MR
CR 56-17	GEB 24 x Ptb 18	—	—	0.9	—	13.8	1.72	0.85	1.90	6	7	9	R
Ptb 18	—	—	—	1.1	—	0.0	1.55	2.16	1.53	2	10	7	R
Ptb 21	-	—	—	1.9	—	0.0	2.63	2.85	2.11	3	3	1	R
Leaung 152	—	—	—	—	—	—	3.14	2.45	0.90	6	0	0	R
Semidwarf varieties													
IR8	Peta x Dgwg	2.07	1.04	20.3	29.5	39.7	—	—	—	—	—	—	S
TN1	—	0.24	1.54	13.6	29.5	46.4	1.25	0.69	Nil	386	1454	135	S
IR5	Peta x T. Rotan	1.97	—	19.2	69.2	41.2	—	—	—	—	—	—	S
Jaya	TN1 x T 141	—	—	—	—	—	2.24	0.14	0.13	190	1053	157	S
RP 6-12	IR8 x Siam 29	—	—	—	—	—	2.58	2.75	0.71[c]	5	19	0	R
RP 6-13	IR8 x Siam 29	—	—	—	—	—	3.50	3.09	0.69[c]	1	9	1	R
RP 6-15	IR8 x Siam 29	—	—	—	—	—	3.05	2.95	1.15[c]	2	4	3	R

[a]Due to heavy infestation, stunted tillers were far higher than silver shoots. [b]R = resistant; S = susceptible. [c]Yields affected by heavy leafhopper or planthopper attack.

nurseries at several locations for screening. The screening tests of 1969-70 included 485 selections from different locations. Each test plot had two rows of 25 plants flanked on each side by a susceptible variety, Taichung Native 1 or IR8. Differences in resistance were readily detectable in such tests. Further, the multi-locational testing ensured a resistance that was broad enough to counter variation in the ecotypes of the pest and it minimized misclassification due to escapes.

Materials with proven resistance are included in AICRIP yield tests at numerous locations every wet season under unprotected conditions. The first test, in kharif 1968, included only tall selections while the tests in 1969 had three semidwarf selections from the cross, IR8 x Siam 29. The data on incidence and grain yields in these tests are presented in Table 2. These tests confirmed the resistance of the selections derived from Eswarakora, Ptb 18, Ptb 21 and Siam 29. Tall, midge resistant selections, like W 1263, while resistant over different test locations and years, do not offer significant advantages in yield over the donor varieties, Ptb 18 and Ptb 21, although they have better grain type and shorter growth duration. The semidwarf selection RP 6-13, on the other hand, has by far the best yield potential. The major weakness of this selection and its sister selections is susceptibility to green leafhoppers and planthoppers. These insects occurred in high populations at Warangal and reduced the yields of these selections.

Dwarf, gall-midge-resistant selections now in yield tests vary widely in maturity. With the exception of W 13400, none possess very attractive grain type, although some have acceptable grain type. Since consumer preference might restrict the acceptability of these varieties, several new crosses have been attempted between gall-midge-resistant dwarfs, like W 12708 and RP 6-13, CR 57-29 and fine-grained, high yielding dwarf selections, like CR 10-4103, CR 36-148, CR 1-6-144, IR20, IR22, Ratna, and IR24. Simultaneously, several primary crosses have been made between new donors for resistance identified from Assam rice collections and the semidwarf, fine-grained varieties.

GENETIC STUDIES

K. V. L. Narasimha Rao (*unpublished*) at AICRIP studied inheritance in two crosses, IR8 x W 1263 and IR8 x Ptb 21. The F_1 stubbles, the parents, and F_2 populations were grown at Warangal during kharif 1969 when the pest load was unprecedentedly high. The resulting data sharply differentiated resistant from susceptible phenotypes. To minimize the errors due to escapes, each F_2 plant (grown in the nursery ahead of the gall midge season) was vegetatively propagated and planted in six hills. Each F_2 plant-row following such vegetative propagation was flanked on one side by a susceptible row of IR8 and on the other by a resistant row of W 1263. In the cross, IR8 x Ptb 21, F_2 plants were not vegetatively propagated, but the data from individual F_2 plants were recorded. If a silver shoot appeared on any one of the tillers of an individual F_2 plant in IR8 x Ptb 21, or on any one of the six clonal F_2 hills of IR8 x W 1263, the relative F_2 plant was considered susceptible. At Warangal, no silver shoots were observed on

W 1263, and only rarely on Ptb 21. For this reason, the criterion of resistance used in classifying F_2 population was rigorous.

The F_1 plants of both hybrids were resistant. In the F_2 population of IR8 x W 1263, which consisted of 4,747 plants, the pattern of segregation fit into the digenic inhibitory ratio of 13 resistant to 3 susceptible (Table 3). This implies that a single basic pair of genes governing resistance was involved with "susceptibility" dominant but suppressed by a dominant inhibitory gene. In the cross, IR8 x Ptb 21, out of 5,469 F_2 plants, the segregation conformed with the tetragenic ratio of 229 resistant to 27 susceptible (Table 3). In this case, three complementary dominant genes govern susceptibility and one of these genes is hypostatic to a dominant inhibitory gene.

Since IR8 is a common parent of the two crosses and since the character under study is the same, the loci involved obviously are the same. It therefore follows that the epistatic-hypostatic loci involved in both hybrids are the same. Susceptibility results from the complementary action of three basic dominant genes. W 1263 is resistant because one of the three complementary dominant genes governing susceptibility is absent, but Ptb 21 is resistant because all three complementary susceptible genes are absent. Both W 1263 and Ptb 21 have the dominant inhibitory gene in addition. IR8, on the other hand, is rendered susceptible by the presence of all three dominant genes and the absence of the dominant inhibitory gene. Thus, IR8 differed from W 1263 in resistance to gall midge at two loci and it differed from Ptb 21 at four loci, inclusive of the inhibitory genes in each case. That explains the digenic and tetragenic ratios obtained in the two crosses. The following gene models are proposed for the three parents.

W 1263:	*gm 1*	*GM 2*	*GM 3*	*I-GM 1*
Ptb 21:	*gm 1*	*gm 2*	*gm 3*	*I-GM 1*
IR8:	*GM 1*	*GM 2*	*GM 3*	*I-GM 1*

MECHANISM OF RESISTANCE

The first-instar larvae of gall midge migrate to the shoot apex without puncturing or feeding on the plant tissue. This finding prompted Y. S. Rao, P. Israel, C. P. Yadara, and J. K. Roy (*unpublished*) to investigate the morphological differences in the pseudo-stems of rice varieties. They reported that the spaces between leafsheaths are small in resistant varieties, like W 1263, Ptb 21, and Leaung 152, and large in susceptible varieties like IR8 and GEB 24. The inference was that the maggots would find it more difficult to reach the shoot apex of resistant varieties because of the smaller interspaces, implying that simple mechanical factors determined resistance. Venkataswamy (1966) associated resistance to gall midge with hairiness of leafblades, although the precise role of this character in determining resistance was not considered.

The observations at AICRIP (1969) do not corroborate the conclusion of Venkataswamy (1966) and Y. S. Rao, P. Israel, C. P. Yadara, and J. K. Roy (*unpublished*). In crosses involving W 1263 and IR8, resistance is not related to hairiness (K. V. L. Narasimha Rao, *unpublished*). Furthermore, by dissecting

Table 3. Segregation for resistance to gall midge in F_2 populations of two crosses, IR8 x W 1263 and IR8 x Ptb 21.

Cross	Phenotypes (no.)		χ^2	P value
	Resistant	Susceptible		
IR8 x W 1263				
Observed	3817	930		
Expected (13R:3S)	3857	890	2.20	0.25 to 0.10
IR8 x Ptb 21				
Observed	4927	542		
Expected (229R:27S)	4892	577	2.37	0.25 to 0.10

infested hills of IR8 and of resistant W 1263 at different times, it was shown that the first-instar larvae in W 1263 became inactive while those in IR8 completed their life cycle. If the resistance is primarily bio-physical, as inferred by Y. S. Rao, P. Israel, C. P. Yadana, and J. K. Roy (*unpublished*), the first-instar larvae would not be expected in the shoot apex of W 1263; nor would many of them be found dead (Table 4).

Similar observations were recorded for W 1263 by H. E. Fernando (*personal communication*) in Ceylon. P. S. Prakasa Rao (*unpublished*) likewise found that the maggots of gall midge migrated to the shoot apices of Ptb 18, Ptb 21, and W 1263 unhindered by the compact disposition of leafsheaths in these resistant varieties. In support of this statement, he cited high incidence of silver shoots under some conditions. All evidence thus strongly indicates that W 1263 exhibits pronounced antibiosis for gall midge larvae. While P. S. Prakasa Rao (*unpublished*) agrees to the role of antibiosis as the principal mechanism of resistance in W 1263, he believes that parasitized larvae are not killed by antibiosis. In his opinion, the silver shoots observed on W 1263 are mostly produced after the larvae have been parasitized. The implications of this observation are significant and must be studied.

Table 4. Condition of gall midge larvae in susceptible and resistant varieties (AICRIP, 1969).

Variety	Date of dissection	Tillers examined (no.)	Larvae (no.)						Pupae (no.)
			1st instar		2nd instar		3rd instar		
			Alive	Dead	Alive	Dead	Alive	Dead	
IR8 (susceptible)	Sept. 20	100	26	3	4	1	6	2	6
	Oct. 23	128	16	3	7	0	3	3	12
	Nov. 6	216	38	9	7	1	4	5	19
	Dec. 4	100	19	–	4	–	4	-	14
W 1263 (resistant)	Oct. 23	188	2	18	0	0	0	0	0
	Nov. 6	85	2	6	0	0	0	0	0
	Dec. 4	108	0	1	0	0	0	0	0

BIOTYPE VARIATION IN GALL MIDGE

The complete resistance to gall midge observed at Warangal is not necessarily observed at other locations. B. Jackson (*personal communication*) said that W 1257 had better resistance than W 1263 in the screening tests of Thailand. Pure seed lots of W 1263 showed only 30 percent resistance in the screening tests at Peradeniya, Ceylon (N. Wickramasinghe, *unpublished*). W 1263 had a higher incidence than its sister selections at Mangalore (Table 2), but not at Warangal and Kanke. Both at CRRI and Sambalpur, W 1263 and sister selections showed some incidence of silver shoots, the number varying with season and time of planting, although the variety is still classified as resistant at these locations.

The selection CR 56-12, bred and rated as resistant at CRRI, had as many silver shoots as susceptible varieties at Warangal (Table 2). Resistant selections made at CRRI and duplicates planted at Cuttack and Sambalpur had discrepant ratings of silver shoots at these two locations (Table 5). While the incidence was lower at Cuttack than at Sambalpur for 12 selections, the reverse was true for four selections. In the same screening tests 116 other selections gave similar incidence at both locations.

Ptb 18, Ptb 21, RP 6-13, RP 6-15, and CR 56-17 were consistently resistant in all test locations and seasons (Table 2). Gall midge screening tests at Pusakenagara, Indonesia, confirmed the resistant reaction of RPW 6-12, RPW 6-13, and RPW 6-15 (J. Leeuwangh, *personal communication*). The difference in reaction among common test varieties may be due to intrinsic variation in the insect itself, which may have differentiated into biotypes. At the same time, the reactions obtained do not seem to be due to pure populations of well-differentiated, location-specific biotypes, but probably to an admixture of biotypes in different locations. The relative frequency of these biotypes may vary among locations and times, causing some minor discrepant reactions among common test varieties.

P. S. Prakasa Rao (*unpublished*) attributes the locational and seasonal variation in the incidence of silver shoots on W 1263 to the variation in parasitization and not to variation in frequencies of the biotypes. His observation indicated that the silver shoots produced on W 1263 are mostly parasitized and that antibiosis is restricted to unparasitized larvae. These observations need to be confirmed in more critical studies of biotypes of the insect.

FUTURE OUTLOOK

The level of resistance to gall midge that has been achieved is a unique experience in breeding for insect resistance. Since excellent sources of resistance are available and the resistance is compatible with the productive semidwarf plant type, breeding for resistance should be the preferred strategy in attacking this problem. We should determine how long the resistance can last and over what range of locations. That the Eswarakora source of resistance held up in India, Ceylon, Indonesia, and Thailand, is gratifying, but within India, some discrepancies (though minor) in ratings of resistant varieties were noticed between Orissa and

Table 5. Discrepant ratings of gall midge incidence at Cuttack and Sambalpur, CRRI screening tests, kharif 1969.

Variety	Cross	Incidence of silver shoots (%)	
		Cuttack	Sambalpur
CR 57-42	IR8 x Ptb 21	10.5	40.5
57-46	IR8 x Ptb 21	13.2	40.0
57-16	IR8 x Ptb 21	5.3	33.3
57-11	IR8 x Ptb 21	5.2	42.3
57-30	IR8 x Ptb 21	8.6	25.0
58-28	Ptb 21 x TN1	8.5	45.4
58-33	Ptb 21 x TN1	7.6	24.3
58-51	Ptb 21 x TN1	10.4	48.9
60-2	CR 56-17 x IR8	10.6	31.4
60-3	CR 56-17 x IR8	10.5	30.6
60-15	CR 56-17 x IR8	17.5	57.3
60-42	CR 56-17 x IR8	12.2	35.2
93-2	CR 55-13 x IR8	11.6	2.2
93-4	CR 55-13 x IR8	12.2	2.1
93-6	CR 55-13 x IR8	18.9	2.0
94-19	CR 55-36 x IR8	25.5	2.1

Andhra Pradesh. These findings indicate possible admixtures in insect biotypes. Since the breeding programs are neither limited to nor restricted by a single source of resistance, even if the problem of biotypes becomes more serious, one of over 50 resistant varieties probably could be imaginatively used in the breeding programs. Future programs should use diverse sources of resistance in breeding and evaluate the reactions of different donors and selections to the pest in different locations. Not only would the development of variation in the biotypes of gall midge be monitored, but also alternate resistant varieties suited to different locations would be identified. The resistance in Ptb 21 and in W 1263 fits a model involving two and four genes. That suggests that the breakdown of resistance due to genetic changes in the insect population could be slower in Ptb 21 than in W 1263. Incorporating more non-allelic genes for resistance may result in varieties with still more prolonged resistance.

The identification of a large number of unrelated varieties as resistant to gall midge indicates that some of the resistance resource could be unrelated genes. Only a few genes have so far been identified in the limited genetic studies involving two resistant varieties. Tests of allelism between the genes in resistant varieties may reveal diverse genetic systems regulating resistance.

According to present data, resistance to gall midge is assured even if one of the three basic loci carries a recessive allele or if the dominant inhibitory gene is present, since susceptibility depends on complementation among three loci carrying dominant alleles. Critical loci governing resistance are, therefore, *GM 1* and *I-GM 1* in W 1263 and Ptb 21. Questions about the nature and quantification of the actions of *gm 2* and *gm 3* genes remain. While W 1263 and Ptb 21 normally are equally resistant, W 1263 had a greater breakdown at Sambalpur and Cuttack than Ptb 21 did at Warangal. It would be interesting to find out whether this difference between the two donors is related to additional resistance genes, *gm 2* and *gm 3*, in Ptb 21. In other words, does Ptb 21 carry resistance to more biotypes than W 1263? Earlier studies ignored the minor variation in incidence, while S. V. S. Shastry and D. V. Seshu (*unpublished*) attributed these differences to differences in relative frequencies of biotypes prevailing in different locations. Future tests seeking the verification of the biotypic differences between locations might reveal the role of different genes controlling resistance.

From the standpoint of breeding, irrespective of genetic systems and of gene action, incorporating resistance genes from diverse sources might overcome the problem of biotypes and extend the duration of resistance in the varieties bred for this purpose. From a rational point of view in breeding, choosing donors bearing non-allelic genes for resistance would ensure continued resistance.

It may be significant that among the varieties resistant to gall midge a few show multiple resistant reaction to other pests as well. For example, the Ptb 18, Ptb 21, Eswarakora, and ARC 11218-2 carry general resistance to gall midge, stem borers, leafhoppers, and planthoppers. Eswarakora is resistant even to more aggressive species of leafhoppers, *N. apicalis* (K. Krishnaiah, *unpublished*), and to thrips. The multiple resistance to pests of Eswarakora has been transmitted *in toto* to all four selections, W 1251, W 1253, W 1257, and W 1263, although these selections were made only on the basis of resistant reaction to gall midge. This apparent block-transfer of diverse factors for host resistance suggests that the basic gene for resistance to gall midge probably has a wide spectrum of activity on several insect species.

It is premature to conclude how extensive multiple resistance is in rice varieties. The varieties resistant to stem borers, TKM-6, CB 1, and CB 2, and varieties resistant to leafhoppers and planthoppers, MTU 15, Latisail, and Mudgo, are susceptible to gall midge. This preliminary observation may imply that, at least in some cases, multiple resistance is a character of varieties resistant to gall midge.

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Progress in mass rearing, field testing, and breeding for resistance to the rice gall midge in Thailand

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Research on the control of rice gall midge through the use of resistant varieties has received increasing emphasis during the past 4 years in Thailand. Because heavy infestation does not always occur under field conditions, a recently developed method for mass rearing the insect has helped speed the research. Five locations in widely separated areas of the country where the insect commonly occurs have been selected for field tests. Thirty-one cross combinations with varieties of Indian origin that have shown the most promise as sources of resistance to gall midge have been completed. Many lines that exhibit high resistance to gall midge also possess short to intermediate height, long grain, resistance to brown planthoppers and green leafhoppers, good tillering ability, and good tolerance to stem borers.

MASS REARING

We use the mass rearing method reported by Leumsang, Bhandhufalck, and Wongsiri (1968). The only difference is that Leuang Tawng (photoperiod-insensitive) and Dawk Mali 3, the susceptible hosts, are replaced by RD1. RD1 is highly resistant to green leafhoppers which had previously contaminated our gall midge cultures and infected the plants with yellow-orange leaf virus. With RD1, 500 to 1,000 adult gall midges are collected from cages daily.

The varieties are screened in an inoculation chamber with a mylar film roof and aluminum screen walls. The chamber is sprayed with water every 6 minutes to maintain high humidity. Results have shown that 100 percent relative humidity favors egg hatching. Twenty- to thirty-day-old seedlings of 100 to 150 varieties are transplanted in trays and placed in the chamber. One adult insect is released into the chamber for every five plants and is left there for 4 days. After inoculation, the trays are removed from the chamber and placed in a screened cage for about 45 days. During this time symptoms are sufficiently expressed so that the number of galls can be recorded.

During 1970, 1,351 lines involving 22 different F_3 or F_4 hybrid populations, mostly from EK lines (India) as the resistant parents, were tested by this mass screening technique. Of these only 150 lines, or slightly less than 10 percent, exhibited high resistance. Most of these were F_3 and F_4 hybrids.

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Table 1. Gall midge infestation of six Indian varieties and selected Thai varieties grown in northern Thailand in the 1969 wet season.

Variety	Infestation (%)
EK 1252	24.4
EK 1263	27.2
EK 1240	27.5
Eswarakora	32.5
EK 1256	33.6
EK 1259	35.3
Muey Nawng 62 M	49.3
RD1	66.8

FIELD TESTS

The high resistance of the Indian varieties to gall midge was first discovered when an experimental field planting in the province of Chiengrai in northern Thailand was severely infested with the gall midge during the 1969 wet season. A total of 124 experimental lines and check varieties were being grown in a randomized block design containing three replications with 4.5- x 0.75-m plots and a 25-cm spacing between single-plant hills within rows.

Infestations ranged from 24 percent for EK 1252 to 70 percent for a hybrid line from the cross Muey Nawng 62M x IR262. All the varieties of Indian origin were superior to the Thai resistant variety, Muey Nawng 62M, but they were not significantly different from each other (Table 1). Previous tests had shown that Muey Nawng 62M was not highly resistant to the gall midge in the northern areas of Thailand although it exhibited a resistant reaction in the northeastern region. Fortunately, crosses had been made in 1967 and 1968 using many of the Indian varieties as resistant parents. Thus, assisted by field tests, breeders were encouraged to select for gall midge resistance in the existing F_2 and F_3 hybrid populations.

In 1970, F_3 seeds of several crosses were exposed to the gall midge in the laboratory by the mass rearing technique (Leumsang et al., 1968). Heavy infestations were obtained in the laboratory and only 20 of 250 lines had no galls. These lines were saved and grown in the screenhouse Seeds obtained from each line were planted during the 1970 wet season for a field test which was expected to confirm the resistant reaction obtained in the laboratory. Field data on 15 selected lines are presented in Table 2. Although infestations were relatively low in 1970, the data strongly suggest that the selections are capable of resisting the gall midge. In addition to apparent resistance to the gall midge, a few of the lines have exhibited good resistance to green leafhoppers, brown planthoppers, and stem borers. Although all the lines had dwarf plant type with medium or long grain, a few were weak strawed and had spreading culms. In the 1971 wet season, 16 lines of good agronomic type were chosen for detailed field tests in areas of Thailand where heavy outbreaks of the gall midge commonly occur.

Table 2. Reaction to gall midge and other insects of promising experimental lines developed from crosses between Indian varieties and experimental lines from Thailand, 1970 wet season.

Selection or variety	Gall midge infestation[h] (%)	Reaction[i] to Green leafhoppers	Reaction[i] to Brown planthoppers	Stem borers[j] (% dead hearts)
6805[a]-2	0.24	R	Seg	16
-7	0.24	S	R	25
-22	0.15	–	–	19
-23	0.44	R	R	29
6806[b]-16	0.91	R	R	27
-18	0.12	R	S	32
-34	0.08	R	S	32
-36	0.25	Seg	S	20
-46	0.14	Seg	S	22
6811[c]-2	0.00	Seg	S	-
6809[d]-51	0.13	–	–	16
-63	0.18	–	–	17
-64	0.10	–	–	18
-74	0.00	–		20
-82	1.90	–		18
RD1[e]	8.35	R	S	29
RD2[e]	5.37	MR	S	43
RD3[e]	3.78	R	S	31
EK 1263[f]	0.06	R	R	15
17-3-10[e,g]	3.65	R	S	

[a]17-1-EK 1252 x RD2. [b]17-1-EK 1259 x RD2. [c]CNT 3176-EK 1263 x RD2. [d]CNT 3176-EK 1256 x RD2. [e]Susceptible check. [f]Resistant check. [g]Leaung Tawng x IR8. [h]Data obtained from field tests in the northern region of Thailand. [i]Data from IRRI tests; R = resistant, S = susceptible, M = moderately, Seg = segregating. [j]Field tests conducted at Rangsit Rice Experiment Station, 1971 dry season.

BREEDING

Eight varieties reported to be resistant to the gall midge were received from India in 1967. They were planted for seed increase and to determine whether they possessed other desirable characteristics. Since then, information has been obtained on their reaction to blast and to some extent on their reaction to bacterial diseases and stem borers (Table 3). The lines EK 1252, Ptb 21, and EK 1259 have exhibited more resistant reactions to blast than the other entries although none appeared to be highly resistant to yellow-orange leaf virus or bacterial leaf blight. Ptb 21 exhibited some resistance to bacterial leaf blight and Eswarakora was somewhat resistant to bacterial leaf streak. All entries, except EK 1240 and EK 1256, appeared equal to the variety TKM-6 in tolerance to stem borers.

Crosses were made with all of the Indian varieties except Ptb 18. The Indian varieties were first crossed with promising long-grain semidwarf selections and in most cases some F_1 plants were also crossed to the glutinous dwarf variety RD_2 to introduce the waxy characteristic, since most farmers in areas with gall

Table 3. Reaction of gall-midge-resistant parent varieties to blast, bacterial leaf blight, bacterial leaf streak, and stem borers (dead hearts) in Thailand.

Variety	Blast reaction by station				Reaction[a] to		Dead hearts (%)
	PSL	BKN	UBN	KGT	Bacterial leaf blight	Bacterial leaf streak	
EK 1240	3	4	5	4	S	S	31
EK 1252	2	5	5	2	S	S	13
EK 1256	4	7	6	3	S	S	25
EK 1259	2	4	7	4	VS	S	20
EK 1263	3	7	7	5	S	S	15
Eswarakora	3	5	5			MR	15
Ptb 18	4	3	7	2	S	VS	15
Ptb 21	3	3	2	3	MR	S	15

[a]S = susceptible, R = resistant, M = moderately, V = very.

midge problems grow glutinous varieties. All lines involving the EK 1240 parent and most of the two-way crosses concerned with EK 1256 have been discarded. Generally, the three-way crosses have appeared to be the most promising crosses for vigor, grain quality, and plant type.

The 20 lines which originally exhibited high gall midge resistance under laboratory conditions (Table 2) are being studied extensively since several have

Table 4. Number of reselections made from promising gall-midge-resistant lines.

Cross	Selection no.	Plants selected (no.)
(LT-IR8 17-1 x EK 1252 F_1) x RD2	BKN 6805-2	136
	-7	61
	-22	47
	-23	108
(LT-IR8 17-1 x EK 1259 F_1) x RD2	BKN 6806-16	21
	-18	117
	-34	107
	-36	59
	-46	99
	-58	108
(LY 34/2-TN1 CNT 3176 x EK 1256 F_1) x RD2	BKN 6809-51	40
	-63	50
	-64	30
	-74	43
	-82	36
(LY 34/2-TN1 CNT 3176 x EK 1263 F_1) x RD2	BKN 6811-5	32

shown promise as potential varieties. Reselections have been made from the more promising lines (Table 4) which we hope will result in lines homozygous for resistance to the gall midge as well as for other major characters. This should permit early release of an improved variety for areas of the country infested with gall midge. Yield trials of the early-generation lines are also under way to determine if reselections from high-yielding lines are equally productive.

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Discussion of papers on gall midge

N. PARTHASARATHY: Is there gall midge infestation in upland rice?

S. V. S. Shastry: No, the insect larvae rely upon a moist surface for the migration to a growing point. This condition, which greatly influences the infestation, is not so commonly encountered in the regions where upland rices are grown.

B. R. JACKSON: What are the parentages of Ptb 18 and Ptb 21? Was W1263 an early-generation line when it was selected?

S. V. S. Shastry: Ptb 18 and Ptb 21 are both pureline selections from local varieties in Kerala. W 1263 was bulked in the F_8 or F_9 generation.

W. H. FREEMAN: Has Dr. Fernando studied the possibility of having biotypes in gall midge?

H. E. Fernando: The work has just begun. We need more critical experiments to provide the answer.

R. F. CHANDLER: Where does the gall midge survive during the dry season and in what form?

H. E. Fernando: In rice ratoons and in wild grasses.

Genetics of resistance to rice insects

D. S. Athwal, M. D. Pathak

The available information on the genetics of resistance to rice stem maggot, stem borer, gall midge, and rice bug is rather limited. According to one report, field resistance to stem borer is polygenic while another report shows it is monogenic. The resistance to the other insects is controlled by one to three major genes. The preliminary results of studies with stem borer at IRRI indicate that resistance is dominant. It was complex in inheritance when the incidence of dead hearts was used as an index of resistance in the field, but it appeared to be simply inherited when mean larval weight was used as a criterion of resistance in the greenhouse. The genetics of resistance to the brown planthopper, *Nilaparvata lugens* Stål, and the green leafhopper, *Nephotettix impicticeps* Ishihara, has been intensively studied at IRRI. Resistance to both insects is simply inherited. One dominant and one recessive gene have been identified for resistance to brown planthopper (*Bph 1*, *bph 2*). Three independently inherited dominant genes (*Glh 1*, *Glh 2*, *Glh 3*) have been identified for resistance to green leafhopper. The two genes for resistance to brown planthopper are allelic or closely linked but independent of the three genes for resistance to green leafhopper. The greenhouse and field reactions to brown planthopper are strongly correlated. The genetic constitution of different sources of resistance to brown planthopper has been elucidated. Several varieties possess a common gene for resistance. All varieties possessing *Bph 1* became susceptible to a new biotype of the brown planthopper under greenhouse conditions. Diverse sources of insect resistance thus should be used in breeding programs. The significance of polygenic resistance for developing varieties with more lasting resistance to rice insects is discussed. The possibility of concentrating, through recurrent selection, minor genes that contribute to a resistant reaction is indicated.

INTRODUCTION

The stability of high productivity of modern rice varieties is greatly affected by control of insect pests. In the past, insecticides were the primary means of control. Unfortunately, no systematic attempt was made to discover and use genetic resistance to minimize or eliminate losses caused by insects. Recent work has shown that genetic resistance is available to almost all major insects against which collections of rice varieties have been evaluated.

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Although about 20 insect species are major rice pests in different parts of the world, only resistance to the brown planthopper and resistance to the green leafhopper have been studied in detail to determine the mode of inheritance and to identify different genes for resistance. Limited information is also available regarding the inheritance of resistance to stem borers, stem maggot, and gall midge.

BROWN PLANTHOPPER

The brown planthopper (*Nilaparvata lugens* Stål) causes damage by feeding on the rice plant and by transmitting the grassy stunt virus. When present in large numbers, the insects cause "hopperburn," which sometimes results in complete loss of crop. The brown planthopper is becoming increasingly important in tropical areas where rice is intensively grown.

Several hundred rice varieties from the world collection at IRRI were screened for resistance to the brown planthopper. Some had a high level of resistance (IRRI, 1967; Pathak, Cheng, and Fortuno, 1969). The development and survival of the insects on resistant varieties is so poor that the insects can do little damage to them.

In 1968, we began studies to determine the mode of inheritance of resistance to the brown planthopper. Two screening techniques, the "bulk seedling test" and the "tiller test," were developed and used in the greenhouse (IRRI, 1970, p. 103). The bulk seedling test consisted of planting the test material in wooden flats, 60 x 45 x 10 cm, and infesting the seedlings at the one-leaf stage with nymphs from virus-free insect colonies. The material was graded according to insect damage. The resistant seedlings showed either no visible damage or partial yellowing of leaves. The susceptible seedlings showed severe stunting, wilting, and gradual death. The tiller test consisted of infesting individual plants with a known number of insects and classifying the reaction on the basis of insect survival. Most insects on resistant plants died within 10 days while those on susceptible plants showed normal growth and development. The chief advantage of the tiller test is that an F_2 plant with a known reaction can be grown to maturity and its phenotypic reaction can be confirmed by studying the breeding behavior of its F_3 progeny. We carried out genetic studies with Mudgo, ASD 7, CO 22, and MTU 15, varieties that are resistant to brown planthoppers. Crosses between resistant varieties and a susceptible one, as well as crosses among resistant varieties, were studied in the greenhouse. A fairly clear-cut segregation for resistant and susceptible reactions was obtained in F_2 and F_3 generations. According to Athwal et al. (1970, 1971), Mudgo, CO 22, and MTU 15 each possess a single dominant gene for resistance to the brown planthopper. The single genes for resistance in these varieties were conditioned at the same locus and appeared to be identical. The common gene for resistance in Mudgo, CO 22, and MTU 15 was designated as *Bph 1*. The resistance of ASD 7 behaved as recessive and was controlled by a single recessive gene, which was designated as *bph 2*.

Table 1. F_3 breeding behavior of Taichung Native 1 x Ptb 18 and Pankhari x Ptb 18 for reaction to brown planthoppers.

Parent or cross	Reaction to brown planthoppers Resistant	Segregating	Susceptible
Taichung Native 1	–	–	13
Pankhari	–	–	11
Ptb 18	24	–	–
Taichung Native 1 x Ptb 18	35	65	32
Pankhari x Ptb 18	90	19	4

All available data on crosses between ASD 7 and other resistant parents indicated that recombination of *Bph 1* and *bph 2* was rare or non-existent. Therefore, the two genes are either allelic or closely linked. However, the ASD 7 gene (*bph 2*) appeared different from the Mudgo gene (*Bph 1*) because the ASD 7 gene was recessive and the Mudgo gene behaved as dominant.

A study comparing the greenhouse and field reactions of F_4 lines of Mudgo and those of a susceptible variety, Taichung Native 1, showed that reactions at two different stages of plant growth and under two different conditions were strongly correlated (Athwal et al., 1971). Thus the same gene in Mudgo, *Bph 1*, controlled both the resistance of the seedlings in the greenhouse and that of the adult plants in the field.

We have now completed studies on the genetics of brown planthopper resistance of two additional varieties, MGL 2 and Ptb 18. The results show that MGL 2 has a single dominant gene for resistance and Ptb 18, a single recessive gene for resistance. We have evidence that the resistance gene in MGL 2 is *Bph 1* and the one in Ptb 18 is *bph 2*.

Although Ptb 18 in crosses with susceptible Taichung Native 1 or IR8 gave a monogenic segregation for reaction to brown planthopper, it behaved differently when Pankhari 203 was the susceptible parent. In repeated tests, the proportion of susceptible plants in Pankhari x Ptb 18 F_2 populations was far lower than expected on the basis of monogenic segregation: only 58 F_2 plants were susceptible in a population of 943 F_2 plants. The comparative data on F_3 breeding behavior of Taichung Native 1 x Ptb 18 and Pankhari x Ptb 18 are presented in Table 1. While about 25 percent of the F_3 lines of Taichung Native 1 x Ptb 18 were homozygous susceptible, as expected, only about 4 percent of the F_3 lines of Pankhari x Ptb 18 were susceptible. The reasons for this variation in segregation of crosses involving two different susceptible parents are not clear.

C. R. Martinez (*unpublished*) studied the genetics of brown planthopper resistance of three IRRI experimental selections, IR747B2-6, IR4-93, and IR1154-243. He found that the resistance of each selection was under monogenic control. The gene for resistance in IR747B2-6 was dominant and allelic to the Mudgo gene, *Bph 1*, and the resistance genes in IR1154-243 and IR4-93 were

Table 2. Reactions of a group of varieties to two biotypes of the brown planthopper.

Variety	Reaction to brown planthopper[a]	
	Biotype 1	Biotype 2
Taichung Native 1	S	S
Mudgo	R	S
CO 22	R	S
MTU 15	R	S
MGL 2	R	S
IR747B2-6	R	S
ASD 7	R	R
Ptb 18	R	R

[a]R = resistant; S = susceptible.

recessive and allelic to the ASD 7 gene, *bph 2*. As both parents of IR747B2-6 and IR1154-243 are susceptible, Martinez proposed that resistance in these two selections originated through mutation. IR4-93 inherited its resistance from a Ceylonese variety, H-105.

Chen and Chang (1971) in Taiwan also studied the inheritance of the brown planthopper resistance of Mudgo and reported that the resistance depended upon a single dominant gene. Kaneda (1971) transferred the Mudgo gene to japonica types. So far no japonica variety has been recorded to be resistant to the brown planthopper.

Brown planthoppers show poor survival on the resistant variety, Mudgo. The insects are normally reared on Taichung Native 1 which is susceptible. IRRI plant pathologists found that the average life span of insects reared on Mudgo for 10 generations improved from 4.2 days in the first generation to 16.0 days in the 10th generation (IRRI, 1970, p. 69-70). The life span of the 10th generation insects on Mudgo was practically the same as the life span of the insects on Taichung Native 1.

We tested Mudgo against brown planthoppers which had been reared on Mudgo for 22 generations and found it nearly as susceptible as Taichung Native 1.

Table 3. Genetic constitution of different sources of brown planthopper resistance.

Source of resistance	Genetic constitution	Reaction to brown planthopper	
		Biotype 1	Biotype 2
Taichung Native 1	*bph 1 bph 1 Bph 2 Bph 2*	S	S
Mudgo, CO 22, MTU 15, IR747B2-6, MGL 2	*Bph 1 Bph 1 Bph 2 Bph 2*	R	S
ASD 7, Ptb 18, IR4-93, IR1154-243, H 105	*bph 1 bph 1 bph 2 bph 2*	R	R

Apparently, continuously rearing the insect on a resistant variety led to the development of a new biotype. Table 2 shows the reactions of varieties to the original culture (designated as Biotype 1) and to the new culture (designated as Biotype 2). The data confirm the findings that the genes for resistance in Mudgo, CO 22, MTU 15, MGL 2, and IR747B2-6 are identical because all were rendered susceptible to Biotype 2. On the other hand, the resistant reaction of ASD 7 and Ptb 18 to Biotype 2 supports the hypothesis that the resistance of these varieties is genetically different from that of Mudgo.

The simultaneous breakdown of the resistance of several varieties to a new biotype shows the need for using genetically diverse sources of resistance in breeding programs. Present knowledge about the genetic constitution of some of the available sources of resistance to the brown planthopper is summarized in Table 3.

GREEN LEAFHOPPER

In addition to causing direct damage by feeding, the green leafhopper (*Nephotettix impicticeps* Ishihara) transmits tungro or tungro-like viruses of the rice plant. Athwal et al. (1970, 1971) reported results of genetic studies with Pankhari 203, ASD 7, and IR8, varieties that are resistant to the green leafhopper. The studies were made in the greenhouse using both the bulk seedling test and the tiller test. The resistance of each variety was controlled by one major dominant gene. A study of crosses among the resistant parents showed that the single genes for resistance to green leafhopper in Pankhari, ASD 7, and IR8 were inherited independently of one another. The resistance genes were designated *Glh 1* (in Pankhari), *Glh 2* (in ASD 7), and *Glh 3* (in IR8).

Our current studies on the inheritance of resistance of Ptb 18 show that this variety has two genes for resistance to the green leafhopper. Only five of 134 F_3 lines of a cross between Taichung Native 1 (susceptible) and Ptb 18 were homozygous susceptible. We do not have conclusive data on the relationship between these two genes and the three resistance genes already identified, but it appears that one of the Ptb 18 genes is the same as the Pankhari gene, *Glh 1*.

RELATION OF PLANTHOPPER AND LEAFHOPPER RESISTANCE

Some rice varieties are resistant to either the brown planthopper or the green leafhopper, while others are resistant to both (Table 4). In general, varieties from East Pakistan and China are resistant to the green leafhopper and varieties from Ceylon are mainly resistant to the brown planthopper. Several varieties from India are resistant to both insects.

Mudgo is resistant only to the brown planthopper; Pankhari and IR8 are resistant only to the green leafhopper. ASD 7 is resistant to both insects. Athwal et al. (1971) showed that the ASD 7 genes for resistance to the two insects (*bph 2* and *Glh 2*) are independently inherited and that the Pankhari gene for resistance to the green leafhopper (*Glh 1*) is inherited independently of the

Table 4. Reaction of rice varieties to the brown planthopper and the green leafhopper.

Variety	Country of origin	IRRI acc. no.	Reaction[a] to	
			Brown planthopper	Green leafhopper
Mudgo	India	6663	R	S
Pankhari 203	India	5999	S	R
CO 22	India	6400	R	SR
MGL 2	India	6218	R	SR
MTU 15	India	6365	R	SR
ASD 7	India	6303	R	R
Ptb 18	India	11052	R	R
H 105	Ceylon	158	R	MS
Mathumanikam	Ceylon	8960	R	SR
Vellanlangalayan	Ceylon	8958	R	SR
DK 1	E. Pakistan	8574	S	R
DV 139	E. Pakistan	8870	S	R
Su-Yai 20	China	7299	S	R
Bir-tsan 3	China	4335	S	R
IR8	Philippines	9925	S	MR

[a]R = resistant; MR = moderately resistant; SR = semi-resistant (intermediate reaction); MS = moderately susceptible; S = susceptible.

Mudgo gene for resistance to the brown planthopper (*Bph 1*). Although we do not have precise data regarding the independent assortment of *Bph 1* and the IR8 gene for resistance to green leafhopper, *Glh 3*, we did not encounter any difficulty in combining these two resistance genes in one line. We tested a selected sample of 437 F_5 lines of the cross IR8 x Mudgo for resistance to the brown planthopper and the green leafhopper and found 247 lines resistant to both insects. Apparently the two genes are non-allelic and probably they are independently inherited.

Since recombination between the genes for resistance to brown planthopper, *Bph 1* and *bph 2*, is rare or absent, it may be concluded that each gene is inherited independently of the three genes for resistance to green leafhopper. Thus the available genetic information shows that several combinations of one or more of the three genes for green leafhopper resistance (*Glh 1*, *Glh 2*, *Glh 3*) with any of the two genes for brown planthopper resistance (*Bph 1*, *bph 2*) can be incorporated in future varieties.

STEM BORERS

There are more than 20 species of rice stem borers, but the striped borer (*Chilo suppressalis* Walker), the yellow borer (*Tryporyza incertulas* Walker), the white borer (*Tryporyza innotata* Walker), the dark-headed borer (*Chilotraea polychrysa* Meyrik), and the pink borer (*Sesamia inferens* Walker), are the most common and economically significant. Stem borer damage is caused by larvae which feed inside the rice stem and cause dead hearts in the early growth stages and white heads after heading.

Varietal resistance to stem borers is reflected by the low survival and slow growth of the larvae which cause the damage. In addition to antibiosis, the moths' non-preference for oviposition on certain varieties is also important. Several structural characters of plants, such as heavily sclerotized stem tissues closely spaced vascular-bundle sheaths, ridged stem surface, and high silica content, are associated with stem borer resistance (Pathak et al., 1971).

Although differences in the susceptibility of varieties to stem borers are due to differences in their suitability as larval hosts, a low survival rate is not always associated with low body weight of the surviving larvae. Also, the resistance at the white head stage may be independent of the resistance at the dead heart stage (Pathak et al., 1971). Thus resistance to stem borer constitutes a rather complex phenomenon. For precise genetic studies, the role of different components of resistance must be clearly understood.

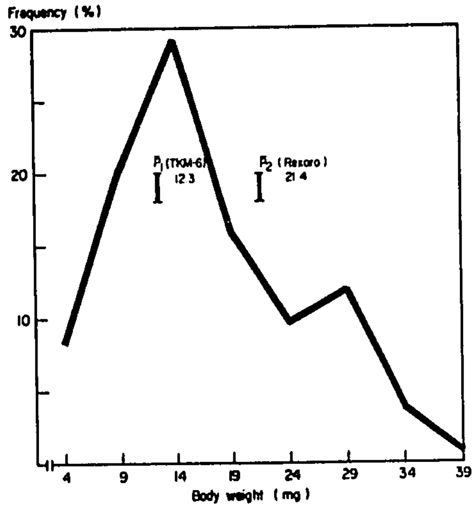
Using borer infestation as a criterion of resistance, Koshairy et al. (1957) showed that in the field the resistance of Giza 14 to stem borer was under polygenic control but few genes appeared to be involved. Another report indicates that the field resistance of TKM-6 to stem borers, as measured by the incidence of white heads, was simply inherited (All-India Coordinated Rice Improvement Project, 1968).

We studied the inheritance of the resistance of TKM-6 to stem borer in the greenhouse and in the field. In the greenhouse, the striped stem borer was used as the test insect. The material was graded according to survival rate and body weight of larvae. In the field, the material was studied under natural infestation conditions and was classified according to the incidence of dead hearts. The striped borer was the predominant species present in the field.

As shown by the survival rate of larvae, the mean body weight of the surviving larvae, and the percentages of dead hearts and borer infestation, resistance was dominant in the F_1 plants of a cross between Rexoro (susceptible) and TKM-6 (Table 5). The contrast between parents as well as F_2 segregation was clearer for mean body weight of the surviving larvae than for any other component of resistance to stem borer. The larval weight was independent of

Table 5. Reaction of F_1 of Rexoro x TKM-6 and parents to the striped borer (mean of five plants each infested with 10 larvae).

Parent or cross	Surviving larvae (no./plant)	Average wt of surviving larvae (mg/plant)	Dead hearts (%)	Infested tillers (%)
Rexoro	6.6	68.6	19.6	42.2
TKM-6	5.4	31.6	8.6	18.0
Rexoro x TKM-6	3.6	51.2	7.4	14.4



1. Distribution of striped borer larvae according to their body weight and frequency on 133 F_2 plants of Rexoro x TKM-6.

survival rate and was used as an index of resistance to stem borer in inheritance studies in the greenhouse. The frequency distribution of the mean body weight of surviving larvae on 133 F_2 plants is plotted in figure 1. The distribution curve is bimodal with about 25 percent of the insects showing a mean body weight equal to or higher than insects on Rexoro. Although the limited data indicate that this particular component of resistance to stem borer may be simply inherited, more information is needed before any hypothesis can be postulated.

Figure 2 shows the frequency distribution of dead hearts in an F_2 population and in parents of the cross, TKM-6 x Rexoro, based on field data. About 30 percent of the plants of the susceptible variety, Rexoro, showed less than 3 percent dead hearts per hill and apparently were escapes. There were probably some escapes also in TKM-6 and the F_2 population. The F_2 distribution curve shows no definite pattern. The inheritance of field resistance appears relatively complex and is probably controlled by several genetic factors. But, as reported by Koshairy et al. (1957), the number of factors cannot be very large because it is easy to recover resistant lines in crosses between TKM-6 and susceptible varieties. In the field we grew unselected bulk populations of the cross, IR262-24-3 (susceptible) x TKM-6, to the F_4 generation. From an F_4 population of about 26,000 plants, 594 plants were selected primarily on the basis of plant type, but also for resistance to diseases and insects, including stem borers, under natural infestation. The F_5 planting was adjusted so that this material reached the maximum tillering stage when all other rice in the surrounding area had been harvested. This ensured heavy infestation of stem borers. The susceptible check variety, Rexoro, was completely killed by stem borers. Of the 594 F_5 progeny, 305 showed a mean of 3 percent or less dead hearts per hill and their level of resistance was comparable to that of TKM-6. Under similar conditions, the susceptible parent, IR262-24-3, had 15 percent dead hearts per hill.

To understand the genetics of resistance to stem borer, it is necessary to define the different components of resistance of a particular variety and to study their pattern of inheritance both individually and collectively. These components should include preference for oviposition, survival and growth rate of larvae, and larval damage expressed as dead hearts and white heads.

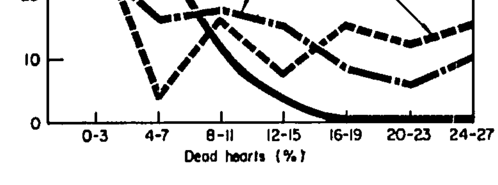
OTHER INSECTS

A species of planthopper, *Sogatodes oryzicola* (Muir), is an important insect pest of rice in South America. It also transmits hoja blanca virus. Jennings and Pineda (1970) found that Mudgo, which is resistant to the brown planthopper, and IR8, which is resistant to the green leafhopper, are also resistant to *Sogatodes*. They found that resistance to *Sogatodes* was highly heritable. Though no attempt was made to determine the number of genes controlling resistance, the F_3 breeding behavior indicated that the resistance was easy to transfer.

Fukuda and Inoue (1962) found many rice varieties resistant to the rice stem maggot, *Chlorops oryzae* Matsumura. In resistant varieties, the newly-hatched larvae died soon after entering the growing point. The F_1 hybrids of resistant and susceptible varieties showed intermediate resistance and the F_2 segregation agreed with a 1:2:1 ratio, showing that the resistance was monogenic.

Rice gall midge (*Pachydiplosis oryzae* Wood Mason) is a serious insect pest in India, Ceylon, Thailand, and Indonesia. S. V. S. Shastry and D. V. Seshu (*unpublished*) studied the inheritance of field resistance of W 1263 and Ptb 21 to gall midge in crosses with IR8, a susceptible variety. On the basis of F_2 data, they hypothesized that one or more basic dominant genes in IR8 govern susceptibility and that their expression is suppressed by a non-allelic dominant inhibitory gene in resistant varieties.

Sethi, Sethi, and Mehta (1937) reported that some rice varieties carry resistance to the rice bug, *Leptocorisa varicornis* F., because the panicle remains



2. Distribution of TKM-6 (235 plants), Rexoro (192 plants), and TKM-6 x Rexoro F_2 (932 plants) according to the frequency and incidence of dead hearts.

enclosed in the extended leaf sheath. They showed that the extension of the leaf sheath was dominant and controlled by three genetic factors in crosses between resistant and susceptible varieties. Apparently the resistance to rice bug results from the leaf sheath as a mechanical barrier and not from antibiosis.

DISCUSSION

Resistance to brown planthoppers and to green leafhoppers is simply inherited but resistance to stem borers appears to be complex. Although monogenic resistance is advantageous because it can be easily bred into new varieties, most workers feel that it is more vulnerable to insect variation than polygenic resistance.

Pathak (1970) reviewed information regarding the genetic basis of resistance of the host plant to different insects as well as the number of biotypes recorded in such insects. Host resistance to European corn borer and sorghum shoot fly is under polygenic control. Biotypes rarely develop in these two insects. On the other hand, several biotypes have been reported in different aphid species and in Hessian fly, host resistance to which is monogenic. This general finding lends some support to the contention that polygenic resistance may be more lasting.

We do not wish to imply that polygenic resistance is necessarily permanent or is always superior to single gene resistance. In work with cereal diseases, the terms "specific" or "vertical" resistance have been used for race-specific, major-gene resistance which generally is short-lived. The more stable resistance that operates against all known races is referred to as "generalized" or "horizontal resistance." There is some confusion regarding the nature of specific and generalized resistance. Caldwell (1968) argues that general resistance need not be always polygenic nor must short-lived resistance be always monogenic.

In our battle against insects and other parasitic organisms, we should exploit all kinds of resistance. Although polygenic resistance or generalized resistance might be more desirable, single-gene resistance has been effectively used against such destructive insects as Hessian fly of wheat. Six races of Hessian fly have been recorded in the U.S., but host resistance to each of these races is available (Hatchett, 1969). In fact, breeding for resistance to Hessian fly was so successful that the insect population was nearly eradicated after the distribution of fly-resistant wheat varieties (Painter, 1968).

The fact that a new biotype of the brown planthopper capable of attacking the resistant variety, Mudgo, was isolated in the greenhouse indicates that brown planthoppers, and probably green leafhoppers, will eventually develop new biotypes when resistant varieties are commercially grown over wide areas. There are some signs that the strain of green leafhopper prevalent in some rice-growing areas of the Philippines may be different from the original strain maintained in the greenhouse. The original strain had an average life span of only 4.3 days on IR8 in the greenhouse, while that of the new strain was more than 15 days on IR8 seedlings (IRRI, 1971, p. 93-94). The potential for such a variation in these insects calls for a well-planned and dynamic breeding program to incorporate diverse genes for resistance in future varieties.

In dealing with potentially variable insects, genetic information regarding the relationship between different sources of insect resistance is indispensable for the success of a breeding program. Our studies have already shown that several sources of resistance to the brown planthopper possess the same gene for resistance. Only two closely linked or allelic genes for resistance to brown planthopper have been found so far. Both genes should be incorporated in future varieties. At the same time, genetic studies should be carried out to identify other genes for resistance in the rice germ plasm. Based on our present knowledge, the prospects for controlling the green leafhopper genetically seem somewhat better than for controlling the brown planthopper because the three sources of resistance to green leafhopper that have been studied possess independent genes for resistance that can be incorporated singly or in different combinations in commercial varieties.

Genetic studies should be carried out to identify diverse sources of resistance to stem borers, gall midge, and other rice insects. A precise genetic analysis of the complex nature of resistance to stem borer will be valuable to breeders. The level of host resistance to stem borers is not as high as the level of resistance to planthoppers and leafhoppers. A high degree of resistance might be developed by combining genes from different sources for non-preference for oviposition, low larvae survival rate, poor larval growth, and for plant histological characters that interfere with larval feeding.

Some rice varieties are known to possess resistance to many insects. In addition to being resistant to both brown planthoppers and green leafhoppers, an Indian variety, Ptb 18, has also been reported to possess resistance to stem borers and gall midge. Our studies have shown that the resistance of this variety to brown planthoppers and green leafhoppers is conditioned at independent loci and probably resistance to other insects is also due to different genetic factors. Another variety. TKM-6, has shown considerable field resistance to rice insects including the brown planthopper though it is moderately susceptible to the insect in the greenhouse. We have found that when TKM-6 is crossed with some other susceptible varieties, it is possible to recover progeny that possess a high degree of resistance to brown planthoppers.

The possibility of concentrating, through recurrent selection, minor genes that act in a complementary fashion to make a genotype resistant or less susceptible should be explored. This can be best accomplished by selection in a composite population that is undergoing a high rate of genetic recombination through outcrossing. In a self-pollinated species like rice, outcrossing can be induced by introducing male-sterile lines in a composite population. The use of recurrent selection in improving the level of insect resistance may have special significance when adequate host resistance is not naturally available or when we gradually run out of the available genes for resistance due to continual variation in the insect.

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Discussion: Genetics of resistance to rice insects

S. V. S. SHASTRY: The genetics of resistance to stem borer has been analyzed at AICRIP under natural infestation. We adopt a field layout plan which overcomes some of the limitations that have been pointed out.

D. S. Athwal: I have read the detailed account given in the AICRIP Report. I think the method you used was good. We have suggested here that in addition to dead hearts or white heads, we should try to determine the basic component or components responsible for the expression of resistance to stem borers and then study the mode of inheritance of that component or those components in addition to their joint effect expressed as dead hearts or white heads.

Improvement of grain quality and nutritional value

Physicochemical properties of starch and protein in relation to grain quality and nutritional value of rice

Bienvenido O. Juliano

The physical properties of the rice grain are more closely related to the gelatinization temperature of starch or to the protein content than to amylose content. A high protein sample of a variety tends to resist milling and grain breakage more than one with normal protein. A high protein content or gelatinization temperature prolongs the cooking time of rice. A low or intermediate gelatinization temperature is a property common to varieties that show extreme elongation when presoaked and cooked, such as Basmati. Waxy rices of good rice cake quality tend to have a higher gelatinization temperature. Aging is accompanied by increased insolubility in water of starch and protein with no change in amylose content. Amylose content is the principal influence on volume expansion, water absorption, texture, and gloss of cooked rice. An increase in protein content of milled rice is accompanied by a less-than-proportional decrease in the nutritional value of protein. Such decrease corresponds to a decrease in lysine, threonine, tryptophan, and sulfur amino acids, and to an increase in the prolamin fraction of protein. The better nitrogen balance in subjects fed high-protein milled rice is related to the rice's higher levels of essential amino acids compared with normal-protein rice.

INTRODUCTION

Starch and protein are 98.5 percent of the constituents of milled rice (Juliano, Bautista, Lugay, and Reyes, 1964). Rice at 12 percent moisture has about 80 percent starch and 7 percent protein. Starch, a polymer of glucose, occurs in the endosperm as compound polyhedral granules, 3 to 10 microns in size. Protein is present as discrete particles, 1 to 4 microns in size, between the starch granules (Del Rosario et al., 1968).

Proteins are polymers of amino acids linked by peptide bonds. The protein content of milled rice ranges from 5 to 14 percent protein (at 12% moisture) (Juliano, 1966). Usually within the same variety, protein content shows a variation of 6 percentage points due to environment. For example, at 12 percent moisture, the protein content of the variety BPI-76 ranges from 8 to 14 percent (Cagampang et al., 1966). Starch content decreases with an increase in protein content. Brown rice from different panicles in the same hill may differ in protein level by as much as 10 percentage points, particularly when high rates of nitrogen fertilizer have been applied. Individual grains in a panicle may vary in protein content by as much as 5 percentage points.

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Protein content is usually determined from Kjeldahl nitrogen multiplied by the factor, 5.95, which is based on the 16.8 percent nitrogen content of the major rice protein fraction, glutelin. In the Kjeldahl protein determination, the digestion is still done manually, but the colorimetric ammonia assay in the digested rice has been automated (Juliano, Ignacio, Panganiban, and Perez, 1968).

Amylopectin is the major and branched fraction of starch; amylose is the linear fraction. Amylose is absent from waxy (glutinous) rice, but in nonwaxy rice it constitutes 7 to 34 percent, dry basis, of the milled rice or 8 to 37 percent of the starch. The amylose content of samples of the same variety may vary by as much as 6 percentage points. For example, the amylose content of milled IR8 rice varies from 27 to 33 percent, dry basis. Individual grains of a sample of a variety may range in amylose content up to 5 percentage points (N. Kongseree, *unpublished*). Amylose content of milled rice is classified as low (below 20%), intermediate (20 to 25%), or high (above 25%).

The amylose content of nonwaxy rice is usually measured by the intensity of its blue-colored complex with iodine. Amylose is determined at pH 9.8 to 10.0 by the method of Williams et al. (1958). A simpler, more accurate, and more rapid method has been tested satisfactorily at different laboratories using a pH of 4.5 to 4.7 and a wavelength of 620 nm (Juliano, 1971*b*). This method has been successfully adapted to an AutoAnalyzer module for screening alkaline dispersions of single-grain samples (10 mg) and bulk samples (100 mg) of milled rice at the rate of 70 per hour. The swelling number of Pelshenke and Hampel (1960) also measures amylose content. The water-extractable amylose from milled rice flour (starch-iodine blue value) at 100 C may be used for screening amylose content of samples with less than 30 percent amylose (Juliano, Cartaño, and Vidal, 1968).

Gelatinization temperature, a physical property of starch, is the range of temperatures within which the starch granules start to swell irreversibly in hot water with simultaneous loss of birefringence (in polarized light) and crystallinity. Final gelatinization temperature ranges from 55 to 79 C in rice starch and may vary by as much as 10 C within a variety (Juliano, Bautista, Lugay, and Reyes, 1964; Juliano, Nazareno, and Ramos, 1969). A high ambient temperature during grain development results in a starch with lower amylose content or higher gelatinization temperature, or with both (Suzuki and Murayama, 1967; Tani, Chikubu, and Horiuchi, 1969). Although gelatinization temperature and amylose content are independent properties of starch, no rice with both high amylose and high gelatinization temperature has been identified (Beachell, 1967). Final gelatinization temperature may be low (below 70 C), intermediate (70 to 74 C), or high (above 74 C). Samples of wild *Oryza* species had the same range of amylose content and gelatinization temperature as cultivated rice (Ignacio and Juliano, 1968).

Rice breeders usually estimate gelatinization temperature or birefringence end-point temperature by the extent of alkali spreading and clearing of milled rice soaked in 1.7 percent potassium hydroxide for 23 hours (Little, Hilder, and Dawson, 1958). This value can be accurately determined with a polarizing microscope that has a Kofler hot stage (Schoch and Maywald, 1956). Heating-cooking tests done below 100 C measure gelatinization temperature (Simpson et al., 1965); they include heat alteration values at 62 C (Little and Hilder, 1960), water absorption at 77 C and 82 C (Halick and Kelly, 1959), and expansion at 80 C (Refai and Ahmad, 1958). At 77 C, rices that have a low gelatinization temperature absorb more water than do those with intermediate or high gelatinization temperatures. At 82 C, rices that have low or intermediate gelatinization temperatures absorb more water than do those with high values.

Because of the variability among varieties in composition of the grain and variability in environment during maturation, drying, and storage (Juliano, Albano, and Cagampang, 1964; Juliano, Bautista, Lugay, and Reyes, 1964; Juliano, Cagampang, Cruz, and Santiago, 1964; Juliano, 1966), it is extremely difficult to obtain meaningful correlations from samples of different varieties grown and stored under different seasons or environmental conditions (Reyes et al., 1965). The ideal samples for these studies are lines that differ only in the property being studied and that are grown under identical management.

PHYSICAL PROPERTIES OF THE GRAIN

Market quality is determined by the physical appearances of the grain such as size and shape, percentage of brokens, and translucency, with little direct reference to starch and protein properties. Size and shape of the grain are not related to protein content, amylose content, or gelatinization temperature (Juliano, Bautista, Lugay, and Reyes, 1964; Simpson et al., 1965).

Nonwaxy rices are translucent. Waxy rices are opaque although their starch granules and protein bodies are also arranged compactly in the endosperm (Del Rosario et al., 1968). In contrast, the opacity of the endosperm of nonwaxy rice is caused by the loose packing of the starch and protein particles of the cells. These opaque portions, such as the white belly of IR8, contribute to a low yield of head rice. The opaque endosperm of "crumbly" rice also is soft. The opacity of the endosperm of waxy rice may be due to the presence of pores within the starch granules (Watabe and Okamoto, 1960). An experimental line with 7 to 9 percent amylose had a "tombstone" white appearance intermediate between the translucency of waxy and nonwaxy rices.

Studies by Cagampang et al. (1966) on pairs of samples of several varieties differing in protein content showed that high protein samples are probably more resistant to abrasive milling. They yielded less bran and polish (Table 1) tended to have higher head rice yields (Nangju and De Datta, 1970), and tended to be more translucent but with a darker color (IRRI [1964], p. 153-161) than low-protein samples of the same variety.

Study of the distribution of hardness in the rice endosperm with a Vickers microhardness tester showed that the variety with high gelatinization temperature, Century Patna 231, had the hardest core (Nagato and Kono, 1963). Although hardness distribution was studied for its correlation with arrangement of cells in the endosperm, its correlation with gelatinization temperature was not studied. Other instruments, such as the Kiya tester, are not very sensitive

Table 1. Mean weight ratios and contents of protein and protein fractions of milling fractions of brown rice of low- and high-protein samples of three varieties.

Fraction	Weight ratio	Content[a] (%)				
		Protein	Albumin	Globulin	Prolamin	Glutelin
			Low-protein samples			
Milled rice	86.9	6.6	0.40	0.69	0.19	4.64
Polish	2.0	11.8	2.81	0.95	0.40	4.85
Bran	11.1	12.4	3.41	3.29	0.51	2.10
			High-protein samples			
Milled rice	89.5	13.0	0.44	0.84	0.35	9.68
Polish	1.5	16.2	3.65	2.17	0.69	6.46
Bran	9.0	14.7	4.01	3.92	0.42	2.39

[a]At 12% moisture. Mean brown rice protein contents, 7.2% and 13.4%.

for this purpose and correlations with gelatinization temperature are either positive or negative, depending mainly on the samples chosen (IRRI, 1966, p. 69-77). Gelatinization temperature is expected to reflect the compactness of the starch granule and probably of the endosperm, as shown by the alkali test. It may be related to hardness and the accessibility of the endosperm to attack by fungi and insects. Gelatinization temperature correlates negatively with the extent of corrosion of starch granules by hydrochloric acid and α-amylase, with water absorption below 80 C (Reyes et al., 1965; Juliano et al., 1969), and with alkali concentration required to gelatinize the starch (Suzuki and Murayama, 1967).

COOKING QUALITY

Milled rice that has a high protein content or a high gelatinization temperature requires more water and a longer time to cook than rices with lower values (Juliano, Oñate, and del Mundo, 1965; Ranghino, 1966; Juliano et al., 1969). Rices that have low gelatinization temperature, such as japonica varieties, start to swell at a lower temperature during cooking than rices that have intermediate or high gelatinization temperature (Nagato and Kishi, 1966). However, these properties may affect the eating quality. Rice that has high protein or high gelatinization temperature tends to be undercooked. For example, Suzuki and Murayama (1967) found that the early-season rice crop, when cooked, was not sticky enough for Japanese consumers even though it had lower amylose content than the later crop. The early-season crop had a high gelatinization temperature so it tended to be undercooked in automatic rice cookers used with the amount of cooking water optimum for most varieties (Suzuki and Murayama, 1967).

Soaked milled rice of Basmati, D25-4, and certain Iranian varieties show extreme elongation during cooking (IRRI, 1967*a*, p. 47-58, 1967*b*, p. 43-58).

This property is not confined to long-grain rices. In fact, the highest elongation ratio was obtained with the medium-grain Burmese variety, D25-4, which has intermediate amylose content. Although many of these varieties have a low to intermediate amylose content, some high-amylose varieties, such as Taichung Native 1, which has a low gelatinization temperature, exhibited a high elongation ratio (IRRI, 1971, p. 16). In contrast, Century Patna 231, which has a low amylose content and a high gelatinization temperature, exhibited poor elongation. Gelatinization temperature seems to be more important than amylose content, as reflected in the data for two Pakistan varieties grown under cool and warm climates (Table 2). The Basmati crop at Dokri which had a poor elongation ratio had a much higher gelatinization temperature and a slightly lower amylose content than a good-quality Basmati crop at Punjab. Crosses have been made between Palman 246, a poor elongation variety, and Basmati 370, D25-4, and Domsiah to obtain materials for a detailed study of elongation.

The water content of brown rice steeped at room temperature correlated negatively with amylose content, but not with gelatinization temperature, in lines from the same cross differing in these two properties (N. Kongseree, *unpublished*). This negative relationship between amylose content and water content of steeped rice has been previously reported (Tani et al., 1969). Equilibrium moisture content of the grain and starch at high relative humidity (above 75%) seems also to be related to amylose content rather than to gelatinization temperature (Juliano, 1964; Juliano et al., 1969; N. Kongseree, *unpublished*). This may be related to the lower absolute density (Reyes et al., 1965) and the presence of micropores (Watabe and Okamoto, 1960) in waxy starch granules. Seeds of waxy varieties lose their viability faster than do seeds of nonwaxy varieties.

EATING QUALITY

Properties of properly cooked rice are better related to amylose content of milled rice than to the physical properties of the starch granule, such as the

Table 2. Physicochemical properties of two samples of Basmati rices from Pakistan differing in elongation ratio.

Variety	Quality rating[a]	Length: width ratio	Elongation ratio[b]	Protein content (%)[c]	Amylose content (%)[d]	Gelatinization temperature (C)
Basmati 6129	good	4.3	2.09	9.0	23.6	62 to 66
	poor	4.2	1.68	7.8	21.4	68 to 76
Basmati 370	good	3.9	1.79	7.5	23.4	65 to 72
	poor	3.7	1.61	7.6	22.2	68 to 75
Palman 246	poor	3.6	1.14	9.4	28.6	66 to 73

[a]Assessed by Dr. G. McLean. [b]Length of cooked grain to length of raw grain. Mean of 10 to 20 grains. [c]At 12% moisture. [d]Dry basis.

gelatinization temperature, that are altered during cooking. Table 3 shows that amylose content is the chief influence on taste panel scores of cooked milled rice for cohesiveness, tenderness, and gloss regardless of water-to-rice ratio (IRRI, 1970, p. 27-43; Juliano, 1968; Juliano et al., 1965). Differences in gloss scores are related to volume expansion and water absorption during cooking, as affected by differences in amylose content (Sanjiva Rao, Vasudeva Murthy, and Subrahmanya, 1952). Differences in texture may be ascribed to the greater ability of the linear fraction, amylose, to form a rigid three-dimensional gel than the branched fraction, amylopectin. The method of cooking rice is less important than varietal differences in determining the relative eating qualities of milled rices from different sources (Batcher, Staley, and Deary, 1963*a*, *b*). Amylose content is an index of resistance to disintegration during cooking, while gelatinization temperature is an index of resistance to cooking.

Waxy rices show the least volume expansion and water absorption during cooking. Cooked waxy rice has a high bulk density and is very moist, sticky, and glossy even after cooling. Waxy rices are used mainly for sweets, puddings, desserts, cakes, and sauces, but in parts of Laos and north and northeastern Thailand steamed waxy rice is the staple food. Although waxy rices range in gelatinization temperature from low to high, boiled milled waxy rices give similar taste panel scores for tenderness, cohesiveness, and gloss (Juliano et al., 1969). Waxy rices however differ in cake quality in Japan despite their constant starch composition of 100 percent amylopectin. Our studies have shown that preferred varieties have higher gelatinization temperatures but lower sedimentation constants than the poor-quality varieties (Table 4). The lower molecular

Table 3. Mean properties of milled rice and mean taste panel scores of cooked rice from low-amylose and high-amylose pairs from three different crosses.

Property	Low-amylose lines	High-amylose lines
Amylose (%, dry basis)	14.2	25.3
Protein (%, dry basis)	10.4	10.4
Final gelatinization temperature (C)	61.5	61.5
	Trial I (Identical water: rice ratio)	
Water: rice ratio	1.8	1.8
Tenderness[a]	7.6	4.0
Cohesiveness[a]	7.3	3.4
Gloss[a]	8.3	4.4
	Trial II (Adjusted water: rice ratio)	
Water: rice ratio	1.6	1.8
Tenderness[a]	6.7	4.1
Cohesiveness[a]	6.6	3.5
Gloss[a]	6.9	4.2

[a]Mean of duplicate assessment by a taste panel of four judges (Home Technology Department, University of the Philippines College of Agriculture). Numerical scores from 1 to 9 were assigned, a score of "1" representing the lowest expression of the property in question and a score of "9" the highest expression.

Table 4. Physicochemical properties of two sets of Japanese waxy varieties differing in cake quality.

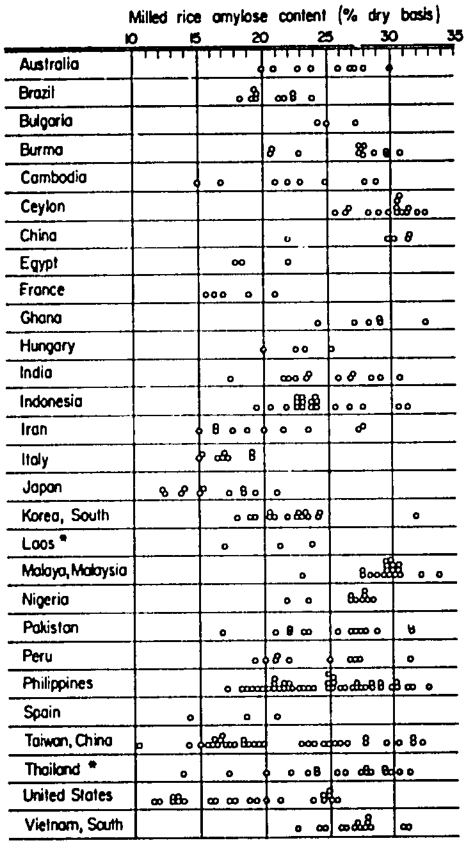
Variety	Cake quality	Final gelatinization temperature (C)	Amylopectin	
			$S_{20,w}$ (Svedbergs)	Mean chain length (glucose units)
Koganemochi[a]	good	67.5	78	25.8
Hatsunemochi[a]	upper interm.	66	60	25.1
Nakatamochi[a]	poor	63	114	26.0
Hatsunemochi[b]	good	68.5	84	25.0
Norin 1[b]	poor	58.5	144	26.6
LSD (5%)		2.7	8.4	n.s.

[a]Obtained from and assessed for cake quality by Dr. H. Kurasawa, Niigata Univ. [b]Obtained from and assessed for cake quality by Dr. S. Saito, Niigata Prefectural Food Res. Inst.

size of amylopectin in these preferred waxy rices probably contributes to a more sticky rice cake.

Most japonica varieties have low amylose content. A few have intermediate amylose content. Indica varieties have a wider range (low to high) of amylose content, however. Low-amylose varieties are moist, sticky, and glossy when cooked, but tend to split and disintegrate more readily than intermediate or high-amylose varieties when overcooked and when the cooked grain is soaked (Halick and Keneaster, 1956; Little and Dawson, 1960). In Japan low-amylose japonica varieties are preferred to high-amylose varieties because they are more sticky, glossy, and better tasting (Kurasawa et al., 1969; Tani et al., 1969). In the United States, low-amylose japonica rices are preferred for breakfast cereals and baby foods. Our study of the cooking properties of indica, japonica, and indica x japonica rices with similar low amylose contents (18 to 20%) showed overlapping properties of cohesiveness and gloss scores of cooked rice (C. Breckenridge, *unpublished*). Japonica varieties are the main varieties grown in Korea, Japan, Spain, Italy, France, and Hungary, but they are also grown along with indica varieties in Egypt, Taiwan, China, United States, and Australia (fig. 1). Rices low in gelatinization temperature, amylose, and protein are preferred for wine- and beer-making.

Most indica varieties have either intermediate or high amylose content. High-amylose rices are common in tropical Asia, even in the Philippines and Indonesia, where the people are partial to intermediate-amylose rice (Juliano, Cagampang, Cruz, and Santiago, 1964). Filipinos and Indonesians, and probably the Thais, also prefer a cooked rice that remains soft even when stored overnight. This kind of rice has less than 25 percent amylose. High-amylose rices cook dry and fluffy and have a hard texture. Most varieties in South Vietnam, Malaysia, and Ceylon are of this type. The long-grain varieties used in parboiling and canning in the United States generally have intermediate amylose content. The



1. Scattergram of amylose content of non-waxy rice varieties from 29 countries. Waxy rices constitute a major portion of the rice consumed in Laos and northern and northeastern Thailand.

semidwarf IRRI varieties that have high amylose (low-gelatinization temperature), when parboiled, are considered too firm in texture. Intermediate- and high-amylose varieties are suitable for noodle-making because they resist disintegration during cooking and subsequent soaking. Such high correlation between texture of cooked rice and amylose content limits the extent to which any one variety can universally meet the different eating quality preferences in various countries. Varieties with very high amylose (above 30 %), such as IR8, show low starch-iodine blue values at 100 C and very high setback values (above 400 Brabender units) in the amylogram, indicating a greater tendency for retrogradation. This is due primarily to the retrogradation *in situ* of amylose in the gelatinized starch granule above the critical amylose concentration (Juliano, Cartaño, and Vidal, 1968) and presumably is not accompanied by a change in molecular size of the starch fractions (N. Kongseree, *unpublished*).

In Ceylon, where all varieties have high amylose content, "samba" varieties (small- and short-grained) are preferred to bold long-grain varieties. Protein content is a secondary factor affecting texture. It is important in countries where the amylose range of the rice varieties is narrow. Protein is the major quality factor in Spain, where amylose content ranges from 12 to 18 percent, although the preferred rice variety is higher in both protein and amylose levels than the other varieties (Primo et al., 1962*a*, *b*). A darker tan color in the raw and cooked rice of a variety may be related to high protein content (IRRI, [1964], p. 153-161), but varietal differences also exist. BPI-76 has a grain that is more characteristically tan-colored than that of most other varieties with the same protein level.

STORAGE AND PARBOILING

Storage for up to 3 to 4 months improves head rice yield and grain hardness and causes the starch and protein fractions to become less soluble in water. Thus, aged rice expands more during cooking and absorbs more water than freshly harvested rice resulting in more flaky cooked rice. During storage, an increase in amylograph viscosity also occurs which cannot be ascribed exclusively to the complexing of fatty acid and amylose, or to crosslinking of carbonyl compounds with protein or amylose (IRRI, 1970, p. 27-43). Such increase in amylograph viscosity during storage also occurs in waxy rice but it is not accompanied by change in taste-panel scores of boiled rice.

Storage changes have been ascribed to after-ripening of immature harvested grain—a decrease in amylolytic activity or a change in colloidal form of the starch from sol to gel (Juliano, Bautista, Lugay, and Reyes, 1964). One objection to the amylase hypothesis is that amylase activity in the mature rice grain is low (Baun et al., 1970) and is concentrated in the germ and aleurone layers (IRRI, 1968, p. 47-58). Hence amylolysis in the soaked rice before inactivation during heating will be minimal.

In countries where flaky rice is preferred, rice is dry-heated or wet-heated to accelerate aging. Rice is parboiled in many Asian countries. It consists of steaming presoaked grains and slowly drying them. The changes are mainly physical and the process results in a harder and more translucent grain. Protein bodies are disrupted and the starch granules are completely gelatinized (Raghavendra Rao and Juliano, 1970). As a result, the protein and starch of parboiled grain are less extractable than those of raw rice. The oil globules in the bran are also disrupted during parboiling (Desikachar, 1967). Although amylograph peak viscosity was reduced markedly in high amylose samples, there was no general relationship with amylose content in parboiled samples, probably because of the presence of some residual physical structure in the gelatinized retrograded starch.

Milled parboiled rice is reported to have higher vitamin content than milled raw rice because during steaming water-soluble vitamins diffuse into the endosperm (Kik and Landingham, 1943). A more likely explanation is that parboiled rice is undermilled compared with raw rice, since it is more resistant to milling. During parboiling, water-soluble vitamins probably diffuse in all directions rather than to the grain core only. This is shown by loss even during soaking in hot water (Subba Rao and Bhattacharya, 1966). Hence if raw and parboiled rice samples are milled to the same degree, parboiled rice should contain less vitamins.

In countries partial to sticky rice, such as Japan, aging of rice above 15 C makes rice deteriorate. Storage changes occur only above 15 C so they are only a problem after the winter season (Tani, Chikubu, and Iwasaki, 1964).

NUTRITIONAL VALUE

Rice is the principal source of protein and calories for Asians. It makes up as much as 80 percent of their total caloric intake. Brown rice contains 8 percent protein and milled rice, 7 percent, at 12 percent moisture (Juliano, 1966). Rice protein has one of the best nutritional values among cereal proteins; its major limitation is its low level in milled rice. Rice protein is unique among cereal proteins in that it contains at least 80 percent glutelin (alkali-soluble protein) and less than 5 percent prolamin (alcohol-soluble protein) (Cagampang et al., 1966; Juliano, 1967) (Table 1). The other Osborne protein fractions are 5 percent albumin (water-soluble protein) and 10 percent globulin (salt-soluble protein). Albumin and globulin are concentrated in the aleurone layers and in the germ (Cagampang et al., 1966).

In a study of samples of the same variety differing in protein content Cagampang et al. (1966) showed that changes in protein content involved principally the percentage in the grain of glutelin and prolamin (Table 1). A corresponding increase in the number of protein bodies in the endosperm accompanied the increase in protein content (Del Rosario et al., 1968), but there was no change in the gross ultrastructure of the protein bodies (IRRI, 1970, p. 27-43). The distribution of protein in the endosperm of high-protein samples is more uniform than in low-protein samples. The difference in protein content between the brown rice and the milled rice tended to decrease as protein content increased. The polish fraction of high protein rice tends also to contain more protein than the bran from the same sample. Kaul, Dhar, and Swaminathan (1969) reported varietal differences in the distribution pattern of protein in the endosperm cross-section of the rice grain. Such differences may not have

Table 5. Levels of essential amino acids and cystine of protein and protein fractions of IR8 milled rice.

Amino acid	Amino acid content (g/16.8 g N)				
	Albumin	Globulin	Prolamin	Glutelin	Milled rice protein
Isoleucine	4.0	3.0	4.7	5.3	4.1
Leucine	7.9	6.6	11.3	8.2	8.2
Lysine	4.9	2.6	0.5	3.5	3.8
Methionine	2.5	2.3	0.5	2.6	3.4
Methionine + cystine	5.4	2.3	0.8	4.1	5.0
Phenylalanine	3.0	3.3	6.3	5.4	6.0
Threonine	4.6	4.6	2.9	3.9	4.3
Tryptophan	1.9	1.3	0.9	1.2	1.2
Valine	8.7	6.2	7.0	7.3	7.2

practical significance since most of the endosperm remains in the milled rice fraction. The protein content of milled rice and that of its outer layer are positively correlated (Primo et al., 1962*a*). A rapid sectioning method for examining cereal endosperm proteins with optional fixing of the sections is applicable to brown rice (Wolf and Khoo, 1970).

High protein rices tend to have lower levels of some of the amino acids essential to man, particularly lysine, than low protein rices of the same variety (Cagampang et al., 1966; Juliano, 1967). However, the drop in lysine content is less than proportional to the increase in protein content and does not occur above 10 percent protein (Juliano, Ignacio, Panganiban, and Perez, 1968; Juliano, 1971*a*). The lower lysine content of protein in high protein rice is partly due to the higher proportion of prolamin in the protein. Prolamin has the lowest lysine content (below 1%) among the protein fractions, followed by globulin, glutelin, and albumin (Palmiano, Almazan, and Juliano, 1968; Tecson et al., 1971) (Table 5). Glutelin has an amino acid composition similar to that of milled rice. Lysine is the first limiting essential amino acid in rice and other cereal proteins. Samples of wild *Oryza* species had ranges of protein content and amino acid composition similar to those of cultivated rice (Ignacio and Juliano, 1968). Waxy rice has an amino acid pattern similar to that of nonwaxy rice (Vidal and Juliano, 1967).

A study in which milled rice samples with 5.7, 7.3, 9.7, and 14.3 percent protein were fed to rats revealed that although protein quality tended to decrease as protein content increased, the decrease in quality was less than proportional to the increase in protein content (Bressani, Elias, and Juliano, 1971) (Table 6). At dietary protein levels of 5 percent and lower, protein efficiency ratios of milled rice overlapped that of casein. Relative quality based on a value of 75 for casein showed values of 75 to 80 for milled rice which are comparable to the biological values of rice protein (Juliano, 1966). Carcasses of rats that had been fed milled rice generally had more fat and less nitrogen than carcasses of rats fed casein. Thus, protein quality indexes based on weight gain, such as protein efficiency

Table 6. Summary of protein quality indexes for four milled-rice samples and casein based on weight gain in white rats.

Protein source	Protein content[a] (%)	0 to 5% dietary protein				Data showing net growth		
		PER[b]	NPR[c]	N growth index	Relative quality[d]	PER[e]	N growth index	Relative quality[d]
Intan	5.68	2.56	3.71	3.49	80	2.04	2.37	47
IR8	7.32	2.20	3.36	3.25	75	2.02	2.30	46
IR8	9.73	1.94	3.07	3.04	71	2.02	2.17	43
BPI-76-1[f]	14.3	1.50	2.57	2.47	57	1.84	2.12	42
Casein	86.2	2.20	3.36	3.23	75	—	3.78	75

[a]At 12% moisture. N x 5.95 for rice protein and N x 6.25 for casein. [b]Protein efficiency ratio at 5% dietary protein. [c]Net protein ratio at 5% dietary protein. [d]Based on a value of 75 for casein. [e]Protein efficiency ratio of 90% rice diet. [f]Corrected for differences in casein values between the two feeding experiments. BPI-76-1 was tested later than the other rice samples.

ratio, net protein ratio, and nitrogen growth index, overestimate the values for milled rice since these indexes assume that the protein contents of carcasses of rats fed different proteins are identical. Nitrogen balance indexes were casein, 0.53; Intan (5.7% protein), 0.49; IR8 (7.3% protein), 0.47; and IR8 (9.7% protein), 0.36.

When only the data showing net growth were considered (3% or higher protein diets), lower protein quality values were obtained for milled rice than for casein (Table 6). Based on a value of 75 for casein, milled rice gave values similar to the relative nutritional value of milled rice of 50 (Hegsted and Worcester, 1967). The BPI-76-1 variety has a relative nutritional value of 47 percent (D. M. Hegsted, *personal communication*), which is close to our estimated value of 42 percent.

The protein efficiency ratios of 90 percent rice diets were identical for the samples with 5.7, 7.3, or 9.7 percent protein and slightly lower for the 14.3 percent protein rice (Table 6). These results indicate that protein content, rather than protein quality differences, is the major influence on nutritional value of milled rice. These results agree with the earlier findings of Blackwell, Yang, and Juliano (1966). The varietal differences in protein quality may be explained by the decreasing level of lysine, threonine, sulfur amino acids, and tryptophan in rice protein as protein content increases. Differences in the levels of these amino acids may be explained by differences in the proportion of prolamin (Palmiano et al., 1968; Bressani et al., 1971) and in varietal differences in amino acid analysis of the protein fractions, such as prolamin and glutelin (Tecson et al., 1971).

The observations in white rats were confirmed by experiments on seven adult human subjects. Equal weights of milled rice of BPI-76-1 (14.5% protein) and Bluebonnet (7.9% protein) were fed to human subjects for a week (Clark, Howe, and Lee, 1971). BPI-76-1 rice caused a highly significant improvement in nitrogen retention over Bluebonnet rice. Clark et al. (1971) attributed the better nitrogen retention with BPI-76-1 rice to the high level of all essential amino acids per unit weight found in the variety by amino acid analysis. Digestibility of milled rice was similar in the two varieties.

Efforts to improve the nutritional value of rice varieties by breeding have been concentrated on increasing the protein content without affecting protein quality (IRRI, 1968, 1970, 1971). High protein varieties were identified by screening the IRRI world rice collection for Kjeldahl protein (Juliano, Ignacio, Panganiban, and Perez, 1968). Many of the selected varieties were japonica varieties, which may have high protein content at Los Baños because of their short growth duration and sensitivity to high ambient temperatures. Six of these high protein varieties were crossed to IR8 and the lines were screened for protein and yield potential. The goal is to improve protein content by 2 percentage points over IR8 while maintaining its high yields.

Amino acid analysis of F_4 brown rice of the breeding lines with the lowest and highest protein contents among the crosses showed that as protein content increased, lysine and tryptophan levels in the protein decreased and glutamic acid and leucine levels increased (IRRI, 1970) (Table 7). But the changes in

Table 7. Contents of glutamic acid, essential amino acids, and cystine of F_4 brown rice of a low-protein and a high-protein line of crosses between IR8 and six high-protein varieties (g/16.8 g nitrogen)[a].

Amino acid	Low protein Range	Low protein Mean	High protein Range	High protein Mean	r^b (n = 12)
Glutamic acid	16.8 to 18.9	17.6	18.2 to 19.8	19.0	0.72**
Isoleucine	4.3 to 4.8	4.6	4.4 to 5.1	4.7	0.36
Leucine	7.8 to 8.0	7.9	8.0 to 8.8	8.4	0.79**
Lysine	4.0 to 4.6	4.4	3.5 to 3.9	3.7	−0.84**
Methionine	2.2 to 3.0	2.6	1.9 to 2.4	2.3	−0.57
Methionine + cystine	3.5 to 5.0	4.3	3.5 to 4.3	4.0	−0.35
Phenylalanine	5.2 to 5.8	5.5	5.3 to 5.9	5.6	0.31
Threonine	3.9 to 4.2	4.0	3.6 to 4.3	3.8	−0.53
Tryptophan	1.1 to 1.6	1.4	0.9 to 1.3	1.1	−0.75**
Valine	6.4 to 7.5	6.7	6.2 to 7.3	6.8	0.15
Protein[c] (%)	5.4 to 7.6	6.7	12.6 to 15.3	14.4	

[a]Recalculated to 95% nitrogen recovery. Mean nitrogen recovery was 93%. [b]Correlation coefficient with protein content of brown rice. [c]At 12% moisture.

amino acid levels were only a fraction of the corresponding increase in protein content. Presumably protein changes through environment and gene recombination have similar effects on the amino acid composition and ratio of protein fractions of the rice grain. By careful selection of parents, however, protein content can be increased by 2 percentage points without adversely effecting the quality of the protein and the color of the starchy endosperm (IRRI, 1971). In fact, the milled rice of some of our lines with 12 percent protein still has up to 4 percent lysine.

The discovery of high lysine mutants of corn (Mertz, Bates, and Nelson, 1964) and barley (Munck et al., 1970) has generated interest in identifying similar mutants in other cereals including rice. Such mutations involve a decrease in prolamin and an increase in nonprotein nitrogen and in albumin. It may be best to screen rice for high content of water-soluble nitrogen since rice already has a very low prolamin content. In fact the endosperm protein of rice already has the same lysine content (3.5 to 4.0%) as the endosperm protein of opaque-2 corn. Tanaka and Tamura (1968) reported high-protein, high-lysine mutants from γ-irradiation, which we verified to have high protein content but normal lysine content (IRRI, 1971). Unlike most cereal proteins, rice protein is mainly made up of one fraction (glutelin) instead of two (glutelin and prolamin) so there is less probability of finding such high-lysine mutants in rice than in other cereals.

Because of the genetic differences in amino acid composition at a similar protein level (e.g., 1 percentage point range in lysine), varieties in the IRRI world collection have been screened for high lysine content in brown rice based on dye-binding capacity (DBC) with Acilane Orange G. An AutoAnalyzer dilutes the supernatant dye solution and records its color intensity. DBC values are correlated with the lysine content of rice protein (IRRI, 1970). Lysine is the only basic amino acid of rice protein that changes in concentration with a change in protein content (Cagampang et al., 1966; Juliano, 1967). The slope of the regression line (DBC as a function of protein content) was lower for entries with 10 percent and higher protein contents than for low protein entries. This reflects the observed greater dependence of lysine content on protein contents below 10 percent than above 10 percent (Juliano, 1971*a*). Lysine analysis by column chromatography of the selected lines based on high DBC values showed a potential improvement of lysine content by not more than 0.5 percentage point.

Nutritionists have advocated the fortification of cereal grains with lysine and threonine to improve the nutritional value of cereals. Although the benefits of fortification have been amply demonstrated in corn and wheat, fortification data on rice are not available, though long overdue. Rice protein is undoubtedly improved by lysine and threonine fortification, but Autret et al. (1968) argued that in the rice diet, enough lysine is contributed by protein from the other foods, so that lysine is not the first limiting amino acid in these diets.

To resolve this controversy, a long-term field study is under way in northern Thailand (being carried out by the Harvard University Department of Nutrition and the Thai Ministry of Public Health) in which synthetic rice fortification granules containing lysine, threonine, vitamins, and iron are being added to rice brought to village mills in the study area (Rosenfield, Gershoff, and Schertz, 1970). Three treatments are involved: One non-fortified, another fortified with vitamins and iron, and a third fortified with lysine, threonine, vitamins, and iron. Health data will be gathered from pre-school children (6 months to 5 years old).

In India, human feeding trials with rice contributing 50 percent of daily calories and protein showed that fortification with 0.2 percent lysine and 0.1 percent threonine for 6 months had no significant effect on height and weight of pre-school children (Begum, Radhakrishnan, and Pereira, 1970). In a second 6-month trial in which rice supplied about 80 percent of daily calories and protein, the children given the fortified rice were not significantly taller than those in the control group (S. Pereira, *personal communication*). These tests were unable to demonstrate any advantage in amino acid fortification of rice diets. Thus, available data show that improvement of the nutritional value of rice is best concentrated on improving its protein content.

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Discussion: Physicochemical properties of starch and protein in relation to grain quality and nutritional value of rice

S. C. LITZENBERGER: In breeding for increased protein content, what measures are taken to determine whether or not the increased protein is truly available to man for improved nutrition? I would raise the same question with reference to amino acid balance.

B. O. Juliano: Our studies showed that increased protein content results in a more uniform distribution of protein in the grain (Table 1). We verify this routinely in the promising lines by analyzing the protein content and amino acid pattern of brown and milled samples. Feeding trials with humans and rats have confirmed the nutritional advantage of high protein content of milled rice.

E. A. SIDDIQ: To what do you attribute the negative correlation between increased protein content and the level of essential amino acids? Please comment on the relationship between protein content and protein distribution pattern.

B. O. Juliano: The decrease in the level of some of the essential amino acids with an increase in protein content in the rice grain is caused mainly by the increase in prolamin (Table 1), which has low levels of these amino acids among the protein fractions (Table 5). A greater proportion of the increase in protein content of brown rice is located in the milled rice fraction as indicated by samples of the same variety differing in protein content in Table 1. We recently found the protein distribution pattern to be unreliable, differing among grains of any one variety. The distribution becomes more even with an increase in protein content.

L. T. EVANS: Does protein storage in the grain continue throughout grain filling or is it completed early? For example, does protein percent fall during grain development?

B. O. Juliano: Histological studies indicate that deposition of protein bodies starts 6 to 7 days from flowering or 2 or 3 days after synthesis of starch granules begins. In the tropics, the dry matter production of the grain, including protein synthesis, is essentially complete 3 weeks after flowering. During this period of starch and protein synthesis, protein content of the grain is essentially constant.

Wheat protein improvement

V. A. Johnson, P. J. Mattern, J. W. Schmidt

Protein increases in wheat as large as 25 percent have been achieved by breeding. Atlas 66 has been the main genetic source of high protein in the ARS-Nebraska program. At least two genes condition protein level in Atlas 66. One of them is linked with a gene for leaf-rust resistance. Although the level of protein in wheat is variable due to environment, the protein advantage of lines derived from Atlas 66 over other similarly grown wheats persists in a wide array of environments. High protein in wheat is compatible with high yield, desirable agronomic traits, and satisfactory processing quality. New sources of high protein have been identified. High protein wheats provide more lysine and other essential amino acids per unit weight of grain than do ordinary wheats. At low protein levels, lysine per unit protein is negatively correlated with protein but no significant correlation exists at high protein levels. Lysine differences ranged from 2 to 4 percentage points among 15,000 common and durum wheats in the USDA world collection. The genetic component of lysine variation appears to be only 0.5 percentage points. High lysine in wheat protein is mainly compensated for by lower levels of the non-essential amino acids, glutamic acid and proline.

INTRODUCTION

A short supply of amino acid lysine is the principal nutritional limitation of wheat protein.

Cooperative work between the Agricultural Research Service of the U.S. Department of Agriculture and the Nebraska Agricultural Experiment Station to improve the nutritional value of wheat began in 1954 when Atlas 66, a soft winter wheat from North Carolina, was introduced into our breeding program. Middleton, Bode, and Bayles (1954) showed that Atlas 66, selected from the cross Redhart x Noll 2 x Frondoso, had more protein in its grain than other soft wheats. In our early research we investigated the heritability of grain protein, the magnitude and stability of the genetic effect, the relationship of grain protein to yield and processing characteristics, and the physiology of high protein content in wheat. Funds from the Nebraska Division of Wheat Development Marketing and Utilization and the Northern Utilization Research and Development Division of USDA aided this early research.

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The ARS-Nebraska protein research was broadened in 1966 to include investigation of the amino acid composition of wheat protein. Supported by funds from the U.S. Agency for International Development, we screened the USDA world collection of wheats for protein and lysine differences and expanded our breeding program for wheat with improved protein. We established an International Winter Wheat Performance Nursery (fig. 1) in 1969 to identify superior winter wheat genotypes and to measure the impact of environment on nutritional quality.

The difference between nutritional quality and milling and baking quality should be clearly understood. The latter refers primarily to the suitability of wheat varieties for a highly mechanized wheat food processing industry. It has little to do with nutritional value.

The nutritional improvement of wheat protein may not be entirely compatible with accepted standards of bread wheat processing quality of the western world. High-grade white flour is composed largely of kernel endosperm. Endosperm protein, however, is relatively poor in lysine (2%) compared with the non-endosperm proteins (over 4%). Since the non-endosperm proteins are mostly eliminated from wheat flour during milling, increasing their lysine content would not change the lysine content of wheat flour much.

In countries where the whole wheat grain is used for food, the site of the lysine-rich protein in the wheat kernel would be of little consequence. Increases in the quantity of any of the proteins or increases in their lysine content would significantly raise the nutritional value of the wheat.

GENETIC VARIATION IN PROTEIN

We have identified substantial genetic differences in the grain protein content of wheat. The source of high protein most extensively used in our program has been Atlas 66. We have been able to raise the level of grain protein by as much as one-fourth in selections from crosses of Atlas 66 with hard winter wheat varieties (Johnson et al., 1963). The high protein trait is conditioned by more than one

Table 1. Average grain yield and protein content of Lancer, a normal wheat variety, NE65307, and a high protein wheat variety, grown with various nitrogen fertility levels in western Nebraska (USA) in 1969 and 1970.

Nitrogen applied (kg/ha)	Yield (t/ha)			Protein[a] (%)		
	Lancer	NE65307	Difference	Lancer	NE65307	Difference
0	2.57	2.55	−0.02	10.8	12.6	1.8
22	2.96	2.71	−0.25	11.2	13.3	2.1
44	3.11	2.92	−0.19	11.8	14.0	2.2
66	3.12	2.97	−0.15	12.6	14.9	2.3
88	3.09	3.01	−0.08	13.2	15.4	2.2
110	3.05	3.02	−0.03	13.6	15.8	2.2
132	2.99	3.08	0.09	14.1	16.2	2.1

[a]Nitrogen × 5.7. Measured at 14% moisture.

1. Fourth International Winter Wheat Performance Nursery - 44 sites in 27 countries.

gene. The ease of recovery of high protein segregates from crosses involving Atlas 66 indicates that the number of genes is not large.

A major gene for high protein in Atlas 66 is closely linked with a gene for leaf rust resistance in adult plants. We have recovered no high protein lines that are susceptible to leaf rust. Our recovery of lines with intermediate protein that are either resistant or susceptible to leaf rust provides evidence of the existence of a second gene for high protein that is not linked with resistance to leaf rust.

Heritability of protein

Environment has a large influence on grain protein. The heritability of protein level is not as high as the heritability of other economic traits in wheat. We have computed estimates of heritability ranging from 0.3 to 0.8 depending on the method of determination (Stuber, Johnson, and Schmidt, 1962).

Stability of protein

Grain protein level cannot be genetically fixed in wheat any more than grain yield can be fixed. The environment in which the wheat is grown is the major influence on both traits. But the genetic potential for high protein and high yield can be built into varieties. We have determined that high protein selections from our program will produce grain with more protein than ordinary wheats grown in the same environment. Our data indicate that the protein genes from Atlas 66 do not affect nitrogen uptake by roots. Rather, they promote more efficient and complete translocation of nitrogen from the plant to its grain (Johnson, Mattern, and Schmidt, 1967).

Evidence of the relative stability of the high protein trait is provided by 2 years of data from Nebraska tests in which a high protein line, NE65307, was compared with variety Lancer with a wide range of nitrogen fertilization rates (Table 1). NE65307 maintained a consistent protein advantage of 2 percentage

Table 2. Average grain yield, protein, and lysine content of nine wheat varieties grown in an International Winter Wheat Performance Nursery in 1969 and 1970.

Variety	Yield (t/ha)	Protein* (%)	Lysine content (% of protein)	(g/100 g grain)
Atlas 66	3.08	17.9	2.7	0.48
Purdue 28-2-1	3.00	17.5	2.8	0.49
NE67730	3.15	16.9	2.8	0.47
Triumph 64	3.28	15.2	2.8	0.43
Scout 66	3.66	14.5	2.9	0.42
Winalta	3.02	14.1	2.9	0.41
Bezostaia	4.34	13.8	2.9	0.40
Gaines	2.87	13.3	3.0	0.40
Yorkstar	3.34	12.8	3.1	0.40
LSD (5%)	6.4	1.1	0.3	—

*Dry wt basis.

points over Lancer at increasingly high levels of protein induced by the nitrogen fertilization.

Further evidence for the relative stability of the high protein trait in diverse environments comes from International Winter Wheat Performance Nurseries grown in 1969 and 1970 (Table 2). Atlas 66, Purdue 28-2-1, and NE67730, all of which possess genes for high protein in common, maintained an average protein advantage of 1.7 to 4.1 percentage points over other varieties with comparable grain yields. The high protein trait was expressed equally well at low yielding and high yielding nursery sites.

COMPATIBILITY OF HIGH PROTEIN WITH OTHER TRAITS

High protein and bread quality

Milling wheat into flour reduces the protein content of the flour below that of the whole grain. The protein reduction ranges from 0.5 to 1.5 percentage points or roughly 10 percent. High protein wheats derived from Atlas 66 exhibit the same magnitude of reduction in protein from milling as do lower protein varieties (Johnson et al., 1963). Thus the high protein trait involves an increase of protein in the endosperm portion of the wheat kernel that permits the protein advantage to persist after milling.

High protein selections from our first cycle of breeding did not possess adequate processing quality. Most lacked the dough development and baking properties required of American bread wheats. The selections, however, had substantial variation for individual quality traits which suggested that problems of combining high protein with satisfactory processing quality would not be insurmountable. This has been borne out in selections from the second and third breeding cycles (Johnson, Mattern, and Schmidt, 1971).

High protein and high grain yield

High protein selections from the first breeding cycle lacked the productivity of popular commercial varieties in Nebraska. In addition, they were too tall, lacked straw strength, and had insufficient resistance to stem rust (Johnson, Mattern, and Schmidt, 1970). One of the selections, NE67730, tested in the International Winter Wheat Performance Nursery was substantially less productive than Bezostaia and several other varieties in the nursery (Stroike et al., 1971). Twenty-six of the first-cycle lines were released as germ plasm by the Nebraska Agricultural Experiment Station and ARS in 1970. The pattern of yield response of one of the lines, NE67730, to nitrogen fertilizer was different than that of Lancer in Nebraska fertilizer trials (Table 1). NE67730 was less productive than Lancer at low levels of fertilizer, but was equal to Lancer above 110 kg/ha N.

Second-cycle, high protein selections currently under evaluation show much more promise. One selection, NE701132, made an average yield of 3.96 t/ha at three sites in Nebraska in 1970 compared to only 3.45 t/ha for Scout 66. Its protein advantage over Scout 66 was 2.3 percentage points or 23 percent. NE701132 and other productive second-cycle, high protein lines combine satisfactory processing quality with moderately short stature and combined resistance to leaf and stem rust (Johnson et al., 1971).

HIGH GRAIN PROTEIN AND AMINO ACID COMPOSITION

Analyses of the USDA world collection of common and durum wheats showed a negative correlation between lysine, expressed as a percentage of protein, and protein. The coefficient for 7,000 common wheats was -0.63. The ratio of gluten to water-soluble proteins and salt-soluble proteins in the kernel endosperm may be involved. The water-soluble and salt-soluble proteins are high in lysine (over 4%), but the gluten proteins are very low (less than 2%). The ratio of water-soluble protein to gluten-protein varies. Low protein wheats usually have a higher percentage of water-soluble protein. This probably explains the tendency of low protein wheats to have a higher percentage of lysine in their protein.

When lysine is expressed as a percentage of dry grain weight, its correlation with protein is strongly positive. The coefficient for 7,000 common wheats was $+0.83$. Obviously, the tendency for protein to be negatively correlated with lysine per unit protein is not sufficient in wheat to overcome the expected increase in lysine per unit weight of grain associated with an increase of protein. This is especially important because it suggests that high protein wheats should provide more lysine per unit weight of grain than wheats with lower protein.

We have used linear regression to adjust lysine values to a common protein level. This technique permits lysine comparisons among wheats that differ in protein content. It is necessary in breeding for higher lysine because it largely overcomes the direct effect of protein on level of lysine. Lysine values, unadjusted for protein variations, could be misleading from a genetic standpoint.

Amino acid profiles were compiled for several of our first-cycle, high protein lines (Mattern et al., 1968). Some lines possessed levels of lysine, methionine, and threonine, expressed as a percentage of protein, that were equal to those of the low protein parent. Other lines did not equal the low protein parent. When lysine was expressed in terms of dry grain weight, however, all lines had higher values than their low protein parent in these essential amino acids.

The amino acid profiles of some high protein lines from the second breeding cycle also have been analyzed. As with the first-cycle lines, the lines varied in their level of lysine per unit protein. Most were superior to a standard variety in the amount of lysine synthesized per unit weight of grain.

GENETIC SOURCES OF HIGH PROTEIN

Twenty-six high protein lines derived from Atlas 66 were released as germ plasm in 1970. Twelve second-cycle, high protein lines were increased in Nebraska and Arizona in 1971. They will be extensively tested in Nebraska and in regional trials. The best lines will be nominated for testing in the International Winter Wheat Performance Nursery. A portion of the 1971 increase seed has been sent to Turkey, Iran, and Afghanistan for agronomic evaluation. The lines combine high protein with outstanding productivity, good agronomic and processing-quality traits, and field resistance to leaf rust and stem rust under Nebraska conditions. Atlas 50, a sister selection of Atlas 66, was used in Kansas and has led to some promising high protein experimental lines.

Other wheats that appear to possess genes for high protein have been identified. One of these, Aniversario, comes from South America and may have a gene or genes for protein in common with Atlas 66 and Atlas 50. A Nebraska male-fertility restorer line, NE542437, also is a potential new genetic source of high protein. It has consistently produced grain that is higher in protein than normal varieties. In addition, it transmits the full effect to its F_1 hybrids. Since the line and all of its hybrids tested to date possessed male-sterile cytoplasm, high

Table 3. Protein and lysine data for four wheat varieties grown for 18 station-years at sites in the United States from 1967 to 1970.

Variety	Protein[a] (%)		Lysine content[b] (%)		Adjusted lysine content (%)	
	Mean	Range	Mean	Range	Mean	Range
			Initial sample — world collection			
Justin	17.0	—	2.9	—	3.1	—
CI5484	14.5	—	3.1	—	3.2	—
CI7337	14.1	—	3.3	—	3.3	—
CI5005	14.0	—	3.5	—	3.5	—
			Nursery data — (18 station-years)			
Justin	18.2	16.2 to 23.0	2.8	2.6 to 3.0	3.1	2.9 to 3.3
CI5484	17.4	11.1 to 25.1	3.0	2.7 to 3.9	3.2	3.0 to 3.8
CI7337	19.1	14.3 to 26.4	2.9	2.7 to 3.5	3.2	2.9 to 3.7
CI5005	15.9	10.9 to 23.1	3.0	2.8 to 3.7	3.2	2.9 to 3.6

[a]At 14% moisture. [b]Based on g lysine/17.5 g N.

protein may be associated with the cytoplasm rather than with nuclear genes. Progenies from reciprocal crosses involving NE542437 in combination with lines derived from Atlas 66 and Aniversario are being studied.

Two wheats from the USDA world collection, C16225 and PI176217, also show promise as new genetic sources of high protein. They hold special interest because they may also be higher in lysine than other varieties. In greenhouse plantings, PI176217 has consistently produced grain with above-normal protein and lysine. We have made numerous hybrid combinations of different high protein wheats to determine genetic relationships and to assess the opportunity of achieving new high levels of protein in wheat.

LYSINE STUDIES

Fifteen thousand common and durum wheats from the world collection thus far analyzed for lysine were grown at Mesa, Arizona in large blocks over a 2-year period. Differential environmental effects should have been minimal. We obtained a range in lysine values from 2 to 4 percent of the protein with a mean of 3 percent. Forty percent of the lysine variation was attributable to variation in protein among the first 7,000 wheats analyzed. Adjustment of lysine values to 13.5 percent protein removed many wheats from the high-lysine class. Six of the 7,000 wheats had adjusted values higher than 3.8 percent and 125 were higher than 3.5 percent (Johnson et al., 1970).

Environmental effect

Some of the wheats with high initial lysine values were regrown at different sites in the United States from 1967 to 1970. Few of the high lysine values were maintained at all sites in all years. Table 3 shows three of the varieties that were tested, and the standard variety Justin. Statistical analyses of data were possible from 12 to 18 test sites. Mean differences for adjusted lysine were small. The adjusted lysine value for CI5484 was significantly higher than Justin in five tests and no different from Justin in seven tests. CI7337 was significantly higher than Justin in adjusted lysine in four tests and no different from Justin in eight tests. CI5005, which had the highest initial adjusted value, was higher than Justin in only one test and was significantly lower than Justin in one test.

Within-year combined analyses revealed that CI5484 and CI7337 were significantly higher in adjusted lysine than Justin in 1968. Not one of the three experimental varieties was different from Justin in 1969, but all were significantly higher than Justin in 1970. It is apparent that environment exerts a strong effect on the lysine level of wheat. This effect complicates the identification and use of genetic sources of high lysine. We are starting research to determine the extent that changes in the ratio of component proteins of the wheat kernel are associated with the environmental effect.

Genetic effect

In wheat, no gene for lysine with the effect of the maize opaque-2 gene has been identified among common and durum wheats. The genetic component of lysine variation among wheats that we have studied appears to be no larger than

Table 4. Protein-amino acid relationships among 90 wheat samples with low protein and high lysine.

Amino acid	Mean[a] (%)	Range[a] (%)	Correlation[b]	
			Protein with amino acids	Lysine with other amino acids
Protein	9.6	6.5 to 16.5	—	—
		Essential amino acids		
Lysine	3.4	2.6 to 3.8	−0.57	—
Isoleucine	3.6	2.9 to 4.0	ns	ns
Methionine	1.5	1.1 to 1.8	ns	ns
Threonine	3.3	2.8 to 3.7	−0.50	0.44
Valine	4.7	3.8 to 5.5	−0.35	0.49
Tyrosine	2.7	2.0 to 3.2	ns	ns
Tryptophan	1.3	0.1 to 1.8	ns	ns
Leucine	7.1	5.9 to 8.1	−0.41	ns
Phenylalanine	4.5	3.8 to 5.2	0.36	ns
		Non-essential amino acids		
Histidine	2.4	2.2 to 2.8	ns	0.50
Arginine	5.0	3.9 to 5.7	ns	0.37
Aspartic acid	6.3	5.0 to 7.3	ns	0.59
Serine	5.2	4.3 to 5.8	ns	ns
Glutamic acid	30.3	24.3 to 35.3	0.38	−0.75
Proline	9.4	7.4 to 11.2	0.50	−0.55
Glycine	4.5	3.8 to 4.9	−0.34	0.55
Alanine	4.2	3.4 to 4.5	−0.58	0.76
Cystine	0.8	0.5 to 1.4	ns	ns

[a]Based on g/17.5 g N for amino acids. [b]Based on 72 samples only; ns = non-significant.

0.5 percent of the protein. PI176217, a variety with high protein and high lysine, was compared with Aniversario, a variety with high protein, in greenhouse tests. Their protein contents were similar but PI176217 consistently showed an advantage of 0.5 percentage point over Aniversario. The genetic component of 0.5 percentage point suggested by our data represents a potential 17-percent advance in the lysine level of wheat. More extensive analyses of other wheats from the world collection could reveal lysine differences larger than 0.5 percentage point.

It may be significant that maize and barley, in which genes with a large effect on lysine have been identified, are both diploid species. In contrast, common wheat is hexaploid and durum wheat is tetraploid. The presence of more than one genome in these wheat species may have contributed to our failure to identify large differences in lysine content. It is possible that a gene in one genome with a large effect on lysine could be masked by genes in the other genomes (Johnson et al., 1971).

Amino acid relationships

Four amino acids in wheat protein are in short supply according to FAO determinations of human requirements (World Health Organization, 1965).

The lysine in normal wheat protein provides less than one-half of man's requirement and is the most critical of the essential amino acids. Isoleucine, methionine, and threonine are also deficient. Phenylalanine and leucine are strongly in excess of requirements.

Little information has been published about the interrelationships of amino acids in wheat. A change in the amount of one amino acid must compensate for a change or changes in other amino acids. We have been particularly concerned with the effect of changes in levels of protein as well as changes in lysine on the levels of other amino acids in wheat protein. Our screening of the world wheat collection afforded an opportunity to obtain such information. Complete amino acid profiles were determined for a group of 90 samples with low protein and high lysine and a group of 47 samples with high protein and low lysine.

We found that protein level was negatively correlated with lysine, threonine, valine, and leucine among the wheats with low protein and high lysine (Table 4). No significant relationship of protein with isoleucine, methionine, tyrosine, or tryptophan could be detected. Lysine was positively correlated with threonine and valine among the essential amino acids. It was not negatively correlated with any of the essential amino acids. The data suggest that selection for high lysine may not be associated with adverse downward shifts in levels of other essential amino acids. The negative correlation of lysine with protein coincides with data from the world collection at large. The negative correlation of lysine with glutamic acid and proline indicates that compensation for high lysine is largely provided by reductions in these two non-essential amino acids.

Correlations for the wheats with high protein and low lysine were notably different from those computed for the wheats with low protein and high lysine (Table 5). Only isoleucine and alanine were positively correlated with protein. Lysine, in contrast to its negative relationship with protein among the low protein wheats, showed no significant relationship with protein when the protein level was high. It can be speculated that wheats genetically high in protein will not be as low in lysine per unit of protein as the general regression of lysine on protein among ordinary wheats would indicate.

Lysine level among the high protein group of wheats was unrelated to levels of other essential amino acids except threonine and valine which were positively correlated with lysine. Among the non-essential amino acids, only glutamic acid was negatively correlated with lysine. These data lend support to our contention that improved levels of protein and lysine can be achieved in wheat without adverse effects upon the levels of other essential amino acids.

Sources of above-normal lysine

Screening of the world collection of common and durum wheats for lysine differences is essentially complete except for recent accessions to the collection. Based upon additional study we have tentatively identified the following as potentially usable genetic sources of improved lysine level: PI176217, CI3285, CI5484, CI6225, CI7337, CI11849, and CI12756. The lysine content of the protein of these wheats is rarely more than 0.5 percentage point higher than that of ordinary wheats. The strong effect of environment may make the advan-

Table 5. Protein-amino acid relationships among 47 wheat samples with high protein and low lysine.

Amino acid	Mean[a] (%)	Range[a] (%)	Correlation[b]	
			Protein with amino acids	Lysine with other amino acids
Protein	19.0	17.5 to 22.5	—	—
		Essential amino acids		
Lysine	2.8	2.5 to 3.1	ns	—
Isoleucine	3.6	3.2 to 3.9	0.50	ns
Methionine	1.3	0.9 to 1.5	ns	ns
Threonine	3.0	2.8 to 3.1	ns	0.52
Valine	4.5	4.1 to 4.8	ns	0.40
Tyrosine	2.5	2.1 to 2.8	ns	ns
Tryptophan	1.1	0.7 to 1.5	ns	ns
Leucine	7.0	6.5 to 7.5	ns	ns
Phenylalanine	4.9	4.4 to 5.2	ns	ns
		Non-essential amino acids		
Histidine	2.4	2.2 to 2.7	ns	0.50
Arginine	4.8	3.8 to 5.4	ns	0.72
Aspartic acid	5.5	4.8 to 6.0	ns	0.50
Serine	5.1	4.6 to 5.4	ns	ns
Glutamic acid	33.4	29.8 to 36.3	ns	−0.70
Proline	10.6	9.4 to 12.0	ns	ns
Glycine	4.1	3.8 to 4.3	ns	ns
Alanine	3.6	3.3 to 3.8	0.52	0.44
Cystine	1.1	0.1 to 1.4	ns	ns

[a]Based on g/17.5 g N for amino acids. [b]Based on 46 samples only; ns = non-significant.

tage disappear in some production situations. Because they also exhibit above-normal protein, PI176217 and CI6225 are being used extensively in our breeding program.

OUTLOOK

The quantity of protein in the grain of wheat can be modified genetically. Although we have increased protein content by as much as 25 percent by breeding, we believe further increases are possible as additional sources of high protein are found.

Varieties possessing genes for high protein maintain their protein advantage relative to other varieties in a wide spectrum of environments. Thus, it would seem that such genes can be effectively used in most winter wheat areas of the world to increase the protein content of wheat.

What is the true contribution of higher protein in wheat to improved nutritional value? At the present time we have only *in vitro* laboratory tests to guide us. They indicate that an increase, on a dry grain weight basis, in lysine and other essential amino acids that are in shortest supply is associated with higher protein content. Theoretically, such wheats should be more nutritious because they provide more of these amino acids.

Our wheat research group in cooperation with University of Nebraska nutritionists recently began feeding tests with mice to better measure the biological value of our high protein varieties. Present nutritional guidelines seem inadequate. Feeding trials with small animals will provide highly useful additional information but our trials must eventually be supplemented with human nutritional tests.

Genetic modification of the amino acid content of wheat protein apparently presents a more difficult problem. Lysine differences that we can identify as genetic are small compared with the total variability of lysine. Incorporation of lysine increases as small as 0.5 percentage point into agronomically acceptable varieties will be difficult.

Moreover, the analytical techniques needed to measure lysine can be effectively done by a few laboratories in the world. The ion-exchange chromatographic system for amino acid determinations is the most reliable method for accurate determinations. The dye-binding technique developed in Sweden offers an apparently adequate alternative method for lysine screening of large numbers of samples generated by breeding programs. Loss of accuracy appears minimal.

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Discussion: Wheat protein improvement

S. K. SINHA: Are there lines with high protein content as well as stability in protein level?

V. A. Johnson: As I pointed out, it is not possible to fix the protein content of wheat or any other crop at a pre-determined level by breeding. Environment exerts a major influence. But we can fix a potential for high protein in wheat, which we have done. Such potential is expressed as an advantage in protein content of high protein varieties over other varieties grown in the same environment, whatever the general level of protein content might be.

B. O. JULIANO: Has the lack of association between foliage and grain nitrogen in wheat been recently verified using your more advanced lines, and leaf blades instead of foliage? We recently found a high level of leaf nitrogen in rices that have a high yield of protein in the brown rice.

V. A. Johnson: No. We have not yet repeated this experiment with our more advanced high protein lines. We plan to do so.

P. R. JENNINGS: Would you speculate why wheat has more protein than rice?

V. A. Johnson: I suppose it is because wheat is grown under lower temperatures and on drier land than rice.

L. T. EVANS: Perhaps the essential difference between wheat and flooded rice in this connection is the extent and duration of their root growth. Roots are a major source of amino acids, and dryland conditions often lead to increased root growth. In support of this postulate, we find that the wild diploid wheat, *T. boeoticum*, which can have up to 38 percent protein in its grain, invests far more in root growth than do modern wheats. Similarly, upland rice may have a more extensive root system than lowland rice.

K. KAWANO: Generally speaking, rice yields more than wheat. Do you think that the generally higher protein content of wheat is responsible for this yield difference?

V. A. Johnson: No, I think not. Wheat and rice are different species that have been developed under quite contrasting ecological situations throughout the world. Even in those production environments in which the yields of wheat and rice are the same, wheat has a sizeable protein advantage over rice. One can only speculate on the reasons for this.

T. H. JOHNSTON: Is there information available on what happens to protein content in the extremely high yielding wheat varieties grown under irrigation and at very high levels of nitrogen fertilization?

V. A. Johnson: We have no information on this except the response of winter wheat varieties in the International Winter Wheat Performance Nursery. In Kabul, Afghanistan, under high fertilization and high productivity of the crop in 1969, the protein content of the varieties remained relatively high.

H. I. OKA: How much is the heritability value of protein and lysine in selection?

V. A. Johnson: We have computed heritability values for protein content in wheat ranging from 0.3 to 0.8 depending on the method of computation. I question the usefulness of such computations even though we have made them. Our research on lysine content has not progressed to the point where heritability estimations were possible.

H. L. CARNAHAN: Were the data showing an association between rust reaction and protein content obtained from seed produced on plants that were not affected by rust?

V. A. Johnson: No. However, phenotypic expression of the high protein trait derived from Atlas 66 lines has been obtained on many occasions in which leaf rust was not present. In other words, although there is linkage between a gene for high protein and one for leaf rust resistance in Atlas 66, expression of the high protein trait is unrelated to the presence of leaf rust.

Breeding for high protein content in rice

Henry M. Beachell, Gurdev S. Khush,
Bienvenido O. Juliano

The IRRI world collection of rice varieties was screened for protein content and varieties with high protein were identified for use in crosses to IR8. These crosses were carried through the F_8 plant generation. Lines were identified which gave 30 percent higher protein content than IR8 check plots and about 70 percent of the rough rice yield of IR8. IRRI breeding lines screened from yield trials were identified which produced 18 to 23 percent higher protein than IR8 check plots but which did not differ significantly in grain yield. Information now available indicates that high yielding varieties with improved plant type can be developed that will produce 20 to 25 percent higher protein than IR8. High protein varieties must yield as well as other varieties if they are to be accepted by farmers. Therefore, they must have high levels of disease and insect resistance along with other essential traits. A close plant spacing and basal nitrogen fertilization was found to reduce environmental variability of protein content.

INTRODUCTION

Rice is a major source of food protein in Asia and other countries where the daily intake of rice is high. Its value as a protein source is enhanced by its high lysine content relative to other cereal grains. The main limitation of rice as a protein source is its low protein content (6 to 8 percent). Any increase in protein content would result in a substantial increase in protein intake by large numbers of consumers provided the quality of the protein is not impaired. For these reasons, breeding for increased protein content is an extremely important objective. Studies on protein content began at IRRI in 1962 (IRRI [1963]). A specific hybridization program was not undertaken until 1967 because of a lack of understanding of the many factors affecting protein content, including the availability of parent varieties with genetically high protein content.

If varieties with high protein content are to be accepted by farmers they must have a grain yield potential and grain quality at least equal to the varieties they would replace. Consequently high protein varieties must possess all the characteristics that breeders are attempting to incorporate into modern semidwarf varieties.

Numerous studies have been conducted at IRRI on factors affecting the quantity and quality of protein in brown rice (IRRI, [1963], [1964], [1965], 1966,

H. M. Beachell, G. S. Khush, B. O. Juliano. International Rice Research Institute.

1967*a*, 1967*b*, 1968, 1970*a*, 1971). Most of the early work was centered in the chemistry department where much information on the knowledge of rice protein was obtained. At present, the breeding program and other phases of the protein improvement work are carried out in a coordinated program among several IRRI departments. A contract with the National Institutes of Health (Contract PH-43-67-726), which started in 1967, resulted in the expansion of the program to its present level.

PROTEIN SCREENING PROCEDURES

We measure protein in brown rice in all screening trials rather than in milled rice since the protein contents of brown rice and of milled rice are highly correlated (Juliano et al., 1964). Furthermore, it is difficult to remove bran uniformly in milling. For example, in a 1968 variety-fertilizer experiment (IRRI, 1968), the brown rice protein content of four improved plant type varieties averaged 8.2 percent and that of the milled rice, 7.3 percent. High protein rice tends to have a lower percentage loss in protein in milling than low protein rice (IRRI, 1970*a*).

Grain samples used for evaluating the protein content of individual plants from pedigree rows are based on 10 fully developed brown-rice grains selected at random from the grain produced by a single plant. This sampling technique appears to be reasonably reliable. Usually three to six plants are taken from each pedigree row. Likewise 20 brown-rice grains are used to determine the protein content of samples from yield trials. Any yield trial sample that shows a high or a low value is re-examined. A more reliable technique for sampling yield trial plots would be useful. Samples are ground in a Wig-L-Bug amalgamator so small samples must be used.

In preparing experimental plots for protein experiments, every effort should be made to maintain soil uniformity. Land to be used should be planted to a single variety the season before. A relatively low nitrogen fertilizer rate should be used on the experiments as well as on the preceding rice crop.

SCREENING THE WORLD COLLECTION

The IRRI world collection of rice varieties was screened for protein content starting in 1966 to identify genetically high protein varieties to be used in the breeding program (Juliano et al., 1968). The mean protein values of the 7,760 varieties ranged from 5 to 17 percent, with an overall mean of 10.6 percent. There were 126 accessions which showed at least 13.5 percent protein based on brown rice samples (wet basis), or a mean of 14 percent for two different crops. Six varieties, selected from the 126 accessions, showed high protein content through four crop seasons (Table 1). They were subsequently used as parents in crosses with IR8 made in 1967. Aside from BPI-76 and BPI-76-1 none of the 126 high protein varieties screened from the world collection have value as commercial varieties in the Philippines. BPI-76-1 was crossed to IR8 and

Table 1. Protein content (of brown rice at 12% moisture) of six varieties screened from the IRRI world collection that were used as parents in crosses with IR8.

Variety	Origin	Protein (%)			
		Planting seed	1966 wet season	1967	
				Dry season	Wet season
Chok-jye-Bo-chal	Korea	17.1	17.0	17.8	15.5
Chow-sung	Korea	15.3		14.8	17.4
Sanho	Korea	16.7	18.2	15.6	15.7
Kasane Sowa 20	Japan	14.5	15.5	14.5	14.0
Omari 39	Hungary	14.7	15.6	12.6	14.3
Cryltiowanon Korn	Korea	16.2	13.5	15.5	14.5

IR12-178 (Mon Cham Vang A x I-geo-tse) and selections from both crosses were screened along with lines from the other high protein crosses.

HYBRIDIZATION PROGRAM

The six high protein parent varieties listed in Table 1 are all japonica varieties except Omari 39 from Hungary which is classified as an indica variety (IRRI, 1970b). These six varieties came from temperate regions and are not adapted to a tropical climate. They mature very early, total dry matter production is low and they are susceptible to several important diseases and insects. The extremely high protein content of the six varieties may be due in part to an environment-genotype interaction brought about by their low grain yield and low total dry matter production. On the other hand, these varieties appear to possess genes for high protein since some of their hybrid progeny show higher than normal protein content combined with improved plant type and higher total dry matter production. The six high protein crosses have been advanced through the F_6 generation. Most of the lines appear to be fixed for most plant and grain characters and many have been tested in replicated yield trials.

There was a wide segregation of plant types coming from the crosses. Some sterility was encountered but this was not a serious problem. Rapid selection pressure for improved plant type and high protein content was exercised each generation starting with the F_2 plant generation. While protein contents as high as the high protein parents were seldom observed, there were many lines that produced consistently higher protein than the IR8 check rows. The range and average protein content of plants selected from each generation are shown for the IR1103 cross in Table 2. The data for IR1100, IR1101, IR1102, IR1104, and IR1105 were similar. Many of the hybrid lines gave higher protein values than IR8 check plants each generation. Likewise, the average protein content of the plant selections made from these crosses was higher than that of the IR8 check row plants in each generation (F_3 to F_6) for each cross.

Table 2. Summary of single-plant brown rice protein analyses (at 12% moisture) of lines from high protein cross IR1103.

Year	Season	Generation	Protein content (%) IR1103[a] Range	IR1103[a] Mean	IR8[b] Range	IR8[b] Mean
1967	Wet	F_2	16.0	16.0	10.0	10.0
1968	Dry	F_3	6.8–12.8	9.7	6.3–9.9	8.0
1968	Wet	F_4	7.2–14.0	10.1	6.4–11.3	8.4
1969	Dry	F_5	6.5–15.9	10.8	7.1–11.1	8.7
1969	Wet	F_6	7.9–15.3	11.2	7.6–10.1	8.7
1970	Dry	F_7	7.0–15.0	10.4	7.5–10.8	8.7
1970	Wet	F_8	6.9–15.2	10.6	6.8–11.7	8.4
1971	Dry	F_9	5.7–15.2	9.7	6.4–9.2	7.5

[a]IR8 x Chow-sung. [b]Check rows.

Table 3. Summary of protein content (brown rice at 12% moisture) and other data on high protein lines and IR8 grown in pedigree rows.

Line	Seeding to heading (days)	Protein content (%) F_7, F_8	Protein content (%) F_9 Avg of two plants	Protein content (%) F_9 Bulk sample	F_9 rough rice yield (g/plant)	F_9 fertility (%)
IR8[a]	104	6.5	7.5	7.5	46.2	89
			IR8 x Chow-sung			
IR1103-1-5	102	10.7	10.6	11.1	44.4	94
IR1103-2-5-1-3	100	11.0	10.7	10.7	49.1	88
IR1103-2-5-1-5	102	10.6	10.6	11.1	39.6	90
IR1103-15-6-4	109	11.6	11.4	11.3	32.1	84
IR1103-15-6-5	105	11.6	10.1	10.7	45.5	87
IR1103-52-2	103	10.9	9.5	9.2	32.5	89
IR1103-66-4	85	10.7	10.0	10.5	33.6	89
IR1103-68-6	104	11.0	9.9	10.3	36.6	85
			IR8 x Cryhtocerias Kara			
IR1104-107-2	107	9.9	8.6	7.6	52.1	89
			IR8 x Rikuto Norin 20			
IR1100-67-5	103	13.0	9.9	10.1	35.4	92
			IR8 x Omirt 39			
IR1101-14-3	85	9.8	7.7	8.3	44.7	83
IR1101-16-3	95	9.9	9.1	8.7	34.3	91
IR1101-29-5	79	12.7	9.2	10.5	35.1	80
IR1101-30-4	76	12.0	10.8	10.5	41.4	87
IR1101-44-3	70	12.8	11.9	11.4	37.8	87
IR1101-45-2	80	12.3	11.1	10.9	30.5	79

[a]Protein values are averages of plants from IR8 check rows grown in nursery each season.

The average protein contents of selected lines based on the F_2 to F_8 seed generation are shown in Table 3. The protein content of six lines exceeded that of the IR8 check plants by 3.5 to 4.5 percentage points or from 41.2 to 52.9 percent. In the F_9 generation these lines exceeded IR8 by from 1.7 to 4.4 percentage points or 22.7 to 58.7 percent. The average rough rice yield per plant of the six lines averaged 77 percent of the yield of IR8. There were four lines which averaged about the same rough rice yield as IR8 and averaged 3.1 percentage points higher protein (41.3 percent more).

ENVIRONMENT AND PROTEIN CONTENT

Considerable variability in protein content is caused by environmental factors such as season of the year (wet or dry season), plant population density, and time and rate of nitrogen fertilizer applied. Usually protein content is higher during the wet season than during the dry season, possibly because grain yields are higher during the dry season.

IR8 plants showed differences in protein content of as much as 75 percent within a season when a 30 x 30 cm plant spacing and split application of nitrogen fertilizer (basal and top dressing) were used. We reduced this variability in the 1971 dry season by using a closer plant spacing (20 x 20 cm) and by applying all nitrogen fertilizer basally before transplanting. The combined effect of the closer plant spacing and the basal N treatment was a reduction in protein content and reduced variability as shown in Tables 2 and 3. In the future, we will plant pedigree nurseries at a spacing of 20 x 20 cm and possibly grow as many as three rows of each selection rather than just a single row. Plants to be evaluated for protein content would be saved from the center row of each line.

Table 4 shows the effect of plant population density on protein content in an experiment conducted by the IRRI agronomy department. The protein content of IR8 varied from 6.1 to 9.0 percent in the dry season and from 6.9 to 9.5 percent in the wet season. IR127-80-1, a low tillering variety, showed an even greater variation between a close spacing and wide spacing.

Table 4. Percentage of brown rice protein at 12% moisture of IR8 and IR127-80-1 (unfertilized) at different plant densities. (Data are averages of three replications.)

	Protein (%)			
	Dry season		Wet season	
Plant spacing (cm)	IR8	IR127-80-1	IR8	IR127-80-1
Broadcast	6.1	6.0	6.9	7.5
20 x 20	6.4	6.4	7.6	7.8
30 x 30	6.7	7.5	7.6	8.4
40 x 40	6.6	8.6	7.9	8.5
50 x 50	7.0	9.3	8.7	9.0
100 x 100	9.0	10.9	9.5	11.3

Table 5. Percentage of brown rice protein of two varieties as affected by time of nitrogen application[a] IRRI, 1969-1970.

Application time	1969 wet season[b]		1970 dry season[c]	
	IR8	IR20	IR8	IR20
Basal	8.8	9.2	8.3	8.9
50% basal and 50% at panicle initiation	8.6	9.6	8.6	9.2
50% basal and 50% at heading	9.0	9.5	8.9	9.9

[a]Data are averages over 15 times of harvest each with three replications. [b]60 kg/ha N applied. LSD (5%) = 0.7. [c]150 kg/ha N applied. LSD (5%) = 0.5.

Late application of nitrogen fertilizer tends to increase protein content and variability as well. Trials by the IRRI agronomy department (IRRI, 1971, p. 131-132) have shown the wide differences that occur in protein content between basal application and split application (Table 5). In our future pedigree nurseries and in preliminary yield trials nitrogen will be applied basally. Lines found to have higher protein at moderate nitrogen levels should eventually be tested at high levels and with split application to determine their overall response. Rate of nitrogen applied and protein content appear to be positively correlated.

SCREENING YIELD TRIALS FOR PROTEIN CONTENT

The varieties and breeding lines grown in most yield trials at IRRI are screened for protein content. From this screening program, IR480-5-9 (Nahng Mon S4/2 x Taichung Native 1) was identified by the agronomy department as a high protein line (IRRI, 1971). IR480-5-9 yielded 6.7 t/ha in a replicated variety yield trial at IRRI in 1967 dry season in which IR8 yielded 7.2 t/ha. This line is not suitable for farm production in the Philippines because of susceptibility to bacterial leaf blight, leafhoppers, and planthoppers. The higher protein content of IR480-5-9 has been confirmed in later experiments. Other lines showing high protein content are IR160-27-3 (Nahng Mon S4 x Taichung Native 1) and IR667-98 (IR8 x [Yukara x Taichung Native 1]). A sister line of IR160-27-3 has been named Sinaloa A68 in Mexico and is being grown commercially, but no information is available on the comparative protein content of Sinaloa A68 and other commercial varieties. The lines from Nahng Mon S4 crosses produce satisfactory milled rice yields and they have attractive grain appearance.

IR667-98, a line with IR8 plant type being widely tested in Korea, gave higher protein content than leading japonica varieties in several 1970 variety-fertilizer trials conducted in Korea as well as in two IRRI yield trials in the 1971 dry season. Further testing of IR667-98 is required to substantiate these findings.

YIELD OF HIGH PROTEIN LINES

Selected F_8 plant lines from high protein crosses, grown in a single-plot observational yield trial are shown in Table 6. A 20- x 20-cm plant spacing was used in this test and all nitrogen was applied basally. The IR8 check plots yielded 4.75 to 5.64 t/ha and with protein contents from 6.0 to 6.6 percent. Several lines in this test approached the yield of IR8 and had considerably higher protein contents than IR8.

Many of the same lines were grown in a replicated yield trial (Table 7). A 20- x 20-cm plant spacing was used and 120 kg/ha N was applied basally. Six hybrid lines in this test did not differ significantly in yield of rough rice from IR8, but had a significantly higher protein content: IR160-27-3, IR773A1-36-2, BPI-76-1, two IR1006 (IR8 x BPI-76-1) lines, and an irradiated IR8 line obtained from the Philippine Atomic Research Center.

In the same replicated yield trial there were six lines from the high protein crosses (IR1100 to IR1105) which averaged 30.1 percent higher protein than IR8 but their average yield was 31 percent lower than IR8. They are shown in Table 7 along with four other lines from the high protein crosses that averaged only 8.2 percent higher protein than IR8 with grain yields 24.1 percent lower than IR8. The two groups of lines did not show statistically significant differences in grain yield but showed highly significant differences in protein content. Apparently this significant difference in protein content is genetically controlled.

The results of five 1971 dry season yield trials in which IR8, IR480-5-9, and IR160-27-3 were grown are shown in Table 8. The average yields of IR480-5-9

Table 6. Grain yield, protein (at 12% moisture), and other data from breeding lines and varieties grown in single observational yield trial plots. IRRI, 1971 dry season.

Line no.	Seeding to heading (days)	Panicles (no.)	Plant ht (cm)	Yield: Rough rice (t/ha)	Yield: Brown rice (t/ha)	Brown rice protein (kg/ha)	Protein content (%): Brown rice	Protein content (%): Milled rice	Amylose content (%)	Gel. temp.[b]
IR1102-25-3[c]	93	13	112	4.23	3.19	322	10.1	8.8	25.6	L
IR1103-64-4	103	12	82	3.54	2.72	169	6.2	5.0	26.9	L
IR1104-16-2	76	8	76	3.53	2.69	250	9.3	8.8	27.4	–
IR480-5-9[a]	96	10	87	4.71	3.52	282	8.0	7.3	22.9	L
IR8[a]	104	13	73	5.15	3.95	243	6.2	5.37	28.5	L
IR160-25-3[a]	104	11	88	4.85	3.66	294	8.03	6.98	24.0	L
IR1105-15-7[d]	77	12	73	4.50	3.56	285	8.0	7.1	25.4	L
IR1100-111-2	102	13	90	4.23	3.21	266	8.8	8.3	Waxy	L
IR1103-1-3-7	96	11	103	4.71	3.71	338	9.1	8.1	28.4	L
IR1103-15-8	108	9	87	3.57	2.75	209	7.6	6.6	27.9	L
IR1103-1-3-5	97	11	99	4.28	3.40	265	7.8	7.6	28.5	L
IR667-98-1	88	11	75	5.53	4.30	353	8.2	7.0	19.1	L

[a]Average of four plots. [b]Gelatinization temperature, L = low. [c]IR8 x Santo. [d]IR8 x Chok-jye-bi-chal.

Table 7. Average rough and brown rice yields and protein content (at 12% moisture) of brown and milled rice and other data of lines grown in replicated yield trial, IRRI, 1971 dry season.

Line no.	Seeding to heading (days)	Panicles (no.)	Plant ht (cm)	Yield: Rough rice (t/ha)	Yield: Brown rice (t/ha)	Brown rice protein (kg/ha)	Protein content (%): Brown rice	Protein content (%): Milled rice	Amylose content (%)	Gel. temp.[b]
IR1100-18-3	74	13	96	4.16	3.24	330	10.2	9.3	25.6	L
IR1101-64-1	73	15	87	4.97	38.1	362	9.5	8.9	22.8	L
IR8[a]	104	12	93	7.01	5.35	392	7.3	6.7	27.8	L
IR773A1-36-2	89	12	85	6.61	5.10	428	8.4	7.8	23.4	L
IR1103-49-4	99	12	89	4.91	3.81	366	9.6	8.4	27.6	L
IR1006-26-1	99	11	96	6.92	5.46	453	8.3	7.6	27.6	L
IR1006-33-1	100	11	95	6.35	4.91	393	8.0	6.9	27.4	L
IR480-5-9	90	10	92	6.04	4.57	416	9.1	8.4	21.8	L
IR160-27-3	97	10	99	7.02	5.50	468	8.5	7.8	23.1	L
IR1103-1-3	95	12	111	4.90	3.89	350	9.0	8.3	25.9	L
IR1103-2-3	89	15	93	5.13	3.29	303	9.2	8.8	26.5	L
IR1103-15-8	101	10	91	4.61	3.57	350	9.8	8.7	24.8	L
BPI-76-1	92	10	129	6.02	4.58	394	8.6	7.8	25.1	H/I
IR1103-52-2	95	12	83	6.73	5.26	400	7.6	6.6	18.0	L
IR1103-64-4	101	13	99	6.54	5.22	360	6.9	6.0	28.2	L

[a]Average of three plots. [b]Gelatinization temperature, L = low, H/I = high/intermediate.

and IR160-27-3 do not differ significantly from IR8 but they exceed IR8 in protein content by a margin of 23 and 18 percent, respectively.

HIGH PROTEIN CONTENT AND OTHER GRAIN PROPERTIES

A taste-panel evaluation of cooked milled rice of some high protein breeding lines conducted by Dr. Luz U. Oñate of the University of the Philippines, College of Agriculture, showed no significant differences in color scores among lines from the same cross that differed by as much as 4 percentage points of protein in the raw grain. The lines compared had similar amylose content (IRRI, 1971). Presumably, an increase in protein content of 2 percent has a negligible effect on the color of milled rice.

Amino acid analysis of F_4 brown rice grains of the lines with the lowest and the highest protein contents among the six crosses, IR1100 to IR1105, showed a decrease in lysine and tryptophan values as protein content increased (IRRI, 1971). It appears that increases in protein content caused by either genetic or environmental factors have similar effects on the amino acid composition of rice protein. Milled rice of F_7 seeds of five lines with 11.4 to 11.6% protein contained 3.3 to 4.0% lysine, 3.4 to 4.1% threonine, 0.9 to 1.2% tryptophan, and 3.0 to 4.6% sulfur amino acids in the protein (IRRI, 1971). These results show that if both parents have normal lysine content in their protein, an increase of 2 percentage points in protein does not necessarily result in a lowering in lysine content, since the lines with similar protein content

Table 8. Summary of mean rough and brown rice yields, protein content (at 12% moisture), milling and other data on IR8 and two high protein lines. IRRI, 1971 dry season.

Line	Yield: Rough rice (t/ha)	Yield: Brown rice (t/ha)	Yield: Brown rice protein (kg/ha)	Protein (%): Brown rice	Protein (%): Milled rice	Brown rice (%)	Total milled rice (%)	Head rice (%)
Replicated yield trial[a] (120 kg/ha N)								
IR8	7.02	5.51	408	7.4	7.0	78.5	67.9	49.6
IR160-27-3	6.56	5.06	430	8.5	7.8	77.1	67.8	44.9
IR480-5-9	6.04	4.57	402	9.1	8.4	75.6	65.5	50.6
Variety x fertilizer trial[b] (60 kg/ha N)								
IR8	7.30	5.69	410	7.2	6.7	77.9	68.1	47.9
IR160-27-3	6.86	5.24	409	7.8	7.6	76.4	69.3	35.8
IR480-5-9	6.31	4.75	413	8.7	8.4	75.2	67.2	44.9
Variety x fertilizer trial[b] (120 kg/ha N)								
IR8	7.13	5.52	475	8.6	8.0	77.8	68.3	41.0
IR160-27-3	7.07	5.43	554	10.2	9.9	76.8	68.5	39.3
IR480-5-9	7.50	5.68	602	10.6	10.3	75.7	67.1	51.3
Variety x spacing x fertilizer experiment[c] (120 kg/ha N)								
IR8	5.64	4.37	315	7.2	—	77.5	68.4	52.4
IR160-27-3	6.19	4.77	415	8.7	8.2	77.1	70.1	48.2
IR480-5-9	6.31	4.81	433	9.0	8.3	76.3	68.4	53.6
Observational yield trial[a] (80 kg/ha N)								
IR8	5.14	3.94	213	6.2	5.4	76.7	66.9	46.7
IR160-27-3	4.85	3.66	289	7.9	6.9	75.4	66.8	38.7
IR480-5-9	4.71	3.52	282	8.0	7.5	74.7	64.4	41.8
Mean of five trials								
IR8	6.40	4.97	358	7.3	—	—	—	—
IR160-27-3	6.24	4.84	412	8.6	—	—	—	—
IR480-5-9	6.08	4.59	416	9.0	—	—	—	—

[a]Four replications. [b]Three replications. [c]Agronomy department trial.

show a range in lysine content and one may select progenies with high lysine values.

When high protein lines of divergent origin are combined in further hybridizations there may be a further increase in protein content. Crosses are being made which combine the different high protein sources. These crosses also include combinations with high yielding, disease- and insect-resistant lines. An increase in protein content of 25 percent without any reduction in grain yield appears to be a reachable goal.

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Discussion: Breeding for high protein content in rice

P. A. LIEUW-KIE-SONG: Have you analyzed F_1 material for protein content?

H. M. Beachell: No analysis was done on F_1 seeds.

A. O. ABIFARIN: How much of the brown rice protein is left after milling?

B. O. Juliano: Brown rice does not exceed milled rice in protein content by more than one percentage point. With brown rice of 8 percent protein, removal of 10 percent by weight as bran-polish during milling leaves about 84 percent of brown rice protein in the milled rice. At about 11 percent protein, the loss of brown rice protein during milling is only about 12 percent based on 10 percent weight removal, leaving 88 percent of its protein in milled rice.

E. A. SIDDIQ: Do you find differences in the levels of protein increase among varieties with increasing rates of applied nitrogen? If so, is it anyway related to the endosperm texture (packing of starch granules)?

B. O. Juliano: Yes, increased protein content from applied fertilizer nitrogen improves grain translucency and the hardness of any variety.

T. H. JOHNSTON: Breeding for higher protein content is also an important phase of the rice improvement programs in the U.S. Determining the protein and lysine content of promising lines is a routine part of the quality testing procedure. Several U.S. researchers have reported that the protein content of brown rice in different crosses did not appear to be simply inherited. Studies on F_2 plants and F_3 lines indicated that the heritability of protein content was low.

Outlook for higher yield potentials

Ecological and genetic information on adaptability and yielding ability in tropical rice varieties

T. T. Chang, B. S. Vergara

Daylength and temperature prescribe the geographic and seasonal adaptability of rice varieties mainly by their effects on growth processes and on growth duration. Differences in varietal reactions to daylength become more obvious when the vegetative growth duration is divided into the basic vegetative phase and the photoperiod-sensitive phase. Varietal reaction to variations in daylength is of four types: strongly sensitive, weakly sensitive, essentially insensitive, and completely insensitive. The effect of temperature is more complicated and it differs at different growth phases of the rice genotypes. A low sensitivity to both daylength and temperature variations is essential for wide adaptability and stable high yields. Genetic control of the different growth phases and of the principal plant characters affecting yield ability was studied in a number of crosses involving parents of contrasting types. Primitive features such as strong photoperiodicity, intense grain dormancy, and extremely tall plant stature were each controlled by a few dominant major genes, though the action of modifiers or inhibitors was also detected in some crosses. For agronomic traits contributing to grain yield, the predominant genetic component was additive effects though some loci showed dominance. Significant genotypic correlation between several traits was observed. This information has important implications for rice breeding and agronomic efforts to increase the yielding capacity of tropical rice varieties.

CLIMATIC FACTORS AND ADAPTABILITY

Rice producing areas extend from 49°N to 35°S and include a wide range of climatic and soil conditions. Among rice varieties, genotypes vary greatly in their response to different climatic factors at various growth stages, even when the supply of water and plant nutrients are adequate. Ecologically, the wide adaptability of a rice variety refers to its high yield performance over diverse climatic conditions.

Plant characters essential to wide adaptability may not necessarily be components of a high yield potential. For example, grain dormancy is needed for wider adaptability in the tropics but not for obtaining high grain yields. On the other hand, varietal resistance to diseases and to insect pests is a requisite for both wide adaptability and high yield potential.

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The climatic factors that affect the adaptability of rice varieties are temperature, daylength, precipitation, and solar radiation.

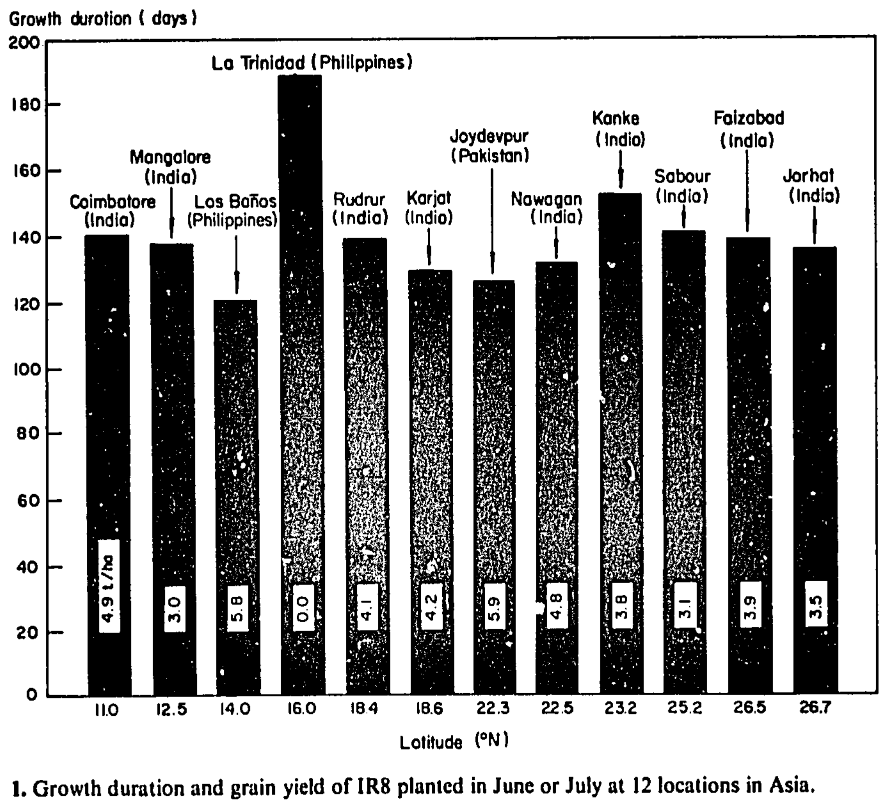
Extensive testing in various rice-growing areas has established the wide adaptability of Taichung Native 1, IR8, and several ponlai varieties for year-round cultivation in the tropics (Chang, 1967*a*). When seeded early, IR8 produces more than 8 t/ha in the Republic of Korea (37°N), in Nepal (28°N, 1,360 m elevation), and in southern Brazil (30°S to 32°S), though its growth duration in these areas is extended to 180 days from its normal duration of 125 days in the tropics.

In recent adaptation trials at eight sites with two fertilizer levels in tropical Africa and Asia, IR8 led a group of 22 varieties in both yield performance and regional stability. Tainan 3 produced top yields at stable levels in three series of trials at 13 sites from central Japan to central Africa (Evelyn et al., 1971).

Four major categories of traits contribute to wide adaptability: insensitivity to daylength, low sensitivity to temperature variation, tolerance to rain and wind effects, and favorable yield response to solar radiation.

Insensitivity to daylength

During the growing season in rice-producing areas daylength varies from 11 to 16 hours (Moomaw and Vergara, 1965). Daylength and temperature are the



1. Growth duration and grain yield of IR8 planted in June or July at 12 locations in Asia.

two important climatic components that affect general adaptability. They determine the growth duration of a variety. How much the growth duration of the variety is affected by daylength or temperature or by both, indicates the range of geographic adaptation of the genotype. The response to photoperiod, being more distinct and more easily controlled, is better understood than the effect of temperature.

In breeding for widely adaptable varieties, insensitivity to daylength is important. Insensitivity insures a le s variable growth duration regardless of the date of sowing. Date-of-planting experiments at 12 locations in tropical Asia indicate that IR8 has wide adaptability and stable growth duration (fig. 1). IR8's growth duration varied within a range of 20 days at latitudes from 11°N to 27°N when planted in June or July, except at La Trinidad, Philippines (15°N, 1,320 m elevation) and at Kanke, India (23°N, 660 m elevation), where there were significant delays in heading dates most likely because of low temperatures during part of the growing season (Chang and Vergara, 1971).

Since photoperiod-insensitive varieties do not have long growth durations, they are not adaptable to the floating-rice or deep-water areas where late-maturing varieties are needed to outlast the period of flooding. On the other hand, early-maturing and photoperiod-insensitive genotypes permit year-round multiple cropping.

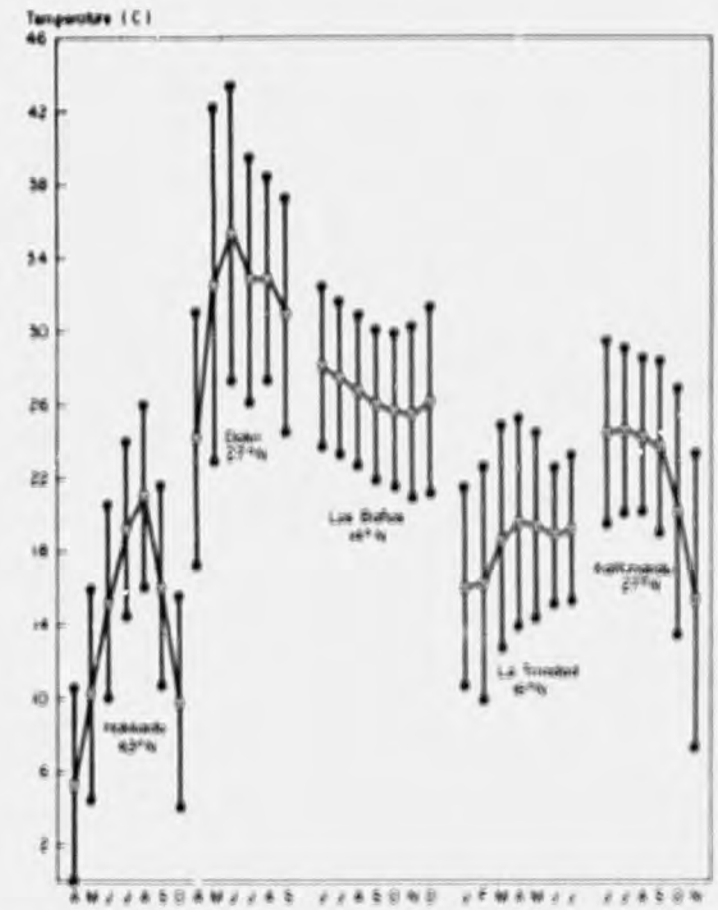
Because photoperiod sensitivity affects the potential adaptability of rice varieties, promising selections from the IRRI breeding program are tested under controlled photoperiods to determine their responses to photoperiod. Tests under three or four photoperiods are more efficient for this purpose than monthly plantings.

Low sensitivity to temperature variations

Patterns of temperature variations during the crop season are more complex than those of daylength. At high-latitude areas, such as Sapporo, Japan, low temperature is the chief limiting factor in rice cultivation. The rice seeds are sown at low temperatures, tillering occurs as temperatures rise, and flowering and ripening are completed as temperatures fall (fig. 2). In tropical areas like Thailand, Philippines, and Indonesia, where rice can be planted any month of the year, the monthly temperature variations differ from country to country though the range is within safe limits. Exceptions to the general pattern are found at high elevations or in special ecologic niches. In subtropical areas where two crops of rice can be planted, the low temperatures can be important. In East Pakistan and Taiwan, the cool temperatures from November to February restrict the seedling growth of many tropical varieties. On the other hand, the high temperatures during the flowering period in parts of West Pakistan (fig. 2) may affect the spikelet fertility of certain varieties.

Varietal reaction to temperature involves different growth stages of the rice plant and the range of temperatures that prevails at each growth phase.

Growth duration. The growth duration of all varieties tested, whether of tropical or temperate origin, is delayed when temperatures decrease from 32 C to 15 C. Both IR8, a tropical variety, and Fujisaka 5, a temperate variety, take



2. Temperature pattern during the rice cropping season at Hokkaido, Japan; Dokri, West Pakistan; Los Baños, Philippines; La Trinidad, Philippines; and Kathmandu, Nepal.

50 days longer to head when grown at the low temperatures normal in La Trinidad than when grown at Los Baños (Philippines). Under normal cultivation methods IR8's growth duration ranges from 120 to 135 days in tropical areas, but the period is greatly extended in temperate areas.

When a tropical variety that requires a long growth duration in the tropics is introduced into the temperate zone, it will not have a chance to produce satisfactory grain yields within the growing season of that area regardless of cultural adjustments (Chang, 1961; N. Parthasarathy, *unpublished*).

High temperatures generally accelerate vegetative growth. Many varieties of the temperate zone will react to high or moderately high temperatures during the seedling stage and develop panicles when only a few tillers have been produced. Such thermo-sensitive types are exceedingly poor yielding when grown in the tropics or subtropics. For instance, Norin 20, which normally matures within 150 to 160 days in Japan, completes its life cycle within 80 days when grown at Los Baños even under a 12-hour daylength (Chang, Li, and Vergara, 1969). Its plant height, panicle size, and plant weight are markedly reduced. At Los Baños, a number of indica varieties from central China also show this type of temperature effect on vegetative growth. The exact threshold level at which the thermo-sensitive response is triggered has not been determined.

Data on IR8 obtained by IRRI cooperators in Australia, East Pakistan, and Nepal indicate that the growth duration of IR8 is negatively correlated with the minimum daily temperature. In contrast to many temperate-zone varieties, IR8 does not appear to have a fixed temperature summation to complete its life cycle. Its temperature summation increases with increase in growth duration. The average minimum temperature during the crop season appears to be the best parameter for estimating the growth duration of IR8 (Chang and Vergara, 1971).

Flowering and sterility. Resistance to cool temperatures from panicle initiation to anthesis is essential for adaptability at high latitudes or altitudes. The rice plant is most susceptible to low temperatures (less than 17 C) during the panicle initiation stage. Temperatures below 22 C during anthesis, however, increase spikelet sterility. A temperature of 22 C or above is needed for the anthesis of IR8 and Fujisaka 5 (Vergara, Chu, and Visperas, 1970).

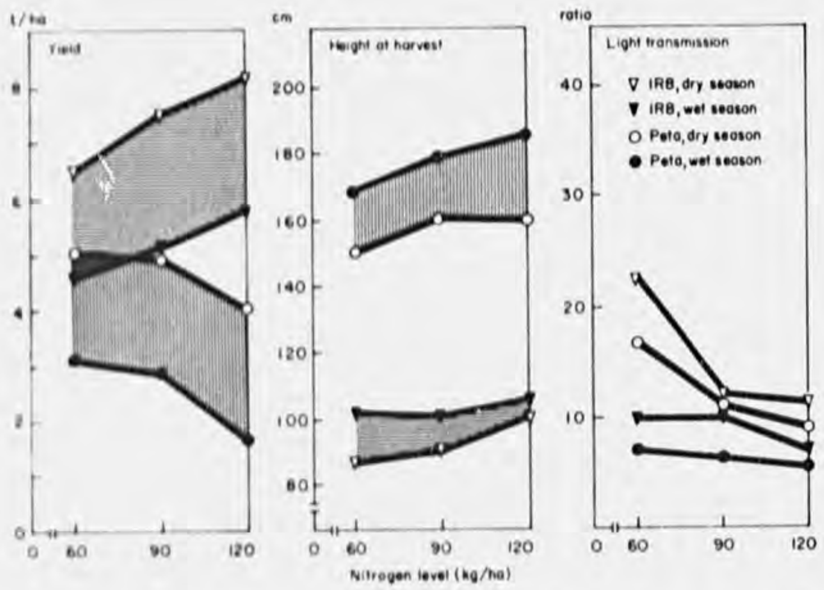
Germination and seedling growth. In areas where seeds are broadcast, tolerance to cool temperatures during germination is needed. A comparison between IRRI varieties and two temperate varieties showed that IR8 has a wider temperature range for optimum germination, a lower minimum temperature requirement, and a higher maximum temperature tolerance than two temperate varieties, Fujisaka 5 and Kulu (Table 1).

In temperate and subtropical areas, cool temperature during seedling growth poses a problem. The ability of the seedlings to survive and to grow at low air and water temperatures is an essential character. Tropical varieties generally lack this type of seedling tolerance to cool spells. Stunted growth and yellowing of seedling leaves, observed in IR8, have been considered signs of low cold tolerance. IR8, however, fully manifests its growth vigor as soon as the temperature rise. Eventually it may tiller more heavily than the tolerant varieties of temperate origin.

Table 1. Optimum, maximum, and minimum temperature requirements for seed germination, 8 days after soaking.

Variety	Temperature (C)		
	Optimum	Maximum	Minimum
IR8	18-35	40	16
Fujisaka 5	26-35	35	18
Kulu	26-40	40	19

Optimum temperature was based on 100 percent germination, while maximum and minimum temperature limits were based on at least 80 percent germination.



3. Differential growth characteristics of Peta and IR8 under different levels of nitrogen and solar radiation values

Reaction to rainfall and typhoons

Although the amount and distribution of rainfall throughout the year follow a pattern, rainstorms are unpredictable. Rainfall is more variable in the tropics than in temperate areas. Typhoons are even more unpredictable. Rice growth and, ultimately, yield are affected by strong winds or rains, which cause lodging, shattering, splitting of leaf tips, or breakage of leaf blades. Under prolonged heavy rain, plants frequently become submerged.

For wide adaptability, varieties require a moderate degree of dormancy, a non-shattering characteristic, and resistance to lodging. Moderate dormancy prevents the maturing seeds from sprouting on the panicle when prolonged rains occur during the ripening stage. Varieties that shatter have lower yields when strong winds or tropical storms occur near harvest causing increased grain shedding. Lodging resistance protects crops when heavy rains or strong winds occur near heading or after. Hitaka (1968) reported that wind speed is more important than wind pressure in breaking rice culms. Raindrops have a more pronounced overloading effect on the rice culms when the wind is weak because the water droplets deposited on the leaf surface produce a greater bending moment than the impact of raindrops.

Response to solar radiation

Mean daily solar radiation values are higher in temperate areas than in tropical areas during the growing season (Gentilli, 1958). In the tropics of the northern hemisphere, March, April, and May usually have the highest solar radiation levels. In the monsoon season solar intensity is much lower though daylength is longer.

Grain yield is positively correlated with solar radiation, especially during the later stages of plant growth (Tanaka and Vergara, 1967; Moomaw, Baldazo, and Lucas, 1967). Adaptability is partly expressed by the potential to produce relatively high yields even with low solar radiation. IR8 has a greater degree of such potential than Peta (fig. 3).

Rice varieties respond subtly to different levels of light intensity. Obviously, the variety that shows the least adverse responses would be more adaptable. For example, low light intensity during the wet season in the tropics is one reason why tropical varieties grow taller and the basal internodes elongate, resulting in lowered resistance to lodging (Chang, 1964*b*; IRRI, [1965], p. 39-42). Since IR8 is initially a short-statured genotype, the adverse effect of low light intensity does not critically affect its yield (fig. 3).

Similarly, when solar radiation is low, Peta has more leaves per unit area and the light transmission ratio is lower (fig. 3). Since Peta has an optimum leaf area index (Yoshida, 1969), it reaches a condition in which the crop growth rate decreases. IR8, on the other hand, has no optimum leaf area index so it is not adversely affected by a large increase in leaf area index during the wet season.

GENETIC ANALYSIS OF THE COMPONENTS OF GROWTH DURATION

The vegetative growth period from seeding to panicle initiation accounts for much of the variability in the growth duration of rice varieties. When a suitable series of photoperiods is used, the two components of vegetative growth, the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP), can be readily identified (Vergara, Chang, and Lilis, 1969). Rice varieties can be grouped into four types according to the two components and the rate of increase in growth duration with increased photoperiod (fig. 4):

1. Completely insensitive very short PSP, long BVP (more than 40 days). Examples. Milfor-6(2), CH-.0, Habiganj-6, Habiganj-2, Dular, Chianung 242, IR12-178-2, IR747B2-6-3.

2. Essentially insensitive detectable increase in growth duration with increased photoperiod, PSP does not exceed 30 days, BVP relatively long. Examples: Century Patna 231, Taichung Native 1, Tainan 3, IR8, IR579-48-1, IR24.

3. Weakly sensitive marked increase in growth duration when photoperiod is longer than 12 to 14 hours; PSP may exceed 30 days, but flowering occurs under a 16-hour photoperiod; BVP varies from short to long. Examples: Bluebonnet 50, Peta, Intan, Tjeremas, Baok, BPI-76-1, C4-63, Sukanandi, Guze, Norin 18, Acheh, Palkweng, IR5, IR20, and IR22. This group has more limited adaptability than the less sensitive types.

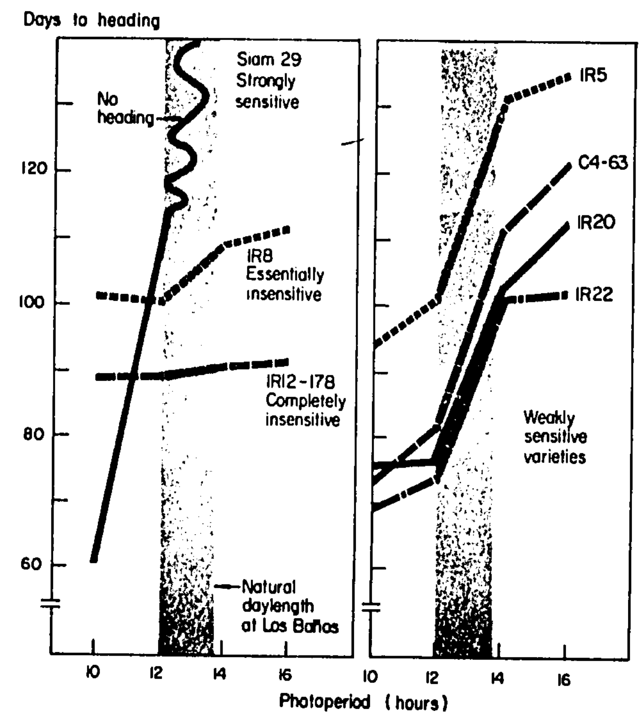
4. Strongly sensitive sharp increase in growth duration with increase in photoperiod, no flowering beyond the critical photoperiod, BVP usually short (not more than 40 days). Examples: BPI-76, Siam 29, Raminad Strain 3, GEB-24, Podiwi-A(8), Puang Nahk 16, FB-121, Latisail. This group can be grown only in the tropics.

When primary tillers from a pure-line parent or hybrid progeny are separated and grown under controlled photoperiods to represent duplicate samples of the same genotype, the concurrent determination of BVP (under a 10-hour photoperiod) and of PSP (under a 16-hour photoperiod) on the same plant becomes practical (Chang, Li, and Vergara, 1969).

Basic vegetative phase

In two crosses involving photoperiod-insensitive parents grown under controlled photoperiods, the difference in BVP between parents ranged from 7 to 40 days. The normal distribution in the F_2 populations could be interpreted by the action of two to four loci with equal and additive effects (Chang, Li, and Vergara, 1969). In a diallel set involving four essentially insensitive parents, the F_1 and F_2 data indicated primary additive gene action and a detectable amount of dominance effect. The dominance of earliness under natural day-length in all parental arrays was iso-directional (Li and Chang, 1970).

In nine crosses, each involving a strongly photoperiod-sensitive parent and an insensitive parent, the parental difference in BVP ranged from 10 to 52 days. The F_1 hybrids in five crosses had a shorter BVP than the short-BVP parent. Two crosses produced F_1 plants with intermediate BVP, and the hybrids in the other two crosses had BVP values that either equalled or slightly exceeded



4. Effect of four photoperiod treatments on the seeding-to-heading period of seven rice varieties.

that of the short-BVP parent. The nine F_2 populations however, showed two common features: a multimodal distribution with a positive skewness showing an excess of short-BVP plants, and a transgressive segregation on both tails of the distribution curve. The distribution of parents, F_1 plants, and F_2 plants indicates the cumulative action of two to three dominant genes controlling short BVP, *Ef 1*, *Ef 2*, and *Ef 3*. These polymeric *Ef* genes also differ in the magnitude of their individual effects on BVP (Chang, Li, and Vergara, 1969).

In four crosses involving the weakly photoperiod-sensitive Peta and insensitive parents, such as IR12-178-2 and Chianung 242, the F_2 distributions also indicated that a short BVP is dominant to a long one, that several *Ef* genes control the total variation in BVP, and that the *Ef* genes have unequal and cumulative effect (IRRI, 1971, p. 216-218).

In a half-diallel set involving four strongly photoperiodic parents, the rather small differences in BVP (from 4 to 18 days) were controlled by genes with additive effect, some of which showed dominance. Dominant alleles controlled a short BVP (Li, 1970).

Photoperiod-sensitive phase

In nine crosses, each involving a strongly sensitive parent and an insensitive parent, the F_1 and F_2 data clearly indicated that either one dominant gene (*Se*) or duplicate genes (*Se 1* and *Se 2*) controlled the photoperiodic reaction. The *Se* gene is epistatic to the *Ef* genes under a long photoperiod. In two crosses, the insensitive semidwarf, I-geo-tze, seemed to carry a recessive inhibitor (*i-Se*) which modified the F_2 ratio.

A duplicate planting of the F_2 population from BPI-76 (sensitive) x Tainan 3 (insensitive) under natural daylength (from March 12 to early November) in the field at Los Baños showed that the expression of the *Se* alleles was affected by a changing daylength, and thus resulted in a modified F_2 distribution of 1 (early): 2 (intermediate): 1 (late). We attributed the difference in F_2 distributions to the complicating effect of the critical photoperiod of BPI-76, expressed under natural daylength ranging from 12.5 hours to 13.5 hours (Chang, Li, and Vergara, 1969).

The two components of a strong photoperiodic response, optimum photoperiod and critical photoperiod, were studied in a half-diallel set involving four strongly sensitive varieties (Li, 1970). The F_1 and F_2 data showed that the short optimum photoperiod was dominant to a long optimum photoperiod and the short critical photoperiod, dominant to a long critical photoperiod. Each of the two components appeared to be controlled by a single gene and probably by a few modifying genes.

In the preceding crosses involving strongly sensitive parents, a genetic association between the sensitive response and a short BVP was frequently observed, indicating a probable linkage between the *Se* gene and one or more of the *Ef* loci. But whether the *Se* gene controls the critical photoperiod or not remains to be elucidated.

More recent studies involving crosses of the weakly sensitive Peta and an insensitive parent suggest that weak photoperiod response is under polymeric gene control and that low sensitivity is partially dominant to weak sensitivity (fig. 5). This indicates a genotypic association between a weakly sensitive response and a short BVP (IRRI, 1971, p. 216-218; F. H. Lin and T. T. Chang, *unpublished*).

By dividing the vegetative growth period into the BVP and PSP, by analyzing the BVP and PSP on vegetative tillers under controlled photoperiods, and by reconstituting the growth period from the two components, we obtained basic information that can be used to interpret or predict a variety of situations if both the genotypes and the environmental factors are known (Chang, Li, and Vergara, 1969).

Reports from Ceylon and India described a genetic association between grain dormancy and photoperiod sensitivity (Chandraratna, 1964). Our genetic studies showed that while a substantial proportion of strongly dormant F_2 progenies were late maturing and probably photoperiod-sensitive, a number of dormant and insensitive progenies could be recovered (IRRI, 1971, p. 218-219). It is likely that one of the *Se* loci is linked with one or more of the dominant polymeric genes that control grain dormancy (Chang and Yen, 1969; IRRI, 1971, p. 218-219).

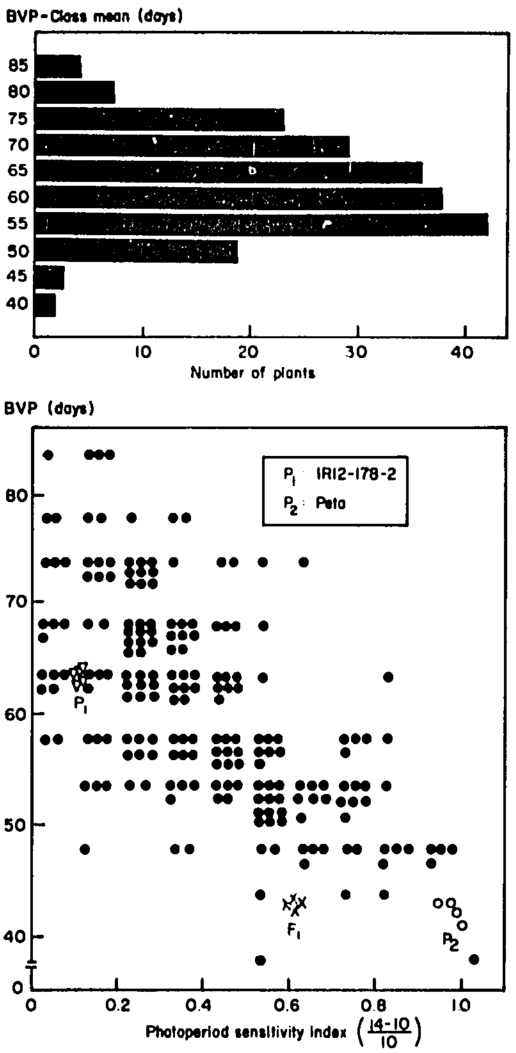
Genetic information on varietal response to temperature variations is lacking. But a number of reports have indicated that high temperatures accelerate panicle development and exsertion and that cool temperatures generally delay heading. Two other reports dealt with the delaying effect of high temperature on flowering (*see* Vergara, Chang, and Lilis, 1969). Critical experiments should be set up under controlled conditions to identify the specific effect of temperature variation at different growth stages, to distinguish between the temperature effects on panicle development and those on emergence, and to study the specific temperature effects on optimum photoperiod and on critical photoperiod.

TRAITS CONTRIBUTING TO HIGH YIELDING ABILITY

Among adapted genotypes possessing adequate resistance to endemic diseases and pests, field experiments at IRRI and elsewhere have identified a number of agronomic traits or complex traits directly related to a high yielding potential in the tropics (IRRI, [1964], p. 13-14, p. 49-51; Tanaka et al., 1964; Chang, 1967*a*; Chandler, 1969*a*). The following discussion deals mainly with the genetic aspects of those traits which contribute to a high yielding potential under favorable environmental conditions.

Short plant stature and resistance to lodging

Rice researchers generally agree that the nitrogen responsiveness and high yielding ability of the new improved varieties are largely derived from their short stature. Among the various sources of plant stature, the recessive semi-dwarfing gene from Taiwan is the most important. It was used in developing nearly all of the improved tropical varieties released after 1966, except BPI-76-1, IR5, C4-63, ICA-10, two Surinam varieties, and several IR5 derivatives.



5. Relation between the basic vegetative phase (BVP) under 10-hr photoperiod and the photoperiod-sensitivity index in the F_2 population of IR12-178-2 x Peta.

Extensive yield trials of the semidwarfs at high nitrogen levels have further indicated the need for both short stature and resistance to lodging. Examples of lodging susceptibility as a limiting factor at high fertility levels have been described for Taichung Native 1 (De Datta, Moomaw, and Dayrit, 1966; IRRI, 1967*a*, p. 81-82) and IR20 (Chandler, 1969*b*).

Sources of short plant stature

One recessive gene primarily controls the semidwarf height in Taiwan's I-geo-tze (Chang et al., 1965) and Taichung Native 1 (Aquino and Jennings, 1966; Heu, Chang, and Beachell, 1968). Our studies of intercrosses among I-geo-tze, Dee-geo-woo-gen, and Taichung Native 1 showed that the recessive gene in all three semidwarfs belongs to the same locus. Several modifying

Table 2. Short-stature types and gene systems.

Plant stature	Parent	Primary genic control
Dwarf (below 50 cm)	Daikoku	One recessive gene for dwarfism and one recessive inhibitor (for tallness)
Semidwarf		
(below 75 cm)	Ai-yeh-lu mutant	Two (duplicate) recessive loci
	Fanny	Polygenes[a]
(100 cm)	Dee-geo-woo-gen, I-geo-tze, Purbachi[b]	One recessive gene[a]
(102 cm)	Acc. 6993 from (CP 231 x SLO-17)	Polygenes[a]
Intermediate types		
(below 115 cm)	"intermediate" and "long grain" mutants	One recessive gene and modifiers

[a]Have negative modifiers (for shortness) in common. [b]Inferred from the cross, Purbachi x IR8.

genes control the minor variation in plant height among the three semidwarfs (IRRI, 1967*a*, p. 67-68). The recessive gene in the Peta x I-geo-tze cross showed a high heritability estimate, 71 to 84 percent (Chang et al., 1965). The dwarfing gene also appears to carry moderately short and erect leaves, moderately high to high tillering, and a moderately long BVP in several crosses (Chang et al., 1965; Morishima, Oka, and Chang, 1967; Heu, Chang, and Beachell, 1968; Chang, Li, and Vergara, 1969).

Another important source of short stature (about 102 cm) came from selections derived from the Century Patna 231 x SLO-17 cross, among which a line from the Beaumont station, B5580A1-15 (IRRI Acc. 6993), has been frequently used in the IRRI crossing program. The polygenic type of short stature in B5580A1-15 (IRRI, 1967*a*, p. 68-69) was incorporated into the IR127 lines and IR661 lines. This source of short stature showed a continuous variation in crosses between this line and either tall or short varieties. It is non-allelic to the recessive gene of Taiwan's semidwarfs (G. C. Loresto, *unpublished*). However, Acc. 6993 and Taichung Native 1 appeared to have in common negative modifiers for shortness (IRRI, 1968, p. 73-74).

We also analyzed selected crosses between the above sources and additional types of dwarfs and semidwarfs in 1967 and 1968 to identify other desirable sources of short plant stature. Several tall x short crosses were also included. The genetic postulates concerning each of the distinct sources of short stature and their allelic relationships are summarized in Table 2 (IRRI, 1968, p. 73-74; G. C. Loresto, *unpublished*).

Four recently acquired sources of plant stature were studied by crossing each of them to IR8. The gene or genes controlling plant height in K4 mutant (112 cm), from Ceylon, and Ch242d3 mutant (80 cm), from Taiwan, are non-allelic to the Taiwan semidwarfing gene. Purbachi, another semidwarf from the China mainland, recently acquired from East Pakistan, obviously shares the same locus for its semidwarf stature (103 cm). The fourth mutant, C53-39, from Burma, continues to produce chlorophyll mutants and is photoperiod sensitive. It probably has the same compound locus as IR8. We observed that the additional sources did not furnish agronomically desirable features, such as growth vigor, plant type, and tillering ability, that were superior to those of the Taiwan semidwarfs.

Interestingly, the recessive gene for semidwarfism is not only widely distributed in varieties of Chinese origin but is also readily induced from a highly mutable locus in several tall Chinese indicas, such as Keh-tze, I-kung-bau, and Shung-Chiang (Hu, Wu, and Li, 1970). Perhaps the semidwarfing genes in Dee-geo-woo-gen, I-geo-tze, Purbachi, and Keh-tze belong to a compound locus. The Taiwan semidwarfing gene appears to express itself fully in crosses involving extremely tall, tropical varieties. In crosses with parents of intermediate or similar height, the segregation into rather discrete height classes became modified. An aberrant segregation was found in the F_2 populations of Basmati 370 x Taichung Native 1 (IRRI, 1967*b*, p. 76).

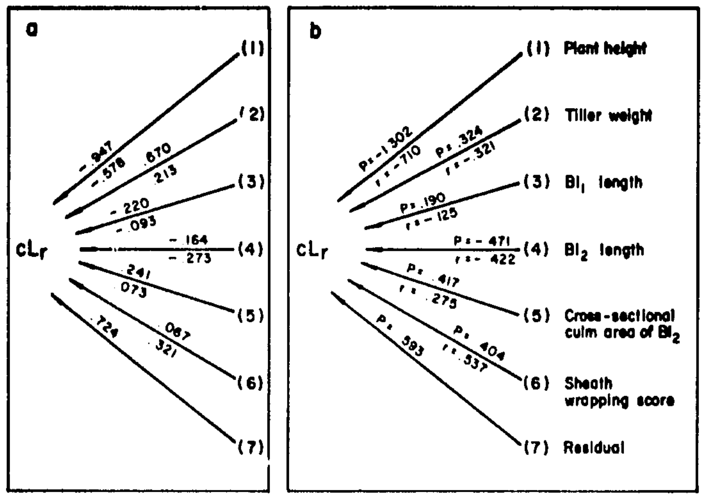
Among parents that are taller than semidwarfs and that differ significantly in plant stature, diallel crosses indicate that height is controlled by genes with additive effect and also by several loci which show dominance. The dominance is isodirectional toward tallness (Wu, 1968*a*; Li and Chang, 1970). A polygenic type of gene action has been reported in crosses involving parents that differ little in height (Mohamed and Hanna, 1964).

Resistance to lodging

In our initial studies on varietal difference in lodging resistance, we pointed out the complex nature of this feature and we emphasized, in addition to short plant height and erect leaves, the pattern of internode elongation, culm diameters and culm symmetry, leaf sheath wrapping, and structural features of the culm as secondary, but essential, attributes of straw strength (IRRI, [1964], p. 23-27, [1965], p. 37-47, 1966, p. 103-105; Chang, 1964*b*). From three crosses, we provided experimental evidence by path analysis that while plant height is the predominant causative factor, sheath wrapping, the length of the basal internodes, especially the second elongated one from the base (BI_2), and the cross-sectional area of the culm at BI_2 (fig. 6) contribute in varying but significant magnitudes to the lodging resistance factor, cL_r, of the culms (IRRI, 1967*a*, p. 79-81; Chang and Liu, 1967; Chang, 1967*b*).

Since several semidwarf selections have lodged at high fertility levels on the IRRI farm, the question is again raised: What traits cause lodging in semidwarfs? While variation in plant height among the semidwarfs is relatively small, differences in the other traits related to straw strength can be substantial. The difference in stem features between IR8 and Taichung Native 1 was described in relation to their difference in lodging resistance (IRRI, 1967*a*, p. 81-82). The rather thin culms and the low slenderness-of-column ratio of IR20 have been pointed out (Chandler, 1969*b*).

Twenty selections, 19 semidwarfs, and one intermediate line (IR127-80-1), that vary significantly in lodging behavior in the field, were selected and planted in the 1970 wet season at two nitrogen levels to determine the effect of heavy fertilization on the important plant characters related to lodging. Analysis of



6. Path diagram and association of six plant characters related to the lodging resistance factor, **cLr, in F_2** plants of (a) MTU-15 x BPI-76, and (b) (Irrad. CP 231 dwarf x Rexoro) x MTU-15.

variance shows that among the six traits recorded for all entries at both nitrogen levels, the effect of nitrogen levels was highly significant for plant height and significant for BI_2 length. Varietal differences were highly significant for all six traits. The interaction between variety and nitrogen was highly significant for five traits and significant for BI_2 length. The entries that showed highly significant differences between the two nitrogen levels, either in plant height, length of BI_2, or sheath wrapping or in two traits combined, belong to the lodging-susceptible strains: IR20, IR532-1-171, IR424-2-1-Pk2, and Thai 12-2-2 (T. T. Chang, *unpublished*).

The preceding observations confirm the association between increased plant height, marked elongation of the BI , or reduced leaf sheath protection and lodging susceptibility in semidwarfs.

Leaf characteristics

Leaf length, width, and angle of openness (measured from the vertical axis to the leaf tip) constitute important morphological features of the improved plant type. Erect and relatively short leaves permit better light penetration into the lower portion of the foliage canopy and contribute to efficient use of light and lessen susceptibility to lodging. Because leaf blades vary in each of these features at different growth stages and differ among tillers of the same plant, the quantitative description of leaf characteristics is a complex problem.

Our data from the Peta x I-geo-tze cross showed that among tall and intermediately tall F_7 lines which varied greatly in the angle of the leaf below the flagleaf, erect leaves were associated with higher yield levels (r_g: −0.605 in intermediate lines, −0.522 in tall lines). Among the six traits measured, path coefficients indicated that the leaf angle produced the largest direct effect on grain yield in both tall and intermediately tall lines (Table 3). In both groups, droopy leaves were associated with tall plants. But the leaf angle differed little among the semidwarf lines and no clear-cut association with yield was detected. On the other hand, the semidwarf lines that had more erect flagleaves had higher grain yields. That trait showed the largest direct effect on grain yield (Chang and Tagumpay, 1970).

Later we selected tropical varieties that have longer and more droopy leaves than Peta and crossed them with semidwarf lines that have shorter and very erect leaves. In Bengawan x IR160-27-3 and BJ-1 x IR40C-5-12, we observed marked differences in leaf angle at 40 days after seeding among the parents and the F_1 plants, though the two parents and F_1 hybrids had fairly large leaf angles, 40 degrees or more. At heading time, the differences became much smaller. The F_1 plants tended to have droopy leaves (fig. 7). The flagleaves of the F_1 hybrids were either intermediate between the parents or showed a partial dominance for erectness (IRRI, 1970, p. 74-76).

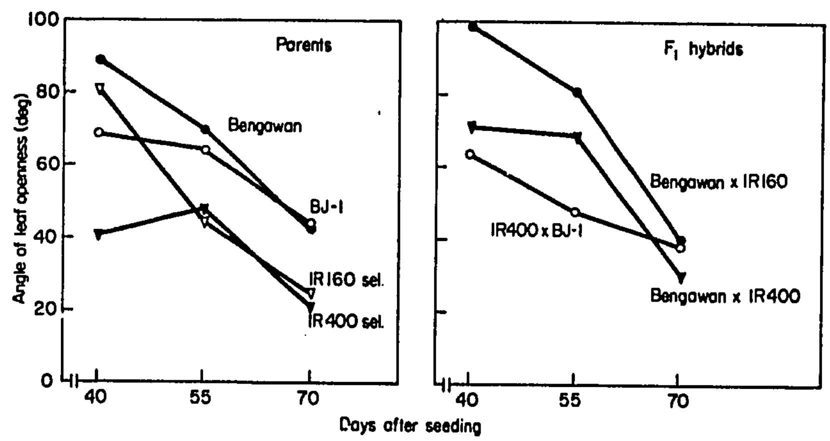
The two F_2 populations showed a predominance of droopy-leaved individuals at 45 days after seeding, but at heading, the distribution became essentially normal; there were slightly more extremely erect-leaved progenies than very droopy plants. The F_2 distribution for flagleaf angle showed an excess of F_2 plants with nearly horizontal flagleaves in both crosses.

Both F_2 populations showed essentially normal distribution for blade length of the leaf below the flagleaf. But leaf width showed multimodal distribution; there was an excess of wide-leaved individuals. Leaf area distribution was essentially normal with a small excess of large-leaved individuals (IRRI, 1971, p. 219-221).

Within each of the F_2 populations, leaf angle was negatively associated with blade width at 75 days after seeding. Leaf angle and leaf length were less positively correlated in the IR400-5-12 x BJ-1 cross only. In both crosses,

Table 3. Path (P), phenotypic (r_{ph}), and genotypic correlation (r_g) coefficients between grain yield and six agronomic traits in short, intermediate, and tall F_7 lines of Peta x I-geo-tze.

Agronomic trait	Coefficient of correlation with grain yield								
	Short			Intermediate			Tall		
	P	r_{ph}	r_g	P	r_{ph}	r_g	P	r_{ph}	r_g
Plant height	−0.071	−0.035	−0.024	0.177	0.093	−0.180	−0.164	−0.252*	−0.486
Panicle number	0.197	0.156	0.046	−0.020	−0.104	−0.537	0.193	0.252*	0.263
Panicle-to-tiller ratio	0.095	0.218*	0.366	−0.007	−0.101	−0.157	0.074	0.110	−0.098
Days to heading	−0.190	−0.053	0.006	−0.237	−0.359*	−0.683	−0.136	−0.108	−0.089
Leaf angle	0.103	0.028	−0.107	−0.347	−0.401**	−0.605	−0.254	−0.323**	−0.522
Flagleaf angle	−0.291	−0.257*	−0.810	−0.091	0.047	−0.024	0.130	0.033	−0.149



7. Differences in the leaf angle (of openness) among tall and short parents and their F_1 hybrids.

flagleaf angle and flagleaf length were positively correlated (T. T. Chang, and O. Tagumpay, *unpublished*).

Tillering ability and panicle number

The desirability of a high-tillering, small-grain variety under the most favorable environmental conditions is debatable (Donald, 1968). But under prevailing environmental conditions in the tropics, a high tillering genotype has the inherent advantages of adapting to varying spacings or planting densities, compensating for missing hills or damaged tillers, and rapidly attaining a favorable leaf area. The requisite for high yield is that a very high proportion of the tillers develop into fertile panicles.

Our F_1 and F_2 data obtained from a four-parent diallel set involving extremely contrasting varieties indicate that panicle number was largely controlled by additive gene effect and to a smaller but significant extent by dominance effect. A high count of panicles was partially dominant to a low count (Li and Chang, 1970). Wu (1968*b*) studied tiller number and panicle number of a five-parent diallel set among varieties having moderate to low tillering ability. The F_1 data likewise indicated that both additive and dominance effects were involved, with higher counts of tillers or panicles showing partial dominance, but different parental arrays varied in the order of dominance. These studies indicated that the loci controlling panicle number differed in the degree of dominance and that different parents carried unequal proportions of dominant and recessive alleles. Our F_2 data (Li and Chang, 1970) indicate a heritability estimate of 39 to 55 percent for panicle number which is higher than the range of 23 to 30 percent obtained in semidwarf F_3 lines of the Peta x I-geo-tze cross (Morishima et al., 1967).

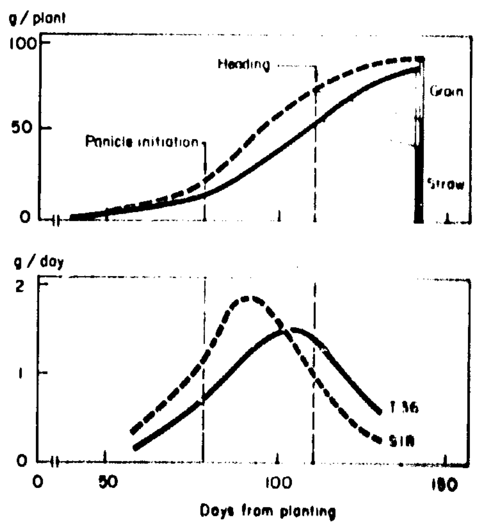
Generally tiller number and panicle number are positively correlated. Tall tropical and subtropical varieties tend to have lower ratios of panicles to tillers (Tanaka et al., 1964). In our cross of Peta x I-geo-tze, the short F_3 lines produced more panicles per plant than the tall lines, but the short lines showed more variability in panicle number between the wet and dry seasons (Morishima et al., 1967). In a large F_7 population of the same cross maintained as a bulk, the association between tallness and a lower panicle-to-tiller ratio was observed only in the tall lines. It did not appear in intermediately tall lines. On the other hand, extremely short F_7 lines produced a lower panicle number and a lower panicle-to-tiller ratio. Among the intermediately tall lines, a high panicle-to-tiller ratio was associated with a longer seeding-to-heading period (Chang and Tagumpay, 1970).

Early and sustained growth vigor

Early growth vigor, as observed in Taichung Native 1, IR8, and IR9-60, contributes to the faster development of a favorable leaf area and is essential to an early-maturing genotype (IRRI, 1966, p. 89-90). This trait also makes the plants more competitive with weeds or other low-tillering varieties (Jennings and Jesus, 1968). IR8 and other high-yielding semidwarfs have early growth vigor and a growth rate that is sustained up to flowering (Yoshida, 1969; Oka et al., 1970). Our data sampled from the Peta x I-geo-tze F_7 lines show that the growth rates at three stages contribute differently to grain yield and that the early-maturing lines tend to have a higher growth rate at heading, which was correlated with the increase in dry matter after heading. The harvest index was negatively associated with the number of days from seeding to heading. Comparison between the tall and short groups suggests that the genetic control of growth rates at different stages is not necessarily correlated with the major gene that controls plant height. It may be inferred that the "early-vigor" and the "late-sustained vigor" types differ in genes that control growth (Oka et al., 1970) (fig. 8).

Panicle features

Next to panicle number per unit area, the weight of grain on the panicles contributes directly to grain yield. Grain weight can also be measured by the number of grains per panicle and mean grain weight. Sometimes it can be



8. Comparison of growth pattern between two F_7 lines having the same maturity. T36 had a higher growth rate at floral (panicle) initiation and a lower growth rate at heading than S18. The grain yield per plant was 28 g in T36 and 33 g in S18 (*after* Oka, Morishima, Chang, and Tagumpay, 1970).

estimated by panicle length. Two diallel analyses showed that longer panicles were partially dominant to shorter panicles, and that larger numbers of spikelets per panicle were partially dominant to fewer spikelets, and that both additive and dominance effects were involved (Wu, 1968*b*; Li and Chang, 1970). The mean degree of dominance was in the direction of longer and heavier panicles. For number of spikelets per panicle, the dominant genes had asymmetrical positive and negative effects. Panicle length was highly stable in two successive dry seasons (Li and Chang, 1970).

In the Peta x I-geo-tze F_2 population, panicle number was negatively correlated with panicle length and with the weight of a single panicle. Long panicles and heavier panicles were associated with F_2 lines of the "early-vigor" type. The sustained-growth type of lines produced more grain per unit length of panicle, however (Oka et al., 1970).

In the six F_2 populations of our diallel cross, phenotypic and genotypic correlation coefficients indicate that panicle length is positively associated with plant height in all crosses and with growth duration in four crosses, and that it is negatively associated with panicle number in two crosses (T. T. Chang, and C. C. Li, *unpublished*). The positive association between panicle length and plant height or culm length in F_2 or F_3 generations was also reported by Nei and Syakudo (1957) and by Chang et al. (1965).

Grain features

Weight of grains is one of the primary yield components. Our earlier experiments with tropical and subtropical varieties showed that while the concurrent variations in yield components are complex and often correlated, varieties differ markedly in 100-grain weight, and that this component has a higher heritability (in the broad sense) than others (IRRI, [1965], p. 32-36). Matsushima (1966) felt that hull size limited the size of the caryopsis (brown rice) in Japanese varieties. Little genetic information on grain size and grain weight is available. Chandraratna and Sakai (1960) estimated that 10 additive genes controlled grain weight in a cross between two Ceylonese varieties. A maternal effect on grain weight was observed in the F_1 and F_2 generations. Inheritance studies on grain length, width, and shape, as well as on the percentage weight of hulls, also had limited scope (*see* Chang, 1964*a*). While grain weight can be readily compensated for by more spikelets on the panicle or by more panicles, varieties that have low grain weight, such as BPI-76, usually have a lower yield ceiling than heavy-grained types, such as IR8 and IR24, under the most favorable cultural system. The japonica varieties also have heavier grains. Concurrent selection for relatively high grain weight in a breeding program does not pose mechanical difficulties.

Another aspect of grain development is the rather high percentage of unfilled spikelets generally found in the tropics, for example, 9 to 29 percent in IR8 (IRRI, 1968, p. 151-159), as compared with the 10-to-20-percent range found in Japan (Murayama, 1971). The higher spikelet sterility in tropical areas may be caused by reduced light intensity (J. B. Lamin, *unpublished*), heavy nitrogen supply (Ota and Yamada, 1965; T. T. Chang, *unpublished*), mutual shading as a result of close spacing (IRRI, [1965], p. 32-36), varietal characteristics (Murata, 1969; IRRI, 1968, p. 30-31, 151-159), cool temperatures at anthesis (Vergara et al., 1970), or genotype-season interactions (Guevarra and Chang, 1965; IRRI, 1967*b*, p. 152-155), or by a combination of any of these factors. The problem of grain fertility would be a rewarding area for physiological studies under precisely controlled environments. These studies could be followed by genetic and breeding experiments.

Duration of the different growth phases

Panicle development and grain ripening need to be sustained by some vegetative growth before panicle initiation. Yield data from IRRI experiments showed that the higher yield levels were obtained from varieties that mature between 120 and 140 days (Vergara et al., 1966). Varieties earlier than 115 days do not produce high yields under the relatively wide spacing in a transplanted crop, unless much denser planting and heavy fertilization are provided (IRRI, 1966, p. 27-30, 1971, p. 25-27).

In the Peta x I-geo-tze F_2 population, the tall and intermediately tall lines showed a positive association between a shorter seeding-to-heading periods (from 85 to 102 days) and higher yield levels (Chang and Tagumpay, 1970). Earliness was also associated with a higher harvest index in the homozygous tall and short F_2 lines (Oka et al., 1970). When the comparison is based on the production of grain per day, the early maturing genotypes have merit for intensive multiple cropping systems (Vergara et al., 1966; IRRI, 1971, p. 25-27). Genetically, the control of earliness by the dominant, cumulative *Ef* genes would facilitate the selection of early maturing strains that combine a moderately long BVP and low sensitivity to photoperiod.

It would be worthwhile to determine if the two components of the reproductive phases, panicle development and grain ripening, could be extended somewhat independently of the vegetative growth period to permit an increase in supply of assimilation products, or storage capacity, or both. In tropical types, the duration from panicle initiation to flowering ranged from 30 to 47 days, though most varieties took about 35 days to complete panicle development (Vergara, Chang, and Lilis, 1969). Varieties also differ in length of the grain-ripening phase. Slowly senescent genotypes of temperate origin often have a longer ripening period. Slow leaf senescence as an indirect selection index for extended grain maturation is worth studying.

IMPLICATIONS OF AVAILABLE GENETIC INFORMATION ON RICE BREEDING AND AGRONOMY

Our studies have shown that some primitive traits, such as strong photoperiodic response, extremely tall stature, and strong grain dormancy, are controlled by one dominant major gene or a few dominant major genes and that these alleles could be readily eliminated from the tropical parents or re-incorporated into improved varieties. The most common type of gene action controlling several economically valuable quantitative traits, such as panicle number, panicle length, and spikelet number, is largely additive, though some loci show dominance. Moreover, the additive effect appeared quite stable over two seasons (Li and Chang, 1970). While most rice breeders are using the recessive gene for short stature and nitrogen responsiveness from Dee-geo-woo-gen, the convergence toward a less diverse genetic background will involve modifications in selection methods. When genotypic variance within a hybrid population becomes largely additive effects, the bulk method of selection or its modifications might be used to good advantage. Recurrent selection for the desired loci may also be tested as a means of accumulating loci that are favorable to higher yield potentials.

While the short-stature gene from Taiwan's semidwarfs has facilitated the recovery of vigorous, high tillering, erect-leaved, and early maturing progeny, its probable genotypic association with the gene or genes controlling susceptibility to the bacterial leaf blight pathogen in Taichung Native 1 (Heu, Chang, and Beachell, 1968) or to the tungro virus in I-geo-tze (T. T. Chang and K. C. Ling, *unpublished*) points to the need for broadening the genetic base of short-stature genes. We need to continue the search for additional sources of short stature which also carry desirable agronomic characteristics.

In this connection, an unexplored area is the potential breeding value of breaking up initial linkage blocks in homozygous parents of naturally self-pollinating species. Continued random intercrossing of several homozygous lines or of their hybrids for a few cycles before selfing could release greater genetic variability by increasing the recombinations within linkage groups (Hanson, 1959). We have made initial crosses to explore the potential usefulness of this intermating technique.

One aspect of our studies indicates the usefulness of including more than one environment in testing different genotypes so that genotype-environment interactions of agronomic interest may be exploited and used to suit specific ecologic niches. One agronomic application is improvement of nitrogen responsiveness and lodging resistance by planting a tall and strong photoperiodic variety during short daylength (Takahashi et al., 1967). Another instance is the finding of genotypes that have weakly dormant grain, such as IR8, which show higher levels of dormancy if rains fall during grain ripening (Chang and Yen, 1969). Similarly, a number of semidwarfs from semidwarf x floating crosses would respond better to rising water level than other semidwarfs or non-dwarfs (IRRI, 1967*b*, p. 63-64). The differential response in root development of different varieties to water stress represents another area where such interactions might be used (IRRI, 1971, p. 214-216; T. T. Chang, G. C. Loresto, and O. Tagumpay, elsewhere in this book).

Genotype-environment interactions of such a plastic nature could also be exploited if certain genotypes that possess higher photosynthetic efficiency under the lower light intensity of the monsoon season were identified.

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Discussion: Ecological and genetic information on adaptability and yielding ability in tropical rice varieties

E. C. CADA: BPI-76 has a high percentage of spikelet sterility, especially at the base of the panicle. Is this genetic or ecological in nature? If it is genetic, will re-selection be effective?

T. T. Chang: This is probably a genetic trait. BPI-76 also suffers from low 100-grain weight. I doubt if re-selection would help.

R. SEETHARAMAN: IR24 is a derivative from IR8 x [(CP 231 x SLO-17) x Sigadis]. Is the short stature of IR24 derived from IR8 or (CP 231 x SLO-17)?

T. T. Chang: Essentially from IR8, because the semidwarfing gene from Taiwan is more potent and has greater penetrance than the polygenes for short stature in (CP 231 x SLO-17), especially in crosses with the tall tropical varieties.

E. A. SIDDIQ: You have listed many component factors of lodging in your path diagram. The mechanical strength of the culm is known to be due to the sclerenchymatous tissues. Our study on the anatomical features of a few varieties including tall, dwarf, and brittle-culmed types reveals differences in the thickness of the wall of the sclerenchymatous cells and not in their number. Have you studied the anatomical features of lodging resistance?

T. T. Chang: We have compared the histological features of many weak- and stiff-culmed varieties. We found distinct differences in the lignification of the mechanical tissues, the symmetry of the inner ring of vascular bundles, and the wall thickness of parenchymatous cells, silica cells, etc. Chemical analysis of culm tissues was also made. But we found it impractical to relate any one histological or chemical feature to culm strength because culm stiffness is more than mechanical strength which usually involves the buckling load, moment of inertia, Young's modulus, and breaking strength. I consider it as the complex and dynamic phase of viscoelasticity of living tissues, which is little understood at this moment.

G. L. WILSON: Referring to your remark about the pros and cons of tillering in different cereals, I suggest that rice is relatively well able to produce some grain even in a small (suppressed) tiller, as compared with the development of barren suckers in corn and sorghum. Therefore, rice is in less danger from over-tillering and losing yield.

Physiological aspects of high yields

S. Yoshida, J. H. Cock, F. T. Parao

The crop growth rate of an improved variety of rice, IR8, increased as leaf area index (LAI) increased up to a value of about 6. Beyond this value, crop growth rate was almost constant. The respiration of the crop increased asymptotically, rather than linearly, with increase in LAI. Gross photosynthesis and respiration showed a similar relationship with LAI. The measured values of respiration of six varieties at different growth stages were centered around 40 percent of the gross photosynthesis. That indicates that the respiration of a rice crop is simply related to the photosynthesis. Grain number per square meter was closely related to nitrogen uptake until heading and to LAI at heading. At Los Baños, Philippines, grain yield was closely related to grain number because filled-grain percentage and grain weight remained almost constant irrespective of grain number and season. Short, stiff culms, erect leaves, and high tillering capacity were considered desirable plant traits. Carbon dioxide enrichment before heading increased grain yield by 29 percent while enrichment after heading increased it by 21 percent. The increased grain yield by enrichment before heading was associated with increased grain number and grain weight. Thus if the yield capacity, as determined by grain number and grain weight, can be increased by some means, neither photosynthetic capacity of the plant nor light nor CO_2 concentration after flowering is likely to limit the grain yield in the dry season at Los Baños. Further yield increase may be made by improving the grain filling, by increasing photosynthetic efficiency or extending the panicle growth period, or by increasing the portion of assimilation products that move to the developing panicle.

INTRODUCTION

At a symposium on the mineral nutrition of the rice plant in 1964, what rice scientists call "plant type" received considerable attention from physiologists and breeders (IRRI, 1965). There was a general agreement that morphological characters of the rice plant are closely related to nitrogen responsiveness and hence to yielding ability of rice varieties. Although the fundamental concept of plant type does not need any change, recent studies on improved varieties demand modifications of some ideas about the physiological basis of high yield, such as optimum leaf area index (LAI), that have been accepted by many rice scientists.

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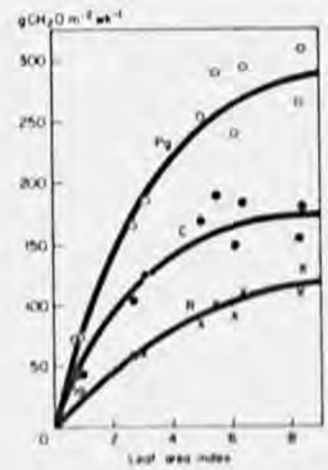
CRITICAL VERSUS OPTIMUM LEAF AREA INDEX

One of the most important concepts in rice physiology is the idea that an optimum LAI exists in the field because of increased mutual shading of leaves. Several reports indicate that an optimum LAI value exists in rice crops in both the temperate regions and the tropics (Yin et al., 1960; Murata, 1961; Takeda, 1961; Hayashi and Ito, 1962; Kanda and Sato, 1963; Tanaka and Kawano, 1966; Tanaka, Kawano, and Yamaguchi, 1966).

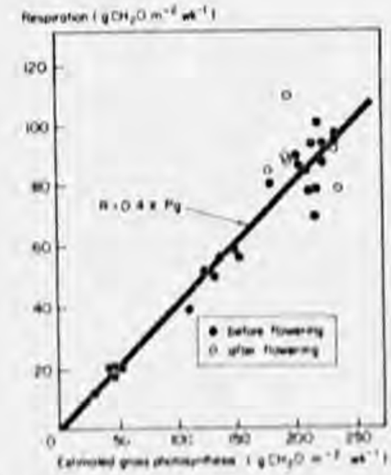
When IR8, an improved indica variety, was released, we began to suspect that there might not be an optimum LAI, or that the optimum LAI value might be much higher for this semidwarf variety than for other varieties. Otherwise, why has IR8, a vigorous growing, high tillering variety, consistently performed well at high nitrogen levels in many parts of the world? If the optimum LAI value of rice varieties is about 5 to 6, a vigorous variety like IR8 should suffer from detrimental mutual shading at high nitrogen levels on fertile soils.

Since it is easy to produce an IR8 crop with an LAI value as high as 10 without lodging, we can eliminate the influence of lodging from experiments. On the other hand, it is difficult to produce such a large LAI value with most japonica varieties without lodging.

Experiments on IR8 indicate that crop growth rate increases as LAI increases up to a value of about 5 at a low light intensity and about 7 at a high light intensity, beyond which it is constant up to 10 (Yoshida, 1969; IRRI, 1970). Figure 1a shows an example of such a relationship obtained recently. In this experiment, the respiration of the crop was measured and was added to crop growth rate to estimate gross photosynthesis. The respiration was estimated from the rates measured at night; it was corrected for temperature, but not for photo-respiration.



1a. Relationship between gross photosynthesis (Pg), crop growth rate (C), and respiration (R) (Variety: IR8).



1b. Relationship between gross photosynthesis (Pg) and respiration (R) (Varieties: IR8, IR747, Jaya, T141, Sigadis, Chianung 242.)

The crop growth rate of IR8 increased with increasing LAI to a value of about 6, beyond which it became almost constant until about 8. Respiration did not increase linearly with increasing LAI; it increased asymptotically. Gross photosynthesis, estimated by adding respiration to crop growth rate, also increased asymptotically with increasing LAI.

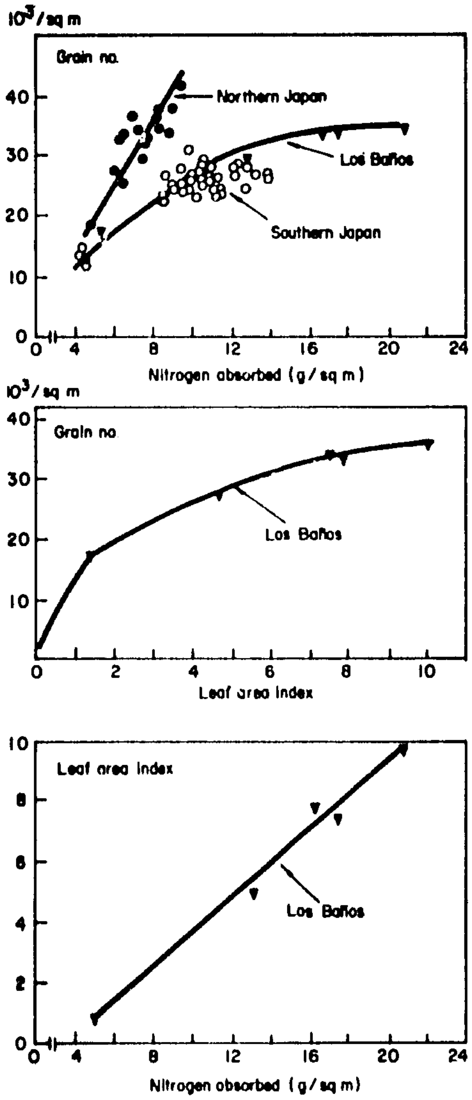
To collect more information on the respiration of a rice crop in relation to the gross photosynthesis, we measured the respiration and crop growth rate of six varieties of different plant types at 2-week intervals from 3 weeks after transplanting until 2 weeks after heading. As shown in figure 1b, the measured values for the respiration were centered at around 40 percent of the gross photosynthesis, which is equivalent to 60 percent growth efficiency (Tanaka and Yamaguchi, 1968). Unlike Tanaka and Yamaguchi (1968), we found no decrease in growth efficiency after panicle initiation. Thus within the experimental range the respiration of a rice crop is simply related to the photosynthesis. Since crop growth rate is the difference between gross photosynthesis and respiration, and since these two have a similar relationship to LAI, it follows that there is no optimum LAI value or at least there is no pronounced optimum LAI value.

Many papers show that the net photosynthesis of rice canopies does not fall even at high LAI values (Wang and Wei, 1964; Tanaka and Kawano, 1966; Tanaka et al., 1966). The detrimental effects of large LAI may instead come from lodging, increased leaf droopiness, and incidence of diseases and insects, all of which make photosynthesis decrease.

GRAIN NUMBER, NITROGEN UPTAKE, AND LAI

The potential yield or yield capacity of a rice crop may be expressed: Yield capacity = (panicle no./sq m) x (grain no./panicle) x grain size. In rice, the maximum grain size is physically limited by the size of hull, a stable varietal character (Matsushima, 1957). At and above normal plant density, panicle number per square meter is negatively correlated with grain number (sum of filled and unfilled grains) per panicle. At IRRI, direct-sown rice produced about 600 panicles/sq m and transplanted rice, about 300 panicles/sq m. But both crops produced the same number of grains per square meter (Yoshida and Parao, 1971). The number of grains per square meter determines the yield capacity of a given variety. It cannot be simply altered by increasing panicle number because of the negative correlation between panicle number and grain number per panicle.

There is a good correlation between the number of grains per square meter and nitrogen uptake by heading as shown in figure 2. The number of grains per square meter increases as the amount of nitrogen absorbed by the crop by heading increases. The efficiency of nitrogen use in producing grains is higher in northern Japan than in southern Japan and the Philippines. Rice plants grown in southern Japan have a low nitrogen content and pass their panicle initiation stage under high temperatures (Ishizuka and Tanaka, 1969). That means that

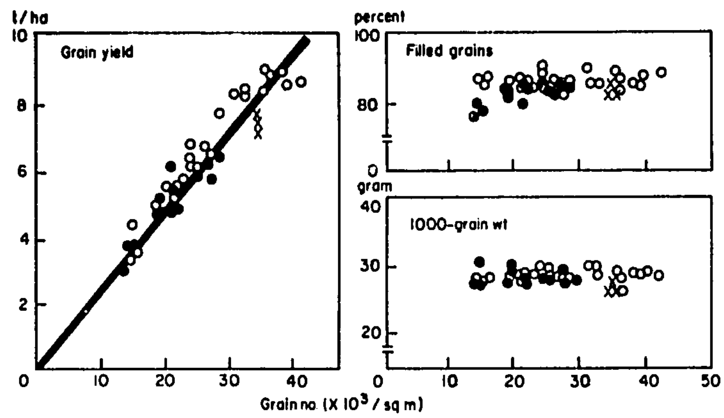


2. Relationship between grain number, amount of nitrogen absorbed by heading, and leaf area index at heading. (Data for Japan are adapted from Murayama, 1967.)

the rice crop stand in southern Japan and in the Philippines must be larger than in northern Japan to ensure the same yield capacity. The increased size of the stand would create a more serious lodging problem in these warm climate regions.

In the above comparison, grain weight (brown rice) is about the same for all locations, 22 to 23 g per 1,000 grains. Hence the grain number can represent the yield capacity.

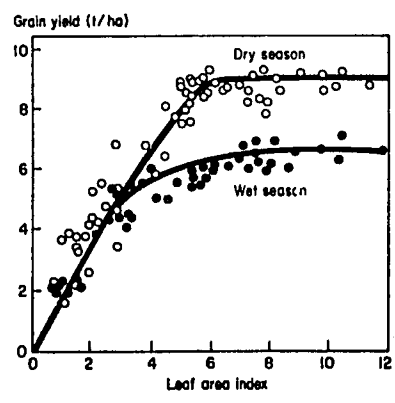
At heading, LAI is closely correlated with nitrogen uptake and hence with the number of grains per square meter (fig. 2). Nitrogen uptake, LAI, and grain number per square meter therefore are closely related to each other.



3. Relationship between total number of grains per square meter, grain yield, filled grain percentage, and grain weight. Variety IR8 (o = dry season; • = wet season; x = direct-seeding).

The grain yield is determined first by yield capacity and then by percentage of ripened or filled grain. In Japan, the ripened grain percentage tends to decrease as grain number per square meter increases (Matsushima, 1957; Wada, 1969). As a result, an optimum grain number may exist for maximum grain yield under certain conditions (Wada, 1969).

But, in our experiments at Los Baños, Philippines, the filled grain percentage and grain weight are about the same regardless of grain number and season (fig. 3). As a result, the grain yield is positively correlated with grain number. At Los Baños, we have two seasons, dry and wet. Within the same season, there is a certain degree of yearly variation in temperature and amount of incident solar radiation (IRRI, 1967*a*, 1967*b*, 1968, 1970, 1971). Nevertheless, the grain yield for each season is rather stable and the dry season yield is consistently higher than the wet season yield. As shown in figure 4, the grain yield and LAI at heading are closely correlated. Clearly, the yield difference between the two seasons is pronounced only when LAI is high.



4. Relationship between grain yield and leaf area index at heading in wet and dry season, 1966-1971. Variety IR8.

Table 1. Morphological characters associated with high yielding potential of rice varieties.

Plant part	Desirable characters	Effects on photosynthesis and grain production	References
Leaf	Thick	Associated with more erect habit. Higher photosynthetic rate per unit leaf area	Baba (1961); Murata (1961); Hayashi and Ito (1962); Tsunoda (1964); Jennings (1964); Tanaka and Kawano (1965); Tanaka et al. (1966)
	Short and small	Associated with more erect habit. Even distribution of leaves in a canopy	Baba (1961); Kariya and Sakamoto (1963); Tsunoda (1964); Jennings (1964); Matsushima et al. (1964); Tanaka and Kawano (1965); Tanaka et al. (1966)
	Erect	Increases sun-lit leaf surface area, thereby permitting more even distribution of incident light	Takeda and Kumura (1959); Baba (1961); Hayashi and Ito (1962); Kariya and Sakamoto (1963); Tsunoda (1964); Jennings (1964); Matsushima et al. (1964); Tanaka and Kawano (1965); Tanaka et al. (1966); Tanaka et al. (1968); Hayashi (1969); Tanaka et al. (1969); Ito and Hayashi (1969)
Culm	Short and stiff	Prevents lodging	Baba (1954); Hayashi and Ito (1962); Tsunoda (1964); Jennings (1964); Tanaka et al. (1964); Chang (1967); Tanaka et al. (1968); Ito and Hayashi (1969)
Tiller	Upright (compact)	Permits greater penetration of incident light into canopy	Tsunoda (1964); Tanaka et al. (1966)
	High tillering	Adapted to a wide range of spacings; capable of compensating for missing hills; permits faster leaf area development (transplanted rice)	Baba (1954); Yoshida and Parao (1971)
Panicle	Low sterility or high ripening percentage at high nitrogen rates	Permits use of larger amounts of nitrogen	Baba (1961); Jennings and Beachell (1965)
	High grain-to-straw ratio (high harvest index)	Associated with high yields	Baba (1961); Tanaka et al. (1964); Hayashi (1966, 1967); Chandler (1969*a*)

VARIETAL CHARACTERS IN RELATION TO HIGH YIELDING POTENTIAL

Table 1 summarizes certain varietal characters probably related to high yielding potential of rice varieties. Most were discussed at the 1964 symposium (IRRI, 1965). We shall discuss only three major characters: short and stiff culms, erect leaves, and high tillering capacity.

Short and stiff culms

Short and stiff culms make the rice plant more resistant to lodging. Among the plant characters associated with lodging, height is most important (Chang, 1967). The increased resistance of improved varieties to iodging appears to be the single character most responsible for high yields (Chandler, 1969*a*). Table 2 gives an example for yield performance of Peta, a tall, lodging-susceptible variety, with and without mechanical support, in comparison with IR8. The mechanical support alone increased the grain yield of Peta by 60 percent in the wet season and by 88 percent in the dry season.

The importance of lodging resistance has long been recognized, but only in recent years has a semidwarf gene been effectively introduced into tropical rice varieties. The recently released high yielding varieties in southern Japan, Hoyoku and its sister varieties, are characterized largely by their increased resistance to lodging (Shigemura, 1966).

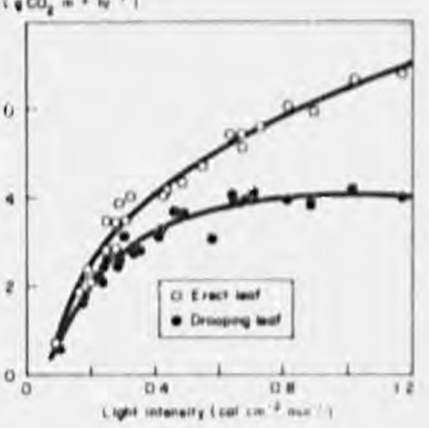
Erect leaves

A close association between erect leaves and high yielding potential has been shown in the past. A real understanding of the physical meaning of erect leaves in terms of light use by a plant community is recent, however (Monsi and Saeki, 1953; Duncan et al., 1967; Loomis and Williams, 1969; Monteith, 1969), as is the finding of empirical evidence that erect leaves are an important varietal character. Tanaka et al. (1969) showed that as light intensity increases, an erect-leaved rice canopy increases its photosynthesis at a higher rate than a droopy one (fig. 5). The effect of erect leaves is more pronounced at high light intensities than at low light intensities.

Table 2. An example of the yield performance of IR8 and Peta in the wet and dry seasons.

Variety	Yield (t/ha)		
	Wet season[a]	Dry season[b]	Mean
Peta not supported	2.83 (100)	3.97 (100)	3.40 (100)
Peta supported	4.52 (160)	7.46 (188)	5.99 (176)
IR8 not supported	6.10 (216)	9.10 (229)	7.60 (224)

[a]1966, 30 x 30 cm spacing, 100 kg/ha N. [b]1968, 20 x 20 cm spacing, 120 kg/ha N.



5. Difference in light-photosynthesis curves between rice populations with erect leaves and with droopy leaves (Tanaka et al., 1969)

When the sun angle is high and LAI is large, an erect-leaved canopy has a larger sunlit leaf surface than a droopy-leaved one, but the erect-leaved canopy receives lower light intensity per unit leaf surface according to the cosine law. The photosynthesis of an individual leaf increases hyperbolically with increasing light intensity, hence photosynthetic efficiency is greater at low light intensity than at high light intensity. Since most daily photosynthesis occurs when the sun angle is high, an erect-leaved canopy must give a higher rate of daily photosynthesis than a droopy-leaved one.

In more detailed consideration of leaf angle, Matsushima et al. (1964) and Isobe (1969) reached the same conclusion, by different reasoning, that plants with erect upper leaves gradually becoming more droopy at low canopy levels appear most desirable.

In rice, the upper three leaves export their assimilation products to the grains during the ripening period (Tanaka, 1958). In one of our measurements of the leaf area distribution of an IR8 canopy at heading when the LAI was 5.5, flagleaf area made up 19 percent of the LAI; second leaf area, 28 percent, and third leaf area, 27 percent. Therefore, 74 percent of the LAI contributes directly to grain yield. So erect leaves, which increase sunlit leaf surface, must be important in increasing yield.

High tillering capacity

Previously, it was thought that medium tillering capacity was desirable for high yielding varieties (Beachell and Jennings, 1965). Low yields of rice varieties were related to a fast growth rate at early stages and excessive LAI values beyond an optimum LAI, which in turn were closely related to high tillering capacity (Takeda and Kumura, 1959; Tsunoda, 1964; Tanaka et al., 1964; Tanaka and Vergara, 1967). As already discussed, however, a large LAI value itself is no disadvantage unless the crop lodges or becomes excessively droopy. In transplanted rice, because of wide spacing, limited leaf area development may reduce grain yield. Under such conditions, high and early tillering varieties have a definite advantage (IRRI, 1966; Yoshida and Parao, 1971). In fact, Hayashi (1968, 1969) found that recent high yielding rice varieties in Japan are short, erect-leaved, and high tillering. These varieties tend to develop larger LAI values with thinner leaves. Furthermore, high tillering capacity gives the plant greater ability to compensate for missing hills which may be caused by poor germination, pests, and diseases. High tillering capacity therefore has many advantages.

Changes in morphological characters of high yielding varieties

In Hokkaido, Japan, Tanaka et al. (1968) studied changes in morphological characters of rice varieties that became commercially available in the past 50 years. That study showed that selection of better varieties has led to shorter plants, higher tillering capacity, and more erect leaves. A similar trend was also observed for rice varieties in southern Japan (Ito and Hayashi, 1969). The increased application of nitrogen must have led the breeders to such selection in the past (Athwal, 1971). The outcome of this selection, however, is in good agreement with the present knowledge of physiological aspects of high yields of transplanted rice.

LIMITING FACTORS OF GRAIN YIELD

Anything that affects rice growth can limit grain yield under certain conditions. Among climatic factors, solar radiation has received considerable attention because it is the source of energy for photosynthesis. The yield of rice has been correlated with solar radiation from 10 to 15 days before flowering until harvest (Murata, 1964; De Datta and Zarate, 1970) and with solar radiation during the ripening period (Moomaw, Baldazo, and Lucas, 1967; Munakata, Kawasaki, and Kariya, 1968). This finding suggests that grain yield is related to the amount of photosynthesis during these periods. Under natural conditions, it is not easy to separate the effects of solar radiation from those of temperature. Shading experiments have demonstrated the direct effect of solar radiation on yield (Stansel et al., 1965; Munakata et al., 1968). Munakata et al. (1968) have shown that the relationship between yield and amount of solar radiation can be expressed by an asymptotic curve. No saturation point seems to exist up to 500 cal cm^{-2} day^{-1}. The close correlation between solar radiation and grain yield reveals when to plant rice to maximize yield.

Analysis of yield components suggests that improving grain-filling is one way to increase grain yield. Low ripened-grain percentage often causes low yields in Japan. It is sometimes as low as 50 percent (Murata, 1969). Under such condition, grain filling tends to determine the grain yield. Even under favorable conditions, the ripened-grain percentage ranges from about 75 to 90 percent (Murayama, 1971), which means that grain yield can only be increased by 10 to 25 percent by improving grain filling.

Low ripened grain percentage has several causes. Under field conditions at high nitrogen levels, lodging is likely to be involved. Ripening also may be affected by the supply of assimilation products, the translocation of assimilation products, and the ability of the grain to accept assimilation products. Any of

Table 3. Effects of CO_2 enrichment before and after heading on growth and grain yield, IR8, 1971 dry season.

Treatment	Yield (t/ha)	Sugar and starch[c] in leaf sheath and culm (%)	Crop growth rate[d] ($g\ m^{-2}\ wk^{-1}$)		Grain		
			Before heading	After heading	Wt[e] (mg)	No. (10^3/sq m)	Filled[d] (%)
Control	9.0	22	173 a	99 b	23.1	46	74 b
CO_2 before heading[a]	11.6	30	224 b	157 a	25.9	51	77 b
CO_2 after heading[b]	10.9	22	173 a	147 a	25.1	45	86 a
LSD (5%)	0.8				0.6	4	--

[a]For 30 days. [b]For 28 days. [c]As glucose. [d]Any two means followed by the same letter are not significantly different at 5% level. [e]Dried at 75 C for 3 days.

these may control ripening. Recently, Nakayama (1969) demonstrated that the senescence of the grain starts with the conductive tissue of the rachilla, suggesting that the translocation may limit grain filling.

The CO_2 concentration in the atmosphere is also likely to limit grain yield. Concentrations higher than 300 ppm increase photosynthesis (Yamada et al., 1955) and grain yield (J. J. Riley and C. N. Hodges, *unpublished*). Crop physiologists must determine whether yield capacity or grain filling, as determined by photosynthesis during the ripening period, limits grain yield.

We have studied the effects on grain yield of CO_2 enrichment before and after heading. Groups of nine plants in the field were enclosed with open-topped plastic chambers. The CO_2 concentration in the chamber was increased to about 900 ppm during the day by adding CO_2 from gas bottles. The CO_2 enrichment before heading increased grain yield by 29 percent above the control and after heading by 21 percent (Table 3). The yield increase by the enrichment before heading was caused by increased grain number and grain weight. Enrichment after heading did not change grain number but increased grain weight and filled grain percentage. The plants that received CO_2 enrichment before heading had identical environmental conditions to the control after heading, yet they had a higher crop growth rate.

In that experiment increased photosynthesis by CO_2 enrichment before heading increased yield capacity which in turn increased photosynthesis after heading and grain yield. This can be regarded as an example of feedback interaction between sink and source.

If the yield capacity can be increased by some means, apparently neither photosynthetic capacity of the plant nor light nor CO_2 concentration after heading is likely to limit the grain yield in the dry season at Los Baños. Thus to increase yield further, some way of increasing the yield capacity must be found.

One possiblity, as suggested by the CO_2 enrichment experiment, is to increase the amount of photosynthesis during panicle formation. Increased photosynthesis may be achieved by increasing photosynthetic efficiency or by extending the time for panicle growth. Some varietal difference in photosynthetic efficiency has been found (Murata, 1957; Osada, 1967; Chandler, 1969*b*). Relatively small differences exist in the period from panicle initiation to heading under normal crop conditions (Akimoto and Togari, 1939; Matsushima, 1957; Asakuma, 1958; Matsushima and Manaka, 1959; Tanaka et al., 1964; Ishizuka and Tanaka, 1969; Vergara, Chang, and Lilis, 1969). But growth duration and the length of the period from panicle initiation to heading are positively correlated. Thus, an early maturing rice crop has a relatively short time for panicle growth (Akimoto and Togari, 1939). Since longer growth duration is not generally desirable, the question arises, can the period of panicle growth be extended independently of whole growth duration?

Partitioning of assimilation products between developing panicles and leaves is probably under some hormonal control. Distribution of a greater portion of assimilation products into developing panicles may produce larger panicles. The flagleaf size of most improved rice varieties is relatively small compared with the second or third leaves. Possibly this results from competition between the flagleaf and the developing panicle. Attempts to understand the mechanism of the partitioning of assimilation products and to find means of controlling it merit much more attention.

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Discussion: Physiological aspects of high yields

L. T. EVANS: In Table 1 you observe that the advantage of a short culm is that it prevents lodging. We have wondered whether it has other advantages in wheat, such as reducing competition between the stem and the ear. However, we found that this competition was not influenced by height *per se*, but by the duration of stem growth. In some tall varieties stem growth ceases well before grain filling begins, while in some short varieties stem growth continues up to the onset of grain filling. Do you have any comparable observations for rice?

S. Yoshida: No. However, we know that the time of stem elongation relative to panicle initiation differs among varieties.

K. HAYASHI: How high are the solar radiation values you have at Los Baños during the rice maturing periods in the wet and dry seasons?

S. Yoshida: The amount of incident solar radiation is subject to yearly variation. Roughly speaking, we have 300 to 350 cal cm $^{-2}$ day $^{-1}$ in the wet season and 450 to 500 cal cm $^{-2}$ day $^{-1}$ in the dry season.

K. HAYASHI: Do you think that the CO_2 enrichment before heading did not increase the translocation of the photosynthate which has been stored before heading?

S. Yoshida: It may account for some of the yield increase. But the high crop growth rate after heading suggests that it is not the sole cause.

A. C. MCCLUNG: I presume that T. Tanaka's data on erect vs. droopy leaves were obtained with Japanese varieties which usually have less erect leaves than IR8. If this experiment were conducted with IR8 to compare the normal leaf angle of IR8 with some strains approximating the leaf angle of the Japanese varieties, would you expect reduced photosynthetic performance?

S. Yoshida: Under cloudy conditions, there will be no detectable decrease. Under sunny conditions, there may be some decrease, but not much.

S. OKABE: You have showed that 1,000-grain weight does not fluctuate or change, irrespective of numbers of grains. Could you explain this? Do you think this is generally true in tropical regions?

S. Yoshida: This is a characteristic of rice whether it is in the tropics or in the temperate region. There may be, however, variations in ripened grain percentage in the temperate region as shown by S. Matsushima.

K. KAWANO: It appears difficult to obtain higher total dry matter production than that of IR8 without simultaneous reduction in the grain-to-straw ratio. On the other hand, it appears feasible to increase the grain-to-straw ratio of IR8 without sacrificing the total dry matter accumulation. On the Peruvian coast, some lines such as IR305-3-15 yield 1 or 1.5 t/ha more than IR8 over several experiments. The yield of IR305 being 11 to 13 t/ha, IR305 had a grain-to-straw ratio of 1.3 to 1.5 while IR8 had 1.1 to 1.2, total dry matter accumulation being more or less the same.

S. Yoshida: To increase grain-to-straw ratio is one way to increase grain yield, if total dry matter remains the same. To increase total dry matter is another matter, if grain-straw ratio remains the same. Our CO_2 enrichment experiment indicates that grain yield can be increased by increasing total dry matter production. Increased dry matter production does not necessarily change the grain-to-straw ratio.

S. C. LITZENBERGER: Your studies show an increased yield with CO_2 enrichment before and after heading. What might be a practical way to produce such a condition in a commercial planting of rice?

S. Yoshida: At present it is uneconomical to enrich CO_2 in the field. The CO_2 enrichment can be economical only for horticultural crops and under greenhouse conditions. It is not our intention to suggest CO_2 enrichment in rice field. The experiment was intended to test if CO_2 concentration in the atmosphere is limiting rice yield and if increased size of sink would produce higher yield without any changes in the environment. Breeding a variety capable of producing more grains per unit land area would be a better solution.

E. C. CADA: High tillering ability is associated with high yield, but grain maturity may not be uniform, so milling recovery and the percentage of head rice may be affected adversely. Is tillering correlated with milling recovery?

S. Yoshida: We have not studied this subject. Judging from tillering habit in the field, however, milling recovery of the high tillering varieties could be lower because many late tillers are developed at wide spacings. At close spacings, however, it is unlikely to be a problem because the high tillering variety approaches the low tillering variety in tillering performance.

S. K. SINHA: Is high tillering capacity advantageous even under moisture stress?

S. Yoshida: It depends on what regime of moisture stress you are considering. Under sustained moisture stress, tillering will be impaired. Therefore, high tillering capacity may not have any advantage or disadvantage. Under variable moisture conditions, however, high tillering capacity may have some advantage by establishing a leaf canopy quickly when there is adequate moisture in the soil, thereby reducing soil moisture loss by evaporation.

S. K. SINHA: Is there any evidence of competition between tillers in the rice plant?

S. Yoshida: Ample evidence suggests that competition exists between tillers for light and nutrients.

G. L. WILSON: Referring to the extension of time for panicle development to permit larger panicles, we found that by freeing tillers of IR22 from competition at the stage of panicle initiation, spikelet number doubled in an unaltered period of development. Therefore panicle size is not limited only by time available.

S. Yoshida: There are many ways to increase panicle size. Extension of time for panicle development may be one way. Exposure of certain tillers by removing other tillers to high light intensity is another, but this will not result in higher yield per unit area of land.

Photosynthetic efficiency in rice and wheat

Shigesaburo Tsunoda

A high nitrogen content per unit leaf area (N_{LA}) is associated with a high photosynthetic rate per unit leaf area, but it is coupled with a decrease in leaf area. Leaves with a lower N_{LA} are effective at low levels of foliage nitrogen per unit ground area (N_{GA}), while leaves with a higher N_{LA} are effective at high levels of N_{GA}. The advantage of high N_{LA} under high levels of N_{GA} is especially noticeable under high intensity radiation. If water supply is not adequate, small leaves with higher N_{LA} values are needed to keep the water balance, regardless of the levels of N_{GA}. Development of vascular bundles, in particular of xylem systems, and arrangement of photosynthetic cells close to the bundles are important to keep the water balance with a low gas-exchange resistance. As observed in wild wheats that have these structures combined with a high N_{LA} (thick, compact mesophyll tissues), a high photosynthetic rate can be achieved. In rice and wheat, primitive varieties had a loose mesophyll structure, while highly nitrogen-responsive varieties had compact mesophyll tissues. The effects of temperature-preconditioning on leaf photosynthesis differed among strains in rice and wheat.

INTRODUCTION

Differences in photosynthetic efficiency among genotypes of plants have been investigated by a number of workers in relation to the amount of proteins, of chlorophyll, and of other components involved, internal structures of leaf, biochemical pathways and activities, size of sinks, etc. I would like to focus on the relationships among nitrogen content of the leaf, leaf structures, and the rate of energy conversion. Their probable significance for adaptability and yield potential of rice and wheat, under different levels of available water, nitrogen, and solar radiation, will also be discussed. In addition, temperature responses observed in rice and wheat will be dealt with briefly.

NITROGEN CONTENT AND PHOTOSYNTHETIC EFFICIENCY OF RICE LEAVES

The angle of inclination of leaves to incidental radiation has claimed attention in breeding cereals for high yield. Changes in the density thickness of leaves or the nitrogen content per unit leaf area seem to have a similar effect to changes in

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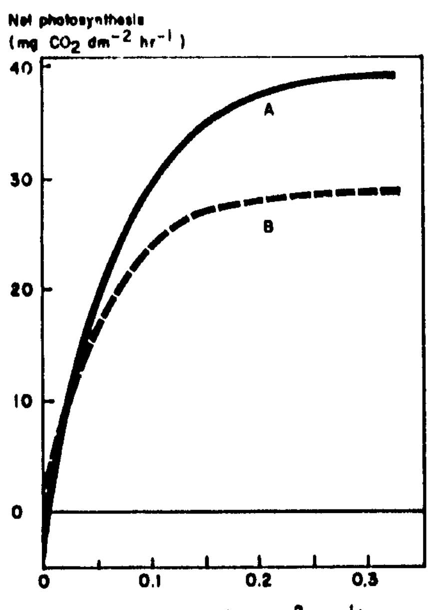
leaf inclination (Tsunoda, 1959, 1965), but this phenomenon has not yet drawn wide attention.

In rice, the photosynthetic rate per unit of leaf area (P_{LA}) is positively related to nitrogen content per unit leaf area (N_{LA}) at high light intensities (Murata, 1961; Osada, 1966; Takano and Tsunoda, 1971). This relationship held whether differences in N_{LA} were due to environment or genotype, as observed also in alfalfa by Pearce et al. (1969) for the relationship between P_{LA} and specific leaf weight (dry weight per unit leaf area). For instance, *Oryza officinalis* and its close relatives, *O. minuta* and *O. eichingeri*, generally showed lower values of N_{LA} associated with lower values of P_{LA}, as compared with many strains of *O. sativa* (Takano and Tsunoda, 1971). Similarly, among different leaves of the one strain, the same relationship was observed; the lower the N_{LA} the lower the P_{LA}. These results suggest that nitrogen content is very closely related to photosynthetic efficiency, possibly reflecting the amount of some functional units in the leaves.

The relationship between P_{LA} and N_{LA} for *O. sativa* varieties at 85 klx (0.310 cal cm^{-2} min^{-1} in the photosynthetically active region) within a range of leaf nitrogen content of 11 to 21 mg/dm^2 was $P_{LA} = -14.38 + 4.88\,N_{LA} - 0.11\,N_{LA}^2$ (Takano and Tsunoda, 1971). This equation shows that, even at the highest nitrogen content observed among rice varieties (about 20 mg/dm^2) the P_{LA} had not reached its ceiling rate. Thus a further increase in N_{LA} due to plant breeding may produce a higher P_{LA}.

As stated, under a high light intensity of 0.310 cal cm^{-2} min^{-1}, leaves having a higher N_{LA} tended to show a higher P_{LA} as compared with leaves having a lower N_{LA}. Under relatively low light intensities, however, differences



1. Light-photosynthesis curves of rice leaves (Kishitani et al., 1972). A) Leaves with a mean N_{LA} value of 17.58 mg/dm^2. (Average of three leaves.) B) Leaves with a mean N_{LA} value of 11.53 mg/dm^2. (Average of five leaves.)

in P_{LA} between leaves with different N_{LA} values were not marked (Takano and Tsunoda, 1971). The dark respiration rate tended to be higher in leaves with high nitrogen content than in leaves with low content (Murata, 1961). Mean dark respiration was estimated at about 0.128 mg CO_2 mg^{-1} leaf nitrogen hr^{-1} at 30 C (Takano and Tsunoda, 1971). Figure 1 sho· .e effect of N_{LA} on net photosynthesis.

Optical properties

Differences in the light reflection, transmission, and absorption rates of leaves were observed among cultivated and wild rice strains in relation to the chlorophyll, nitrogen, and dry matter content per unit of leaf area (Takano and Tsunoda, 1970). Among rice varieties, nitrogen content was closely associated with chlorophyll content and hence positively related to absorption rate and negatively to reflection and transmission rates. Between them, the following relationships were estimated (Kishitani, Takano, and Tsunoda, 1972):

$$\mathrm{Log}_e\, R = 2.28476 - 0.01417\, N_{LA} \quad (1)$$

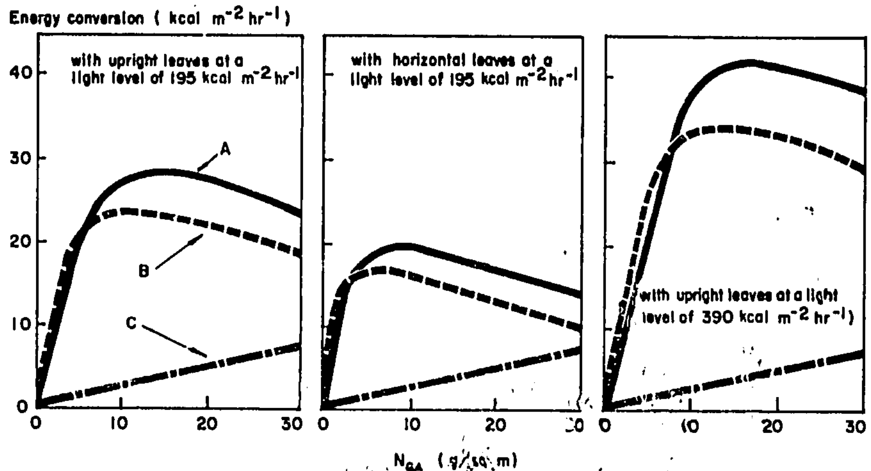
$$\mathrm{Log}_e\, T = 2.27738 - 0.04280\, N_{LA} \quad (2)$$

where R is the reflection as a percentage of the light received, T is the transmission, and N_{LA} is the nitrogen content per unit leaf area in milligrams per square decimeter. As seen from equations (1) and (2) the transmission is more strongly affected by the nitrogen content than is the reflection.

Strains of *O. officinalis*, *O. minuta*, and *O. eichingeri* exhibited a fairly high chlorophyll content for their nitrogen content as compared with *O. sativa* varieties and, simultaneously, a higher light absorption rate for their leaf-nitrogen content (Takano and Tsunoda, 1970).

Canopy photosynthesis

The relationship between the nitrogen content of single leaves and photosynthetic rates of leaf canopies should be clarified. What is the optimum nitrogen content per unit leaf area of single leaves for maximizing canopy photosynthesis under a certain condition? Kishitani et al. (1972) attempted to answer this question. They made a simulation with the data for optical and photosynthetic properties of rice leaves in equations (1) and (2) and on some simplifying assumptions for other factors involved. In figure 2, the photosynthetic rates were measured at two levels of light intensity in the photosynthetically active region, 30 C and 300 ppm CO_2. The respiration rate was measured at 25 C and was estimated to be proportional to foliage nitrogen per unit ground area (N_{GA}) and independent of N_{LA}. Figure 2 shows that leaves with a higher N_{LA} are effective at high levels of N_{GA}, while leaves with a lower N_{LA} are effective at low levels of N_{GA}. The relationship between N_{LA}, N_{GA}, and canopy photosynthesis is similar to that between leaf inclination, leaf area index, and canopy photosynthesis which has been reported by Duncan et al. (1967). The effect of increasing N_{LA} is similar to that of having more inclined leaves, and it seems that the latter can complement the former to some extent. Canopies with horizontal leaves (fig. 2) lack this complemental effect, so an increase in N_{LA} seems to be required even at



2. Photosynthesis and respiration rates of leaf canopies estimated at different levels of foliage nitrogen per unit ground area (N_{GA}) (Kishitani et al., 1972). A) Net photosynthesis with a N_{LA} value of 1.758 g/m². B) Net photosynthesis with a N_{LA} value of 1.153 g/m². C) Dark respiration, independent of values for N_{LA}.

lower levels of N_{GA} to achieve greater photosynthesis. With rice, however, the inclination of the leaves can be changed, thus the complementary relationship of leaf inclination and N_{LA} must be considered in designing ideotypes of rice.

The advantage of having a high N_{LA} under high levels of N_{GA} is noticeable under high light intensity (fig. 2). Long, warm nights may reduce the advantage to some extent because of an increase in the respiration during the night. Furthermore, some other computations show that at N_{GA} levels around or below 1 g/m², a canopy composed of horizontal leaves with a low N_{LA} (1.153 g/m²) arranged in a close layer without overlapping with a canopy density of 1.0 achieves the highest canopy photosynthesis. This is exactly the canopy architecture I previously presented schematically as an ideal assimilation system adaptable to low levels of fertilization (Tsunoda, 1959).

NITROGEN CONTENT AND PHOTOSYNTHETIC RATES OF WHEAT LEAVES

Photosynthetic rates are closely related to nitrogen content in wheat, too. Figure 3 shows that strains of wild species generally exhibited a higher level of N_{LA} associated with a higher photosynthetic rate per unit leaf area (P_{LA}), while cultivated wheats showed a lower N_{LA} value associated with a lower P_{LA} (Khan and Tsunoda, 1970*a*). The highest values for N_{LA} and P_{LA} were observed in a strain of wild diploid species, *Triticum aegilopoides* var. *boeoticum*, and the lowest values for the content and the rate were observed in a strain of cultivated hexaploid bread wheat, *T. vulgare* var. *erythrospermum*.

On the other hand, a higher N_{LA}, together with a smaller seed size, is associated with a lower leaf area (Khan and Tsunoda, 1970*a*). Evans and Dunstone (1970) also observed that P_{LA} was higher in wild progenitors than in cultivated wheats, while the area of individual leaves and the total leaf area was higher in cultivated types than in wild types.

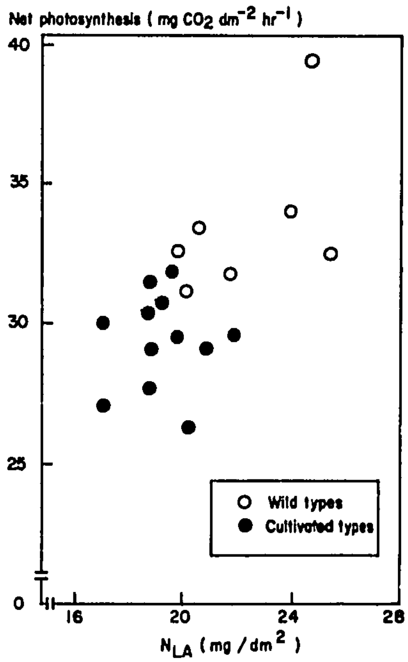
Figure 4 shows that in six commercial varieties of the bread wheat (*T. vulgare*), N_{LA} and P_{LA} were also positively correlated (Khan and Tsunoda, 1970*c*). Mexi-Pak, a modern semidwarf variety that yields well with high fertility and good irrigation showed higher N_{LA} and P_{LA} values than old Pakistani varieties. On the other hand, Mexi-Pak showed a lower leaf area ratio (leaf area/total plant dry weight) as compared with other varieties (Khan and Tsunoda, 1970*d*).

In short, N_{LA} was higher in wild progenitors than in cultivated wheats. But among cultivated wheats, a modern fertilizer-responsive variety showed the highest N_{LA} value. In all cases, a higher N_{LA} was associated with a higher P_{LA}. On the other hand, a higher N_{LA} was coupled with a smaller leaf area.

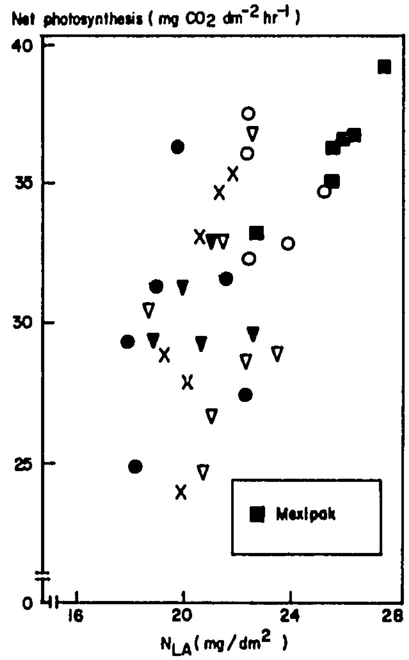
LEAF STRUCTURE AND PHOTOSYNTHETIC EFFICIENCY

Wheat

Recently, Khan and Tsunoda (1970*e*, 1971) studied leaf structures of wild and cultivated wheats in relation to leaf photosynthesis. On the basis of leaf structure, the genera of *Gramineae*, excluding the *Bambuseae*, have been divided into two



3. Relationship between N_{LA} and photosynthesis in wheat in 19 strains of different species; average of January and February observations under greenhouse and glasshouse conditions (Khan and Tsunoda, 1970*a*).



4. Relationship between N_{LA} and photosynthesis in six commercial wheat varieties of West Pakistan including Mexi-Pak, a modern high nitrogen responsive variety, observed in March (Khan and Tsunoda, 1970*b*).

5. Leaf of *Triticum vulgare* var. *erythrospermum*, a strain of cultivated bread wheats as observed in transverse plane shows a loose, thin arrangement of larger mesophyll cells, many of them being non-radiate at intervals between sparsely located vascular bundles.

major groups, the festucoid and the panicoid (Metcalfe, 1960). The wheats belong to the festucoid group. Indeed, *T. vulgare* var. *erythrospermum*, a strain of cultivated wheat which had the lowest P_{LA} value in figure 3, showed the festucoid leaf characters, (fig. 5): many mesophyll cells not arranged radiately around the vascular bundles and the bundles being located sparsely. However, in *T. aegilopoides* var. *boeoticum*, a wild plant which showed the highest P_{LA} value in figure 3, the mesophyll cells showed a radiate arrangement around the vascular bundles and the bundles were numerous and closely crowded (fig. 6). Here, too, the "chlorophyllous parenchymatous bundle sheath" observed in maize, sorghum, and tropical grasses that belong to the panicoid group is not developed. But the radiate, close, compact arrangement of mesophyll cells around the well-developed vascular bundles is far from the festucoid leaf characters. It is rather panicoid-like in structure. The chlorophyllous parenchymatous bundle sheath (CPBS) has drawn attention in relation to drought resistance (by V. V. Korkunov in 1905 and V. G. Arexandrov in 1924 according to Maximov, 1951) and to high photosynthetic rate (El-Sharkawy and Hesketh, 1965; Akita, Miyasaka, and Murata, 1969). It is interesting that the panicoid-like leaf structure of *T. aegilopoides* var. *boeoticum*, though it lacks the CPBS, was associated with high photosynthetic rate. The distribution center of this wild wheat lies in the fertile crescent belt of south Turkey, north Iraq, and adjacent territories in Iran and Syria (Zohary, 1970). The panicoid-like leaf structure observed in this wild wheat probably is a result of adaptation to its arid habitat.

6. Leaf of *T. aegilopoides* var. *boeoticum*, a wild wheat, as observed in transverse plane, shows a compact, thick, radiate arrangement of small mesophyll cells around the densely located vascular bundles.

The ratio of the mesophyll thickness to the vascular bundle distance was positively related to the P_{LA} among 19 strains of different species (Khan and Tsunoda, 1971). *T. aegilopoides* var. *boeoticum* showed the highest P_{LA} with the highest ratio, while *T. vulgare* var. *erythrospermum* was among the lowest in both the rate and the ratio. In addition, *T. aegilopoides* var. *boeoticum* had compactly arranged small mesophyll cells, while *T. vulgare* var. *erythrospermum* had loosely arranged large mesophyll cells. A negative correlation between mesophyll cell size and P_{LA} has been already pointed out with other crop plants by El-Sharkawy and Hesketh (1965) and Wilson and Cooper (1967).

Among six Pakistani commercial wheat varieties, Mexi-Pak had more compact mesophyll cells than older varieties.

The differences in the compactness of mesophyll tissues observed between wild and cultivated wheats and between primitive and modern varieties may be closely related to the evolutionary trends of wheats in N_{LA}.

Rice

Representative indica rices, old japonica rices, and modern japonica rice varieties were compared in leaf structures by Tsunoda and Khan (1968). The mesophyll tissues, including chloroplasts, were most compact in Fujisaka-5, a modern japonica, intermediate in Hosogara, an old japonica, and least compact in Mao-zu-tao, a Chinese indica. This result coincides with that obtained with six Pakistani wheat varieties.

In a preliminary study, S. Kishitani and I (*unpublished*) found a positive correlation between the ratio of xylem area to leaf area and P_{LA} among 14 rice varieties. Xylem area was measured as a total cross-sectional area of all xylems at the base of leaf blade. The correlation was highly significant, when P_{LA} was observed at a low relative air humidity (35 to 40%). Bluebelle, a U.S. variety, showed the highest P_{LA} with the highest ratio.

IDEOTYPES FOR DIFFERENT LEVELS OF AVAILABLE WATER, NITROGEN, AND RADIATION

Significant changes in leaf structure and nitrogen content have occurred in cultivated plants in the course of evolution. Cultivated mesophytes generally have thinner leaves with a lower N_{LA} than wild xerophytes. The change from thick toward thin leaves may help the plant adapt to the mesophytic condition of cultivated land because thinner large leaves can receive, absorb, and use a larger amount of solar energy when moisture supply is well balanced. This may be followed by a change in the reverse direction when nitrogen supply is abundant. Leaves with a higher N_{LA} are effective at high levels of N_{GA}. The advantage of having a high N_{LA} under high levels of N_{GA} are especially noticeable under high intensity radiation.

Water supply

Wild wheats grow over a wide range of soils and climates (Zohary, 1970). Some are found in rain-soaked forests, while others thrive in cultivated wheat fields. However, many grow on the dry steppes and even on the margins of deserts.

Wild wheats showed a higher N_{LA} than cultivated wheats. This characteristic was coupled with a high P_{LA}, and, on the other hand, with smallness of the leaves. In contrast, cultivated types tended to enlarge the leaf area with a lower N_{LA}. If we may use here the term "thick," meaning a higher nitrogen content per unit leaf area and "thin," a lower content, wild wheats tended to have "thick" small leaves and cultivated types "thin" large leaves. This pattern coincides with that observed between wild xerophytes and cultivated mesophytes in *Brassica* and its allied genera (Tsunoda, Kanda, and Takano, 1967). Possibly the "thick" small leaves of the wild plants are an expression of their xerophytic nature, and the "thin" large leaves of the cultivated wheats are an adaptation to improved water supply and water balance. With "thin" leaves or with a lower N_{LA}, the P_{LA} of cultivated wheats is rather lower than that of its wild relatives. This low N_{LA}, however, is associated with the enlargement of leaf area which may bring about an increased use of solar radiation when moisture supply is well balanced. The photosynthetic rate per unit leaf-nitrogen was higher in leaves with a lower N_{LA} than in leaves with a higher N_{LA} (Khan and Tsunoda, 1970*a*).

Maximov (1951, p. 29) pointed out that both P_{LA} and transpiration rate per unit leaf area were higher in many xerophytes than in mesophytes. Wild wheats showed high values not only in P_{LA} but also in transpiration rate (Khan and Tsunoda, 1970*b*). Plants must increase the gas exchange resistance to keep the water balance when the moisture supply to the mesophyll is not sufficient. This change causes a decrease in the transpiration rate and, at the same time, a decrease in P_{LA}. The development of vascular bundles, in particular of xylem systems, and the arrangement of photosynthetic cells close to the bundles, may be important for maintaining the water balance with a lower gas exchange resistance. With these leaf structures combined with a high N_{LA} (thick, compact mesophyll tissues), a high P_{LA} as well as a high transpiration rate can be achieved. Xerophytic leaf characters, suggested above, may also be required to some extent in varieties grown with a limited supply of water.

Nitrogen supply

Nitrogen supply may increase the leaf area and N_{GA} of plant communities. Inclined upright leaves may have an advantage in relation to uniform illumination of leaves when a large leaf area index is achieved (Boysen Jensen, 1932). I suggest that, besides having inclined upright leaves, a large amount of leaves per unit ground-area can be maintained in a well-organized situation in another way (Tsunoda, 1959, 1960, 1965); that is by having "thick" small leaves, instead of "thin" large leaves. Leaves with a higher N_{LA} are effective at high levels of N_{GA}, while leaves with a lower N_{LA} are effective at low levels of N_{GA}. With rice and wheat, the complementary relationship between upright leaves and increasing N_{LA} must be considered.

The mean values for N_{LA} and N_{GA} of actual rice communities under current conditions of rice culture in Japan are estimated at 1.16 g/m^2 and 5.99 g/m^2, respectively, at the heading stage, from data presented by the Japan International Biological Program/Production Processes-Photosynthesis, Local Productivity

Group (1969, 1970, 1971). From the results shown in figure 2, the optimum N_{LA} at around 6 g/m^2 of N_{GA} can be estimated to be between 1.153 and 1.758 g/m^2, under a mean light intensity for the heading time of rice with upright leaves in Japan. This difference between the estimated optimum N_{LA} and the observed mean N_{LA}, 1.16 mg/m^2, seems reasonable since the N_{GA} value reaches a maximum around heading and the mean values of N_{GA} before and after heading are smaller than 6.

In annual crop plants, i.e. rice, the N_{GA} is so small during the early stages of growth that leaves with lower N_{LA} values are effective in promoting growth and in bringing about a higher N_{GA} at later stages. But if the plants are not adequately supplied with water, leaves with higher N_{LA} values are needed to keep the water balance, regardless of the levels of N_{GA}.

Light intensity

Figure 2 shows that the advantage of leaves with higher N_{LA} values at high levels of N_{GA} is noticeable under high radiation intensity. Further increases in N_{GA} by improved methods of cultivation combined with high incident light intensity may pave the way for leaf canopies that exhibit high N_{LA} in addition to erect leaf distribution. Some modern varieties of rice and wheat actually exhibit high N_{LA} values with compact mesophyll tissues.

Under low light intensities, however, differences in P_{LA} between leaves with different N_{LA} are not marked. Low N_{LA} values of *O. officinalis* and allied species seem to be a result of adaptation to shady habitats. Their chlorophyll content per unit leaf area was fairly high for the nitrogen content.

ADAPTATION TO DIFFERENT TEMPERATURES

Leaves of winter types of wheat tend to show a more compact mesophyll structure than do spring types (Khan and Tsunoda, 1970*e*). The compactness of mesophyll tissues might have bearing on cold tolerance, in addition to drought resistance and nitrogen response stated above.

The effects of temperature preconditioning on leaf photosynthesis were observed with wheat (Khan and Tsunoda, 1970*b*) and with rice (S. Kishitani and S. Tsunoda, *unpublished*). In wheat, P_{LA} was higher in spring types in the warm season while it was higher in winter types in the cold season. In rice, decrease in P_{LA} due to a low temperature preconditioning of 17 C was most remarkable in indica varieties, such as Panbira, Taichung Native 1, IR8, and N-136. It is interesting that Calrose, which is grown in California and irrigated with cool water, showed the highest tolerance. Plant characters responsible for such differences are now under investigation. Size of sinks and photorespiration at low temperature might have a bearing.

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Discussion: Photosynthetic efficiency in rice and wheat

S. YOSHIDA: What is the nature of the effect of leaf nitrogen (N_{LA}) on leaf photosynthetic rate (P_{LA}) in terms of diffusion resistance of CO_2 transfer?

S. Tsunoda: High N_{LA} tends to be associated with a high density thickness of the leaf, and, generally speaking, high density thickness may increase the diffusion resistance. To have a lower gas-exchange resistance under such circumstances, a well-developed vascular system, including xylems, and a radiate, close arrangement of photosynthetic cells around the vascular bundles seems to be essential. The leaf structure of the wild wheat that I mentioned may serve as an example. With such a leaf structure, the water balance can be kept with a low gas exchange resistance, and we can expect a high photosynthetic rate.

K. HAYASHI: Please indicate the thickness and erectness of leaves of the variety that can perform well in both wet and dry seasons in Southeast Asian countries.

S. Tsunoda: We are discussing how to maximize the yield potential and, therefore, I pointed out the possibility of increasing yield by having leaves with a high density thickness under intensive cultural conditions and high light intensities. But, for wide adaptation to the current cultural conditions in the Southeast Asian rice-producing countries, including the low light levels of the wet season, canopies with erect, but relatively thin leaves seem desirable.

E. A. SIDDIQ: Thickness of leaf is considered to be negatively correlated with leaf area index. Do you find any difference in photosynthetic efficiency among erect-leaved types having thin and thick leaves?

S. Tsunoda: Genotypic increase in leaf thickness tends to be associated with a decrease in leaf area index, at least when moisture supply is well balanced. So, when we cannot expect to have an optimum or abundant leaf area index, canopies with thinner leaves may be more effective than canopies with thick leaves.

A. O. ABIFARIN: Is there any difference between the nitrogen content of the top leaves and the lower leaves?

S. Tsunoda: We used simple models for simulation without changing the nitrogen content of leaves within the depth of canopies. However, in actual rice canopies, top leaves may have a higher nitrogen content than the lower leaves. This difference may be effective to increase the photosynthetic efficiency of the canopies.

A. O. ABIFARIN: In light of your statement about wild species having high chlorophyll content and high light absorption rate, how do you explain the differences in grain yield of the species mentioned versus that of *O. sativa*?

S. Tsunoda: The species mentioned, *O. officinalis*, *O. minuta*, and *O. eichingeri*, are wild species and are poor grain-producers. Therefore, their grain yields cannot be compared with those of the cultivated varieties.

J. H. COCK: When we grew IR8 at one level of nitrogen we had N_{GA} values of about 12 to 20 g/m^2. As N_{GA} increased, N_{LA} decreased. There was no decrease in CGR as N_{GA} increased. Please comment.

S. Tsunoda: By N_{GA}, I meant the total leaf-nitrogen per unit ground-area. It is not the total nitrogen absorbed by the plant. In Japan the range of N_{GA} at the heading stage seems to be from about 3 g/m^2 up to a little more than 10 g/m^2. I cannot comment at this moment on the rice communities with such high N_{GA} values as you have observed.

L. T. EVANS: Since most of the protein in the leaves is ribulose diphosphate carboxylase, high N_{LA} presumably means high RUDPC, and if this is associated with high P_{LA}, it could imply that photosynthesis is limited by RUDPC content per unit leaf area. Our recent work with wheats from all evolutionary stages does not support this conclusion in that the highest P_{LA} rates were associated with average RUDPC contents. Therefore, I wonder if the relation you observed between N_{LA} and P_{LA} is only an indirect one; high N_{LA} could reflect small cell size and this, by increasing stomatal density per unit leaf area or by increasing the surface/volume ratio of cells, or in some other ways, may provide a more direct relation with P_{LA}.

S. Tsunoda: We have observed an association of RUDPC contents and P_{LA} values at the full expansion stage and in the course of leaf senescence with rice leaves. However, the number of varieties observed is limited and we have no data from wheat in this respect. To reach a conclusion, more observations are needed.

Efficiency of respiration

Akira Tanaka

Because the growth efficiency (unit dry matter produced per unit substrate used) of seedlings germinating in the dark was about 0.60, regardless of temperature or variety, it is difficult to believe that there is varietal difference in efficiency of respiration for growth. The growth efficiency of a photosynthesizing rice population was 0.6 during early stages of growth and it decreased at later stages of growth. The decrease was caused by an increase in the proportion of maintenance respiration and also by retranslocation of substances from old organs to new organs. A population with good plant type probably has a small proportion of maintenance respiration and a high growth efficiency even at later growth stages. Limitation in sink size in comparison with activity of source causes accumulation of photosynthetic products and acceleration of uncoupled respiration, which result in a decrease of growth efficiency and photosynthetic rate. Improvement of the efficiency of respiration should be approached through the plant type concept and from the source-sink theory. The first approach may not be feasible because many improvements along this line have already been made. The second approach, however, may have promise for raising grain yield beyond the level achieved through the plant type approach.

THE CONCEPT OF GROWTH EFFICIENCY

Respiration is often discussed as if it is a useless leakage of carbon to the environment. But it is indispensable. Respiration supports growth and maintenance of cells by providing a variety of carbon skeletons as well as energy as reduced co-factors and as nucleoside triphosphates. The energy is also used for absorption of nutrients and translocation and redistribution of substances.

In addition to essential respiration, there is also wasteful respiration. How can coupled (useful) respiration be increased and how can uncoupled (wasteful) respiration be decreased, so that growth can be favorably influenced? The crux of this question is whether variability exists in efficiency of respiration that can be used in breeding varieties for higher yields. Information about efficiency of respiration, however, is extremely limited. For this reason, discussion in this paper is more or less speculative, rather than a presentation of available information.

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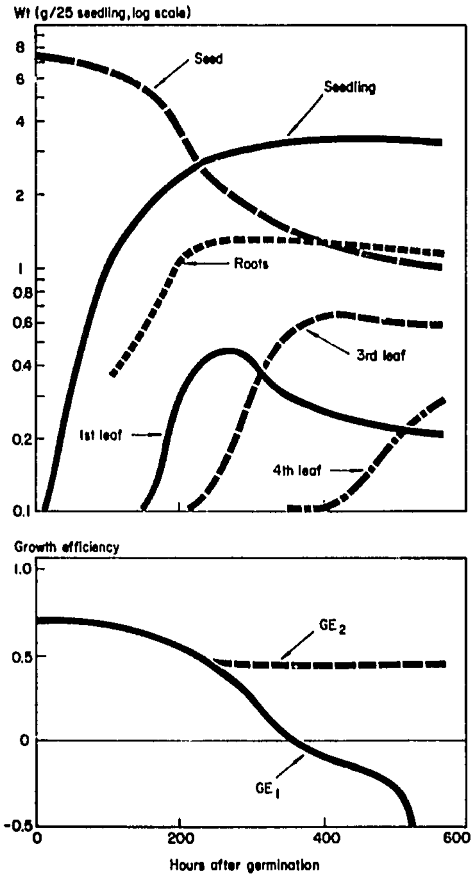
In discussing dry matter production (ΔW) the equation $\Delta W = P\text{-}R$, where P and R are photosynthesis and respiration, is generally used. Because of this expression, it is generally considered that P is gain and R is loss.

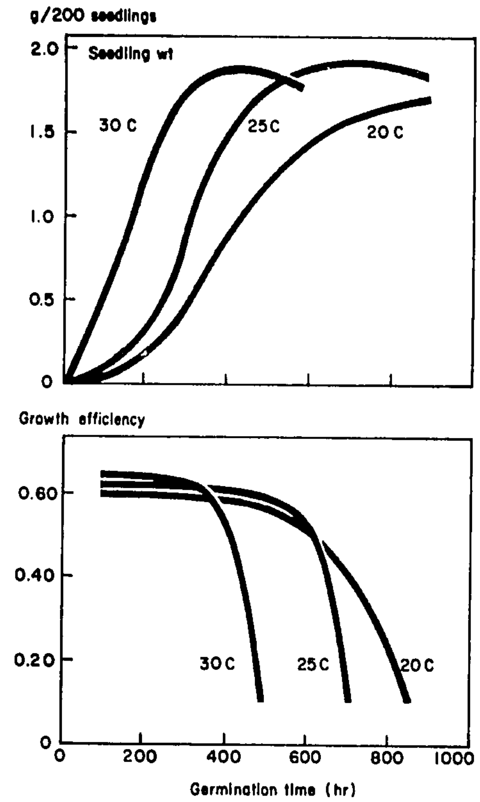
To express the efficiency of respiration quantitatively, the term "growth efficiency" (GE) was introduced: $GE = \Delta W/(\Delta W + R)$ (Tanaka and Yamaguchi, 1968*a*). In growing plants whose dry matter production depends mostly on photosynthesis, growth efficiency can be expressed as $\Delta W/P$, because the raw materials for dry matter production are mostly immediate products of photosynthesis. In other words, $\Delta W = P(GE)$. If the growth efficiency is constant, dry matter production is a simple function of P.

Respiratory usage in plants is frequently taken to be one-third of the total CO_2 assimilated in estimating potential dry matter production (Loomis and Williams, 1963). With this assumption, $GE = 2/3$, and $\Delta W = 2/3\ P$. However, the growth efficiency is not always constant. Thus, the factors controlling the growth efficiency should be studied more in detail.

Growth efficiency, defined here, is similar to the relative yields which is the ratio between the weight of the end-product and the weight of the initial product, $\Delta W/\Delta W + R$, defined by F. W. T. P. de Vries (*unpublished*).



1. Growth and the changes in growth efficiency of maize seedlings germinating in the dark (GE_1 = growth efficiency calculated on the bases of weight of seedlings and seeds; GE_2 = growth efficiency calculated on the bases of weight of organs gaining or losing weight).



2. Growth and growth efficiency of rice seedlings grown in the dark at various temperatures.

GROWTH EFFICIENCY OF GERMINATING SEEDLINGS

The most simple measurement of growth efficiency is with seedlings germinating in the dark, in which all materials for growth are components of seeds. In this case ΔW is the final weight of seedlings, and $\Delta W + R$ is the loss of weight by the seeds.

Maize seeds were germinated in the dark and the weight of seeds and of seedlings were determined with the course of germination. The growth efficiency remained at about 0.65 until the substances for growth of seedlings in the seeds had been exhausted (fig. 1) (Tanaka and Yamaguchi, 1969). When rice seeds were germinated in the dark at various temperatures, the growth rate of seedlings was higher at 30 C than at 20 C and active growth was discontinued earlier. But, the growth efficiency was about 0.60 regardless of temperature so long as active growth of seedlings continued (fig. 2). When temperature was as low as 15 C or as high as 40 C, the efficiency was lower. Thus, it can be concluded that although temperature has significant effect on the rate of growth, the efficiency of respiration for growth of seedlings remains constant within a certain range of temperature. Temperature affects the rate of respiration and of growth, but does not alter the efficiency of respiration.

The growth efficiency of soybean seedlings germinating in the dark was 0.73, and for maize seedlings, 0.65. The value for soybean was apparently

Table 1. Weight and growth efficiency of seedlings of two rice strains having different seed weight.

Strain	Seed weight (g/1000 seeds)	Seedling weight (g/1000 seedlings)	Growth efficiency
338	11.3	1.15	0.605
448	31.4	2.35	0.610

higher than that observed in rice (Tanaka and Yamaguchi, 1968*b*). It was also reported that the efficiency was 0.90 for peanuts and about 0.65 for maize and bean. These values were not changed by temperature (F. W. T. P. de Vries, *unpublished*). These differences among species might be attributable to the differences in composition of seeds. Seeds of soybean or peanut are high in fats and those of rice and maize are high in carbohydrates. If the substrates of respiration are different, the efficiency of respiration may also differ.

With microorganisms it is reported that 1 mole of ATP produced by respiration leads to the production of 10 g of dry matter (Bauchop and Elsdem, 1960). Assuming that 38 moles of ATP is produced from 1 mole of glucose by aerobic respiration, growth efficiency can be estimated to be 0.68. This means that the efficiency of aerobic respiration in dry matter production is almost the same for microorganisms as for higher plants.

Seeds of two rice strains that have different seed size were germinated in the dark for 10 days. The strain that had larger seeds produced larger seedlings than the strain that had smaller seeds, but the growth efficiency was the same for both strains (Table 1).

Seeds of maize populations, which were 13 combinations of parents and their F_1 hybrids, were germinated in the dark. There was no heterosis in the seed weight. Heterosis in the seedling weight was significant, but no heterosis was observed in the growth efficiency. Examples of the data are given in Table 2 (Tanaka and Hayakawa, 1971).

From these preliminary observations, it can be speculated that varietal difference in the growth efficiency of seedlings growing in the dark is negligible,

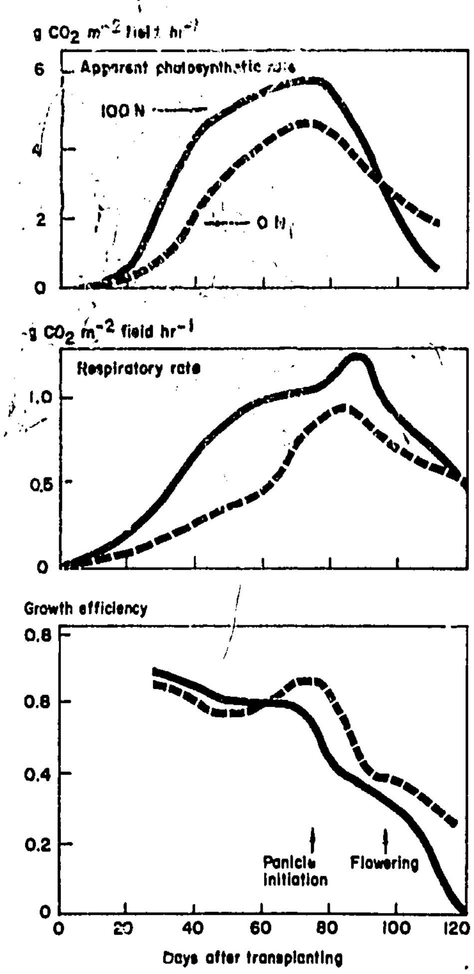
Table 2. Weight and growth efficiency of maize seedlings in parents and their F_1 hybrids.

Population	Seed wt (g/100 seeds)	Seedling wt (g/100 seedlings)	Growth efficiency
W9 (P_1)	17.0	2.06	0.73
WM13^R (P_2)	19.8	2.12	0.66
W9 x WM13^R (F_1)	18.5	3.22	0.71
Ma 21547 (P_1)	16.8	2.41	0.62
C13 (P_2)	30.7	2.81	0.68
Ma 21547 x C13 (F_1)	22.2	3.58	0.66

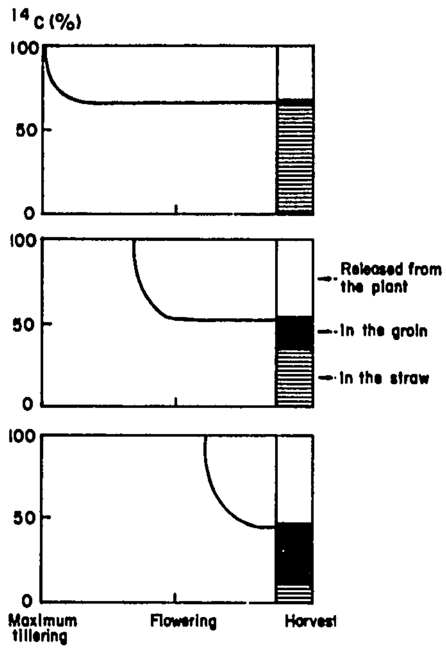
even if there are differences in the growth rate of seedlings or seedling vigor. The efficiency of respiration is the same among varieties although the rate is different due to differences in the amount of substrates, the condition of growth regulators, etc.

GROWTH EFFICIENCY DURING GROWTH

Rice plants were grown in the field with and without nitrogen application. The rates of dry matter production and of respiration were determined and the growth efficiency at successive stages of growth was calculated (Tanaka and Yamaguchi, 1968*a*). The rates of apparent photosynthesis and of respiration of the population were low at early growth stages. They increased gradually as the plants grew, attained their maximum at about booting, and then decreased (fig. 3). These rates were higher with added nitrogen than without added nitrogen at early growth stages. This trend was reversed by the end of growth, however. These tendencies are similar to those reported earlier by several authors (Takeda,



3. Growth efficiency of a Peta population at 0 and 100 kg/ha N.



4. The fate of carbon assimilated at different stages of growth.

1961). At early growth stages the growth efficiency remained at about 0.60, it started to decrease after panicle initiation, and it continued to decrease until the end of growth. Growth efficiency was slightly higher with added nitrogen than without it at early growth stages, but this trend was reversed at later stages.

These tendencies were confirmed by the fate of carbon assimilated at different growth stages. At various growth stages, $^{14}CO_2$ was fed to a rice population and the release of $^{14}CO_2$ from plants by respiration and the ^{14}C in the plant at harvest were determined. The release of $^{14}CO_2$ was rapid for about 5 days after $^{14}CO_2$ treatment and then became extremely slow. Based on the amount of carbon assimilated at early growth stages, about 60 percent of the carbon remained in the plant until harvest. The percentage was lower when the carbon was assimilated at later growth stages (fig. 4) (Lian and Tanaka, 1967). Figure 4 also shows that the carbon assimilated after flowering went to the grains more efficiently than the carbon assimilated at early growth stages.

The amount of carbon respired by the panicle at the milky stage was estimated to be about 15 percent of the amount of carbon which was translocated into the panicle. The high growth efficiency value of the panicle during ripening occurred because the substance produced is mostly starch. Formation of starch from sucrose, which is the major substance translocating into the grain, requires less energy than the formation of protein, etc.

It has been demonstrated that retranslocation of substances from decomposing old organs to growing new organs causes a decrease of growth efficiency. Figure 1 presents a case of low growth efficiency when re-use of substances occurs. When the substances for growth in the seeds are exhausted, materials in old leaves or roots start to be reused for the growth of new organs. The weight of old organs decreases and that of new organs increases. If the growth efficiency is computed from the increased weight of new organs and the decreased weight of old organs, it remains about 0.5 for a long time. Here, the substrates for respiration or for growth are different from those in the seeds. Re-use of substances in vegetative organs for grain development is indicated, and this may be one reason for the low growth efficiency of the whole plant after flowering.

These data demonstrate that the growth efficiency of photosynthesizing rice plants is about 0.6 when the vegetative organs are growing actively, and it decreases during the reproductive phase or during ripening. After initiation of panicle primordia the internodes elongate and the growth rate of leaves decreases. After flowering, grain development progresses rapidly, but the weight of vegetative organs decreases. During these periods the growth efficiency of the reproductive organs themselves is high, especially when the starch is formed in the grain, but the growth efficiency of a whole plant is small, because of re-use of substances in vegetative organs, respiration of elongated internodes, and limited storage capacity.

PLANT TYPE AND MAINTENANCE RESPIRATION

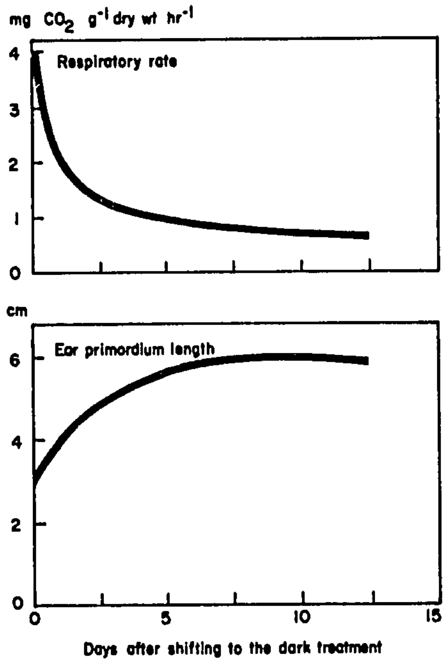
The efficiency of respiration of a population is frequently expressed as P/R. The P/R can be written as $f \times p_0 \times LAR/r$, where f is the light receiving coefficient of the population; p_0, the photosynthetic rate per unit leaf area; r, the respiratory rate per unit plant weight; LAR, the leaf area ratio (Osada and Murata, 1962). From this expression, growth efficiency can be written as $1 - r/f \times p_0 \times LAR$. This expression demonstrates that the growth efficiency is the function of r, p_0, and the plant type which can be expressed by f and LAR. Of course real phenomena are not so simple because these parameters are not independent and they interact with each other. Nevertheless, it is quite possible that growth efficiency is influenced by plant type.

Considering plant type in relation to growth efficiency, the respiration of organs which are not directly linked with growth should be examined. Respiration can be divided into two categories: for growth and for maintenance.

Energy is needed to keep existing structures functioning. Turn-over of molecules, especially of proteins, is always taking place, and consumes energy. The turn-over rate has been estimated to be 5 to 10 percent of protein per day (F. W. T. P. de Vries, *unpublished*).

Maize plants at the tassel-initiation stage were placed in the dark, and the respiratory rate and the length of the tassel primordia were determined successively with time. The elongation of the primordia stopped after 5 days. At this stage the respiratory rate was about 1 mg CO_2 hr^{-1} g^{-1} dry matter (fig. 5) (Yamaguchi and Tanaka, 1970). This rate may be considered the respiratory rate without growth, in other words, the maintenance respiration. With the given experimental condition, it occupies about 25 percent of the total respiration.

Maintenance respiration takes place whether the plant is growing or not. It occupies only a small portion of the total respiration when the plants are



5. Changes in respiratory rate and length of ear primordium after shifting a maize plant to the dark.

young and growing rapidly. Under such conditions the growth efficiency of the rice plant remains at about 0.6. But, at later growth stages, elongated internodes and mutually shaded lower leaves occupy a large proportion of the total plant weight and the respiration of these organs occupies a large proportion in the total respiration. In this sense, growth efficiency is the function of the proportion of the respiration for maintenance to the total respiration. The proportion is influenced by the plant type. Populations supplied with nitrogen have larger elongated internodes and also more mutually shaded lower leaves at later growth stages. This condition results in a higher proportion of maintenance respiration, and a smaller growth efficiency (fig. 3). For the same reason, varieties that are tall and leafy have a larger proportion of maintenance respiration and low growth efficiency (Table 3) (Tanaka, Kawano, and Yamaguchi, 1966).

These discussions suggest that the story of varietal difference in the efficiency of respiration is much the same as the story of varietal difference in plant type.

OPTIMUM LAI AND CEILING LAI

Nitrogen application increases the nitrogen content of leaves. Increase of the protein content of leaves causes an increase of p_0 as well as of respiratory rate, and the p_0 and the respiratory rate per unit leaf area are positively correlated (Murata, 1961). If this is true, growth efficiency may be kept constant. Under some circumstances, such as under low light intensity, however, the decrease in p_0 is more than the decrease in respiratory rate, and this tendency is more prominent when more nitrogen is supplied (Navasero and Tanaka, 1966).

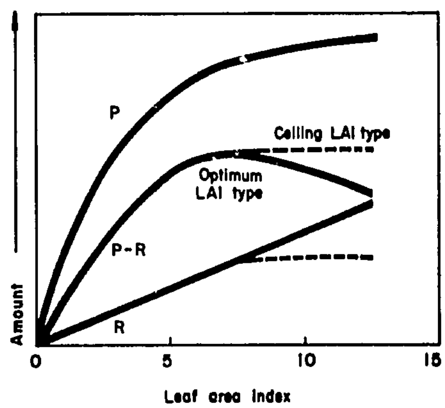
Table 3. Growth efficiency during ripening of populations of four rice varieties with different plant type.

Variety	Plant ht (cm)	Growth efficiency
Hung	222	0.32
Century Patna 231	174	0.47
Chianung 242	149	0.48
Taichung Native 1	122	0.53

With maize plants, Yamaguchi and Tanaka (1970) also demonstrated that when plants are supplied with excess nitrogen, the respiratory rate is high and growth efficiency is low because under such conditions more protein is produced which requires more energy for production and for maintenance. Such discussions are not realistic however. Nitrogen application also causes an increase in leaf area and which in turn, causes various changes in the crop environment.

Let us consider the classic concept of the optimum leaf area index. It stipulates that with an increase in the LAI of a population, P increases more or less proportionally until higher values of LAI are reached when the rate of increase of P decreases because of mutual shading of leaves. On the other hand, R increases almost proportionally to the increase in LAI because it is generally considered to be uninfluenced by mutual shading. For these reasons, dry matter production, which is $P-R$, reaches maximum at the optimum LAI (fig. 6) (Takeda, 1961).

The upper leaves of maize plants at tasseling were fed with $^{14}CO_2$ and the release of $^{14}CO_2$ by respiration from various organs at 3 days after feeding was determined. The release was most active from the ear and only a small portion of the respiration took place in lower parts of the plant or in the roots. But when the lower leaves were shaded, the release of $^{14}CO_2$ from the roots and the



6. Schematic explanation of optimum LAI and ceiling LAI. (P = photosynthesis, R = respiration.)

Table 4. Release of ^{14}C by respiration from various plant parts at 3 days after $^{14}CO_2$ feeding from upper leaves as affected by shading of lower leaves in maize plants (percentage on the bases of total ^{14}C released from the plant).

Treatment of plant parts	Control (%)	Shaded (%)
Ear	56.0	32.2
Upper leaves	18.3	11.1
Upper culm	9.4	6.4
Lower leaves	0.8	1.5
Lower culm	6.0	11.3
Roots	9.5	38.5
Total	100.0	100.0

lower internodes became large (Table 4). The use of photosynthetic products by the respiration of the lower culm and roots may be one reason for the existence of optimum LAI. These data demonstrate that the loss of carbon by respiration from shaded lower leaves is rather limited.

Another conceivable explanation of optimum LAI is the decrease of p_0 when leaves are shaded for a prolonged period (Tanaka and Kawano, 1966).

Optimum LAI has been repeatedly observed in populations of leafy rice varieties. However, S. Yoshida (*unpublished*) reported that no optimum LAI exists in populations with good plant type, such as IR8. Rather there is a ceiling LAI. The ceiling LAI means that no change of dry matter production occurs as LAI increases above the ceiling LAI. The explanation for the existence of ceiling LAI is that with an increase of LAI, the plant weight increases, but the respiratory rate per unit plant weight decreases. Thus, R increases with an increase of LAI till a certain LAI value is reached, and above that value R remains constant, and $P-R$ is also constant (fig. 6).

When maize plants were grown at graded levels of light intensity by giving shading treatment (Yamaguchi and Tanaka, 1970) decrease in light intensity caused a decrease in photosynthesis which was accompanied by a proportional decrease in respiration and dry matter production (fig. 7). Thus, growth efficiency remained almost constant within a wide range of light intensity. When light intensity is extremely low, however, the level of carbohydrates in the plant becomes low and nitrogen compounds become the substrate of respiration. Under such conditions, growth efficiency becomes low.

It must be mentioned that growth efficiency remained constant within a wide range of light intensity. This means that respiration is a function of photosynthesis. The respiratory rate per unit plant weight is higher when the substrate of respiration is more abundant. Under low light intensity or at a large LAI, the respiratory rate may become smaller because the substrate for respiration does not accumulate in organs, especially in the lower leaves, lower culm, and roots. With these conditions, the ceiling LAI exists.

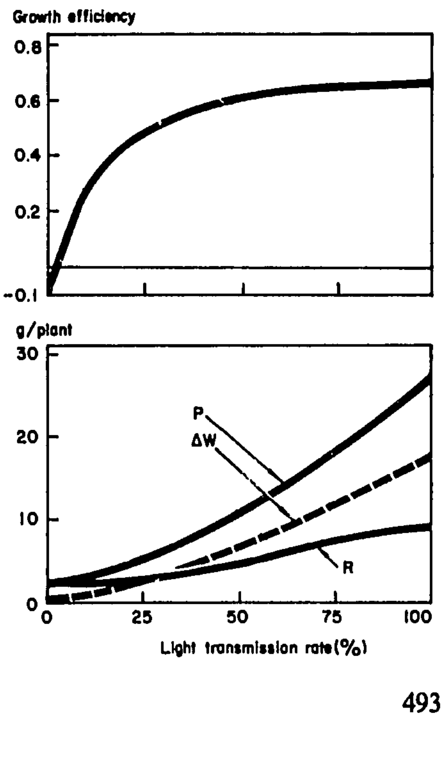
A change of respiratory rate in response to the photosynthetic rate is important in deciding whether there is an optimum LAI or ceiling LAI.

This discussion leads to the conclusion that populations of varieties with good plant type have a ceiling on LAI and those of inferior plant type have an optimum LAI. With the ceiling type of LAI, growth efficiency is kept constant under wider range of LAI values, and with the optimum LAI type growth efficiency decreases, if LAI exceeds the optimum. The ceiling type of LAI is much better than the optimum LAI because with the former excessively cloudy weather has no adverse effect.

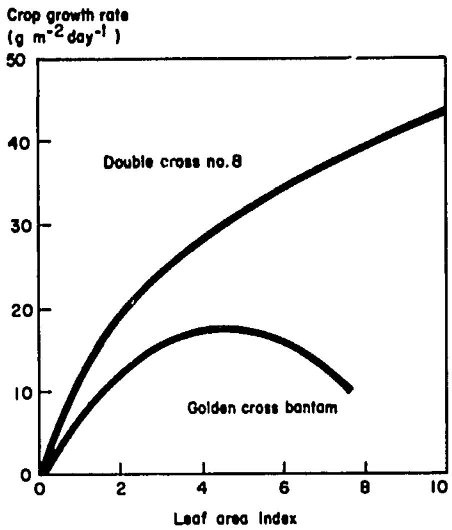
THE SOURCE-SINK THEORY

Tsuno and Fujise (1965) argued that the photosynthetic rate of a leaf is a function of the velocity of photosynthate removal from the leaf. Removal of the sink—for example, removal of panicle during ripening—causes an immediate decrease in photosynthetic rate (King, Wardlaw, and Evans, 1967). When the sink is smaller than the source, photosynthetic products accumulate in leaves and in conductive tissues. This accumulation promotes respiration and retards photosynthesis (Tanaka and Fujita, 1971).

From this evidence it can be concluded that the sink is the cause and the source is the result. This statement, however, contrasts with the statement I made earlier that the respiratory rate is a function of the photosynthetic rate. These arguments are somewhat similar to the story of the chicken and the egg. The answer depends upon conditions.

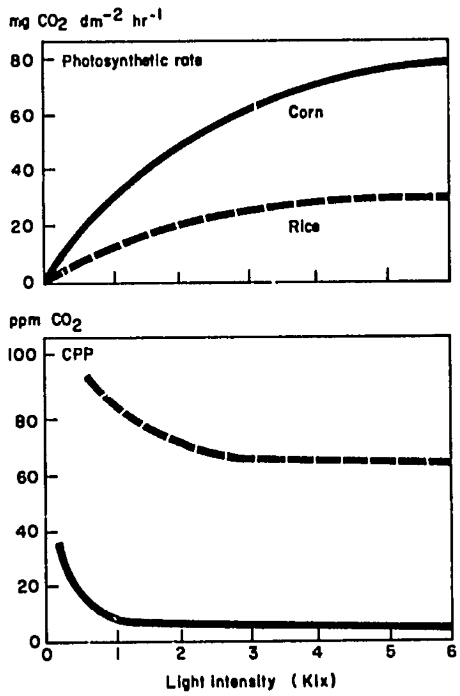


7. Effect of shading on photosynthetic rate (P), respiration (R), dry matter (ΔW), and growth efficiency.



8. Relation between leaf area index and crop growth rate of two corn varieties during ripening.

These points shed light on the existence of optimum LAI. With an increase in planting density or nitrogen application, increases in LAI and spikelet number take place proportionately: the increase in LAI value results in a proportional increase in the photosynthetic rate of the population, which is accompanied by a proportional increase in respiration. Growth efficiency thus remains constant and the grain yield increases proportionally to the increase in photosynthetic rate. Under such condition the ceiling LAI exists.



9. Response to light intensity of photosynthetic rate and CO_2 compensation point (CCP) of rice and maize leaf.

On the other hand, if the increase of spikelet number (the sink size) can not catch up with increase in LAI, photosynthetic products accumulate in the vegetative organs, and the accumulation promotes respiration and retards photosynthesis. Under such conditions optimum LAI exists. For example, populations of some maize varieties at high planting density have a high percentage of barren plants and high sugar content in the culm. On the other hand, in some varieties, the barren plant percentage is low even at high density and the ceiling LAI is observed (fig. 8) (Tanaka, Yamaguchi, and Yamagami, 1970).

In this connection, Yoshida and Ahn (1968) reported that a high content of sugars occurs in the culm at flowering in tropical rice, especially in the wet season. The carbohydrates that accumulate in the culm have been reported to be mostly starch in temperate rice. With accumulation of sugars there may be more chance for respiratory leakage than with accumulation of starch.

Nakayama (1969) demonstrated that senescence of rachilla causes senescence of grains. Senescence of rachilla causes weakening of the sink, which in turn results in a decrease in photosynthetic rate and in growth efficiency. Extension of the ripening period is one important way to increase grain yield. Senescence of the sink may be a major problem in making the duration longer.

To improve the efficiency of respiration at a high LAI, not only the concept of plant type, but also the source-sink theory, may be useful.

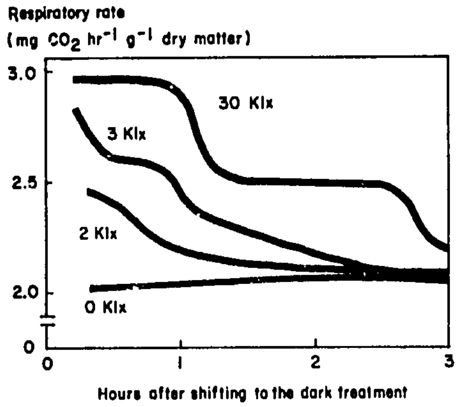
NATURE OF RESPIRATION

The discovery of a large difference in p_0 between one group of plants and another opened an important avenue of study. Higher plants are divided into two groups, the "efficient group" and the "non-efficient group." Maize, sugarcane, sunflower (Hesketh and Moss, 1963), bahiagrass, and bermudagrass (Murata and Iyama, 1963) belong to the efficient group, while rice belongs to the non-efficient group. The efficient group has a high p_0, does not have photorespiration, and has a low CO_2 compensation point (CCP). The p_0 and CCP of rice and maize are illustrated in figure 9.

The respiratory rate of rice plants in the dark was higher when the light intensity immediately before the measurement was higher (fig. 10). But the difference disappeared within a few hours period in the dark (Yamaguchi and Tanaka, 1967). Perhaps rice plants have photorespiration and perhaps there are two types of substrates for respiration, i.e. direct products of photosynthesis and reserved substances.

Scientists are now interested in comparing the p_0 or the CCP among species or among varieties of a species. There is no doubt that varietal differences in p_0 exists, but the significance of the differences in relation to dry matter production or to grain production is still obscure. The p_0 of active maize leaves at high light intensity is about twice that of rice. No such large consistent difference between these two crops has been demonstrated in the net assimilation rate however.

Assuming that the respiratory rate in the light is the same as in the dark, the growth efficiency is more or less the same, 0.6 to 0.7, for rice and maize. On the other hand, if maize plants do not respire in the light as actively as in the dark, the growth efficiency should be much higher in maize than in rice.



10. Changes in respiratory rate of rice plants subjected to different light intensities before being moved to the dark.

It seems simple to consider that the higher the p_0 of a variety, the more likely it is to produce high yield. Thus a variety that has a high growth rate, by implication, is a good variety, but much evidence contradicts this statement. Jennings and Jesus (1968) and Kawano and Tanaka (1969) showed that excess vegetative vigor is frequently associated with low nitrogen response.

The story is really not so simple. The p_0 of a leaf fluctuates with age and cultural condition. It is also different in leaves at different positions in a plant. The influence of these factors on the p_0 are not exactly the same among varieties. Thus, under what conditions varietal comparison of p_0 can be made should be answered before any breeding effort is made along this line. It must be determined whether the p_0 is under direct genetic control.

The changes in the respiratory rate of various organs and in photosynthetic rate per unit leaf area under different physiological conditions must be more widely studied to provide a full understanding of the efficiency of respiration. Preliminary observations have demonstrated that plants suffering from nitrogen or phosphorus deficiency have low growth efficiency. These phenomena indicate that the pathway of respiration changes under conditions of nutrient deficiency. There is also evidence that uncoupled respiration increases under stress conditions, such as drought, existence of toxic substances, and disease infection. These points should also be clarified.

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Discussion: Efficiency of respiration

L. T. Evans: I agree with your analysis that plants may be very similar in their respiratory conversion efficiencies regardless of genotype or environmental conditions, but may differ in maintenance respiration as a function of their growth habit. But these latter differences may not always be in the direction as you have described and illustrated in figure 3. For example, we have found stem respiration rates (per gram of dry weight) to be three times higher in dwarf wheats than in tall ones. Are there similar differences among rice varieties?

A. Tanaka: I have no data.

L. T. EVANS: Do you have any direct evidence that uncoupled respiration occurs in rice when assimilates accumulate? For example, when the sink is removed, does flag leaf respiration rise? We found no evidence that this occurred in wheat.

A. Tanaka: We found this type of phenomena in maize as stated in my paper.

T. H. JOHNSTON: Do you feel that growth efficiency can be affected to a considerable degree by split applications and time of topdressing of nitrogen fertilizer, especially with moderately leafy varieties?

A. Tanaka: If the manipulations of nitrogen application result in a substantial change in plant type, my answer is yes.

Storage capacity as a limitation on grain yield

L. T. Evans

Feedback interactions between photosynthesis, translocation, and storage make it difficult to determine which limits yield most, but several lines of evidence suggest that in wheat, storage capacity is a major limitation to grain yield. An estimate is made of the potential yield of rice in relation to incident radiation: the crop growth rates from an intermediate step in the calculation are close to maximum recorded rates, but actual grain yields are substantially below those estimated, suggesting that storage capacity may also limit grain yield in rice. Variations in four yield components -- inflorescence per unit area, spikelets per inflorescence, grains per spikelet, and grain volume and weight -- are examined for both wheat and rice. In rice the first two, the earliest to be determined, are the dominant variables, whereas in wheat all four vary substantially. Storage capacity in wheat is therefore more responsive to environmental conditions during the later stages of crop development. All yield components are strongly influenced by light intensity, but the effects are only partly in response to changed supply of assimilates. Photomorphogenic and correlative processes are also important, and require further investigation. Since spikelet number per inflorescence in wheat varies considerably with the rate of floral induction, insensitivity to daylength may therefore affect spikelet number and grain storage capacity.

INTRODUCTION

The evolution of wheat, from a wild diploid grass to hexaploid cultivars, has been accompanied by a fivefold increase in weight per grain (fig. 1) and an even greater increase per ear, without any increase in photosynthetic rate or relative growth rate (Evans and Dunstone, 1970). In essence, then, evolution in this crop, as in many others, has been characterized by a progressive increase in the storage capacity of, and investment in, the organs of use to man. With highly evolved crops. therefore, we may have reached the point where yields are as much limited by photosynthetic or protein synthetic capacity as by capacity for storage. Indeed, many plant breeders favor the view that the supply of photosynthetic assimilates primarily limits yield.

One reason for this idea is the negative correlation frequently observed between yield components. A striking example for rice is the decrease in spikelets per panicle as the number of panicles increases (Matsushima, 1970,

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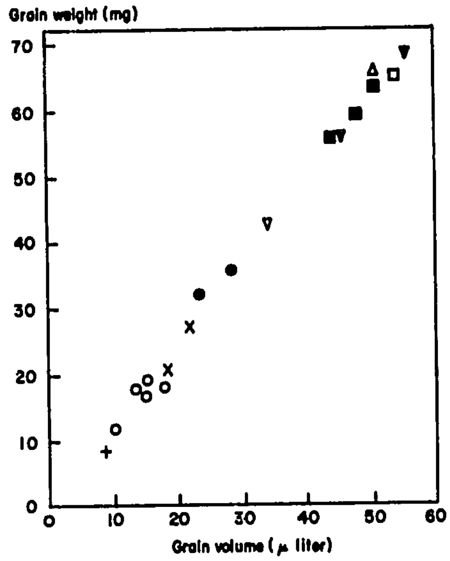


1. Relation between weight per grain and volume per grain for a range of wild and cultivated wheats and related species: x = *Aegilops speltoides*, + = *A. squarrosa*, ○ = *Triticum boeoticum*, ● = *T. monococcum*, ▽ = *T. dicoccoides*, △ = *T. dicoccum*, ▼ = *T. durum*, □ = *T. spelta*, ■ = *T. aestivum* (unpublished data of R. L. Dunstone and L. T. Evans).

p. 151). Adams (1967) pointed out, however, that such negative correlations do not necessarily imply an overall limitation by assimilate supply. In his experiments the negative correlations were lowest in the highest yielding lines, and had little to do with establishing actual yield levels. In fact it is extremely difficult to determine whether yield is limited by the capacity for photosynthesis, by the capacity for translocation, or by the capacity for storage because of pronounced and rapid feed back interactions between these processes.

After examining briefly some of these effects, we will consider evidence which suggests that photosynthetic capacity may not limit grain yields in wheat and rice and then discuss the various components of storage capacity in these two cereals.

INTERDEPENDENCE OF PHOTOSYNTHESIS, TRANSLOCATION, AND STORAGE

Photosynthetic rate responds to the demand for assimilates. For example, during grain-filling in wheat plants, when most of the assimilate from the flagleaf is translocated to the ear, removal of the ear leads to an accumulation of assimilates in the flagleaf and to a fall in its photosynthetic rate to about half the initial rate within hours. If the lower leaves are shaded, so that the flagleaf has to support the rest of the plant, the assimilate is exported at a high rate again and the photosynthetic rate rises to its original level (King, Wardlaw, and Evans, 1967). Such pronounced feedback effects have not always been found probably because alternative sinks for assimilates, such as young tillers, were present. But even in intact plants, alternative sinks are not always available and feedback effects on photosynthesis may occur as they do in wheat at about anthesis. At that stage, when tillering and growth of stem have slowed but grain growth has not begun, flagleaves export less of their assimilates (Rawson and Hofstra, 1969), and their photosynthetic rates may fall by more than 30 percent before rising again as grain growth increases (Evans and Rawson, 1970; Rawson and Evans, 1971). Since leaf photosynthetic rates can reflect the demand for assimilates, varietal differences in photosynthetic rate or leaf area duration, which parallel differences in yield, may do so not because the supply of assimilates limits yield, but because higher storage rates elicit higher photosynthetic rates.

Demand for assimilates can also influence the rate, velocity, and pattern of translocation in wheat (Wardlaw, 1965; Rawson and Evans, 1970) and presumably in other plants. Photosynthesis, translocation, and storage are so closely interdependent that it is difficult to determine which limits yield most.

DOES PHOTOSYNTHETIC CAPACITY LIMIT YIELD?

Several lines of evidence suggest that yield in wheat is not limited by photosynthetic *capacity* even in highly productive modern varieties. First, evolution in wheat has been accompanied by a progressive fall in photosynthetic rate (Evans and Dunstone, 1970; Khan and Tsunoda, 1970) and even among modern varieties there is no clear relation between photosynthetic rate and yield. Admittedly, leaf size has increased at a faster rate than photosynthesis has fallen in the course of evolution, but since ear size has increased even more than leaf size, the supply of assimilates could not have been limiting.

Second, balance sheets of the supply and demand for assimilates throughout grain development, for several productive varieties grown under controlled conditions, show that even at the period of peak demand ample amounts of assimilates were available for grain filling (Evans and Rawson, 1970).

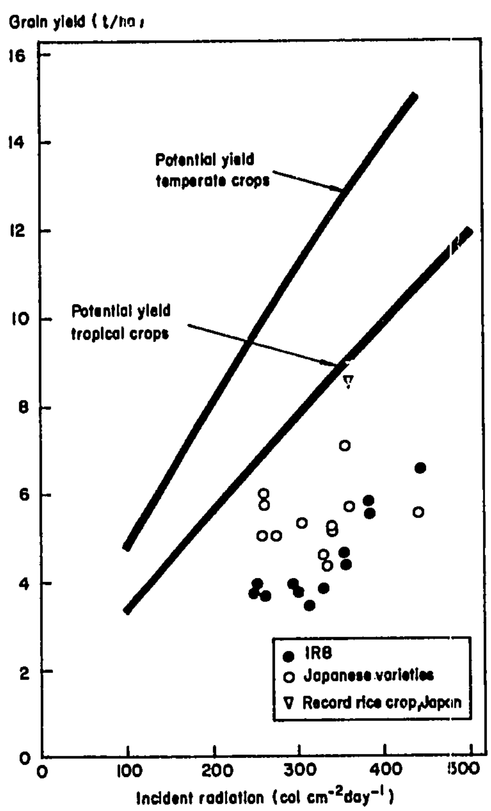
Third, both in the field and under controlled conditions, shading or leaf-removal treatments have had only small effects on grain growth and yield, implying that the supply of assimilates was not limiting. In our experiments with several Mexican wheats, for example, increases in the rate of flagleaf photosynthesis and in the mobilization of stem reserves compensated for inhibition of ear photosynthesis (Rawson and Evans, 1971). Another indication of surplus supply of assimilates is the almost linear increase in grain weight per ear during the middle period of grain filling under controlled temperature in spite of substantial variations in incident daily radiation. We have found this linear increase in Triple Dirk wheat (Rawson and Evans, 1970); it has been noted also in maize (Duncan, Hatfield, and Ragland, 1965).

Fourth, treatments involving sterilization of the most advanced florets in ears of Triple Dirk wheat at anthesis unexpectedly increased the total grain set and yield per ear by 20 percent or more (Rawson and Evans, 1970). One implication of these experiments is that assimilate supply does not limit grain yield.

Lowland rice lends itself to a different, but less conclusive, approach to the question of whether photosynthetic capacity limits yield. We are nearing the stage where photosynthesis in a field crop grown without stress from water and nutrient supply, diseases, pests, and extreme temperatures can be modelled and estimated reasonably well. With further assumptions about the extent of respiration losses and mobilization of reserves, we can estimate the amount of assimilates that are available for grain filling (i.e. the potential yields when storage capacity is not limiting, at various radiation levels) and that can be compared with the actual crop growth rates and grain yields. Such a comparison is made in figure 2.

Estimates of potential rice yields have also been made by Murata (1965*b*) and by Tanaka, Kawano, and Yamaguchi (1966). There are substantial differences between their assumptions and mine. The potential yield estimates in figure 2 are based on the following assumptions:

1. Forty-five percent of the incident radiation is active in photosynthesis.
2. Ten percent of this visible radiation is lost by reflection or absorbed by photosynthetically inert components within a closed crop canopy (Yocum, Allen, and Lemon, 1964; Loomis and Williams, 1963).
3. Eight quanta are required to reduce each molecule of CO_2; over the visible spectrum this is equivalent to an average conversion efficiency of 26 percent.
4. As light intensity increases, some light saturation becomes evident at atmospheric CO_2 levels; the extent of reduction below the eight-quantum rate



2. Relation between grain yield of rice and incident radiation during the period of grain filling. Actual grain yields were all reduced by 14% to allow for moisture content. Variety IR8 was broadcast-seeded at Los Baños 1968/69 with 120 kg/ha nitrogen, 30 kg/ha P_2O_5 (De Datta and Zarate, 1970). The published yields were for rough rice and have been reduced by 19% to allow for glumes. The Japanese varieties were grown at several sites in Japan, 1968 (Japan International Biological Program/Production Processes-Photosynthesis, Local Productivity Group, 1970). The record rice crop was made with variety Ootori, in Japan, in 1960 (Y. Murata, *personal communication*). The solid lines give estimates of the maximum potential yields of rice, based on assumptions described in the text.

was estimated from data for wheat communities (King and Evans, 1967) and compared with curves of photosynthesis and light intensity for communities of rice examined by Tanaka et al. (1966). Murata (1965*b*) did not allow for such light saturation, which can be substantial at high intensities.

5. A conversion factor of 3,500 cal/g dry weight was taken.

6. Respiration losses were estimated as the sum of two terms (McCree, 1970): i) a maintenance term for protein turnover, ion uptake, translocation etc., equivalent to 1.5 percent (temperate crops) or 2 percent (tropical crops) per day of the accumulated dry weight (taken as 1 kg/m^2), and ii) a storage term of 32 percent of the residual gross photosynthesis representing an average cost for the conversion of sugars into plant tissue (Penning de Vries, *unpublished data*). For cereals during grain filling the cost of conversion may be lower, because much of the newly synthesized material is starch for which the efficiency of conversion is high. Nevertheless, the total respiration loss estimated in this way agrees well with that measured by Tanaka et al. (1966).

7. Grain filling was assumed to continue for 30 days in the temperate zone and for 21 days in the tropics, and to receive 90 percent of the net assimilates during that period. For the record rice crop of "Ootori" in Japan, however, the interval between anthesis and maturity was 53 days. The period of active grain filling is likely to be much shorter than the period between anthesis and grain maturity (Daynard, Tanner, and Duncan, 1971).

8. Of plant material accumulated before anthesis, 20 percent was assumed to move to the grain in rice. With a standing crop of 1 kg/m^2, these reserves would be 2 t/ha, as assumed by Tanaka et al. (1966), but much less than Murata's (1965*b*) assumption that reserves are equivalent to net photosynthesis from the preceding 2 weeks. Tanaka et al. (1964, p. 16) found up to 20 percent carbohydrate in rice straw at flowering, and some data of De Datta, Tauro, and Balaoing (1968, p. 645) also suggest that mobilizable reserves in rice are about 2 t/ha.

The reasonableness of the first six assumptions can be tested by comparing estimated crop growth rates with the highest actual rates measured. At 500 cal cm^{-2} day^{-1}, the estimated rate was 55.5 g m^{-2} day^{-1}, which is very close to the highest rate actually found by Tanaka et al. (1966), 55.4 g m^{-2} day^{-1} under 564 cal cm^{-2} day^{-1}. While crop growth rate under favorable conditions is close to the estimated potential maximum, the grain yields in figure 2 are considerably lower, however, suggesting that either translocation or storage capacity is limiting. There are too many uncertainties in these estimates—for example in the terms for respiration and mobilizable reserves—for this conclusion to be compelling. But the estimates may give plant breeders some idea of how closely they are approaching the yield asymptote, and perhaps also persuade people not to expect more green revolutions.

Murata (1965*a*, p. 395) presented data showing a good correlation between the photosynthetic rate of flagleaves of six rice varieties and their crop growth rate, but little correlation between their photosynthetic rate and grain yield at a given level of nitrogen supply, again suggesting that the supply of assimilates did not limit yield. Data supporting this conclusion are given by Yin, Shen, and Shen (1958), and by Murata (1969, p. 240), at least for the 1961 crop in which yield was closely related to spikelet number per square meter, suggesting that storage capacity limited yield. In the 1962 crop, however, spikelet density was higher and yield was more closely related to the proportion of filled grains. In this crop, supply of assimilates may well have limited yield.

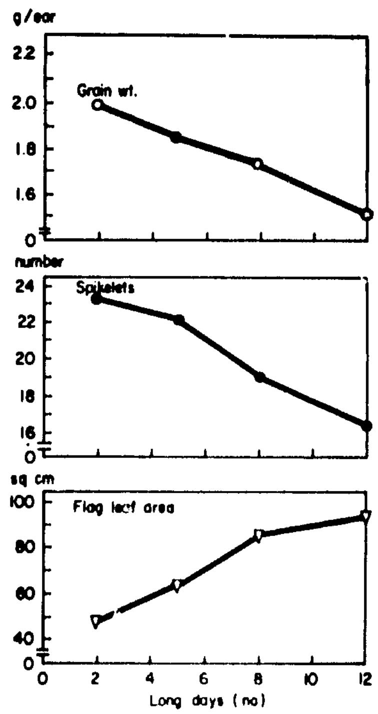
COMPONENTS OF STORAGE CAPACITY

Number of inflorescences

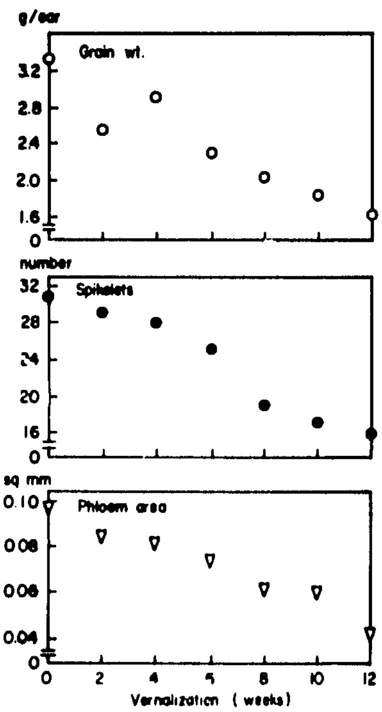
Donald (1968) proposed the uniculm as a characteristic of the ideotype for cereal breeding, based on past trends in maize and on the argument that shoot density could then be fully controlled by sowing rate. But the capacity to tiller is one of the major advantages of cereals like wheat and rice. Tillering helps the plant recover from injury from frost, drought, insect, or insecticide. Similarly, since the storage capacity of each inflorescence is limited, tillering allows crops to take full advantage of unusually long or favorable seasons. The record crops of Gaines wheat and Ootori rice both occurred in seasons of prolonged grain-filling. Whether additional inflorescences or more prolonged filling of the early ones (Daynard et al., 1971) contributed more to the high yield (12.37 t/ha dry weight for wheat and 8.64 t/ha for brown rice) is not known.

Moreover, late tillering may be associated with late root growth, and therefore with the continued movement of cytokinins (Yoshida, Oritani, and Nishi, 1971) and root-synthesized amino acids from the roots, possibly delaying leaf senescence and allowing protein storage to continue. The tillers of grass and cereal plants form an integrated system in which vegetative tillers do not compete strongly with inflorescences, and can supply not only assimilates but also much of their nitrogen to the inflorescences (Rawson and Donald, 1969). Thus, there should be little disadvantage in aiming at a crop with high leaf area index (LAI) and panicle density when water and nutrient supply are adequate. Restricted tillering may be advantageous where drought stress is likely and very heavy tillering probably wastes some plant material. Certainly, many successful modern wheats tend to form few tillers with a high proportion surviving to support an ear (Bingham, 1969). Rawson (1971) has shown that grain yield per ear in several varieties of wheat, under a range of temperatures and plant spacings, is proportional to the weight of the tiller at heading, which in turn is directly related to the age of the main shoot and true leaf-tillers. The weight of the prophyll tillers and of their ears was only about half that of the synchronous true leaf tillers. With wheat, therefore, the goal should be varieties which do not develop prophyll tillers, and which develop true leaf tillers early and rapidly. This prescription may not apply to barley, in which prophyll tillers contribute more to grain yield in modern varieties (Cannell, 1969), or to rice.

Crop photosynthesis reaches a plateau rather than passes an optimum at high LAI in both wheat (King and Evans, 1967) and rice (Tanaka et al., 1966). Crop growth rate and grain yield also reach a plateau in IR8 rice, but tall varieties such as Peta display an optimum LAI (IRRI 1968, p. 22-23). With



3. Effect of the rate of floral induction on spikelet number and grain yield per ear of wheat with increased exposure to long days in variety Triple Dirk (data of Rawson, 1970)



4. Effect of rate of floral induction on spikelet number and grain yield per ear of wheat with increased duration of vernalization in variety Late Mexico 120 (data of Evans et al., 1970)

dwarf varieties, grain yield increased as panicle number per square meter increased up to about 300, above which it reached a plateau (IRRI, 1968, p. 29). Thus there was no yield disadvantage in high panicle density, but in the plateau regions more panicles were associated with fewer grains per panicle.

Number of spikelets per inflorescence

Grain yield per ear in wheat can be closely related to the number of spikelets per ear, as indicated in figures 3 and 4, in spite of possible compensatory variations in weight per grain and grain number per spikelet. Thus, the extent of spikelet differentiation can be a major determinant of storage capacity and yield in wheat, as it also is in rice (Murata, 1969, p. 240, 241).

High light intensity and high nitrogen levels during spikelet differentiation increase spikelet number per inflorescence in both wheat (Friend, 1965) and rice (Matsushima, 1970, p. 131, 139). Another powerful, but less known, influence on spikelet number is the rate of floral induction as controlled by daylength or vernalization. In the wheat variety Triple Dirk increased exposure to long days hastened inflorescence initiation, but it also hastened the differentiation of the terminal spikelet even more, thereby reducing both spikelet number and grain yield per ear (fig. 3). An interesting feature of this experiment was that flagleaf size increased as inflorescence size decreased. Nevertheless, although the smallest flagleaves had to support the ears with the most grains, average grain size was unaffected. In rice there is some evidence that a comparable response may occur. Inflorescence development in rice usually is accelerated by short days. Vergara, Chang, and Lilis (1969) and Owen (1969) found that exposure to longer photoperiods increased spikelet number per panicle.

With the wheat variety Late Mexico 120, increased vernalization sped up ear initiation and, even more, differentiation of the terminal spikelet so that spikelet number and grain yield per ear were halved. It is interesting that the change in the cross-sectional area of phloem at the top of the culm paralleled the change in spikelet number and eventual grain yield (fig. 4). Less vernalized plants had more and larger vascular bundles, implying that the extent of vascular differentiation and the capacity for translocation are by some means coupled to the extent of spikelet differentiation (Evans et al., 1970).

These results further imply that the plant breeding objective of indifference to daylength and vernalization, to aid trans-world adaptation of varieties, may, by hastening floral induction, reduce spikelet differentiation, storage capacity, and potential grain yield. If indifference to daylength was associated with an extended juvenile phase in wheat, during which potential spikelet sites would accumulate at the apex, spikelet numbers might not be greatly reduced. Such an association does occur in rice (Chang, Li, and Vergara, 1969), but no potential spikelet sites accumulate at the apex of the rice shoot.

Grains per spikelet

Like the primitive einkorn wheats, most varieties of rice have only one floret per spikelet. But modern wheats may set four or more grains per spikelet. This difference has contributed much to increased yield potential in the course of evolution. Even so, many more florets differentiate than produce grains. In Ranger wheat, for example, we found 7.8 florets with anther primordia in the eighth spikelet 9 days before anthesis, but only 4.5 reached anthesis, and only 3.3 set grains. The onset of rapid stem growth may have prevented further differentiation of the three distal florets, but why should at least one floret in each spikelet reach anthesis and yet fail to set grain?

Low-intensity light at anthesis tends to reduce grain set in both wheat and rice. In wheat this effect is more marked at high temperatures (Wardlaw, 1970); nitrogen level has little effect (Hoshikawa, 1959). In rice it is most pronounced when nitrogen level is high (Togari and Kashiwakura, 1958), causing failure of anther dehiscence. Such effects are usually interpreted in terms of reduced supply of assimilates. For example, Wang and Yan (1964) found that grain setting in rice was more sensitive to low light intensity than was grain filling. They concluded that more assimilates are needed for grain initiation than for grain filling.

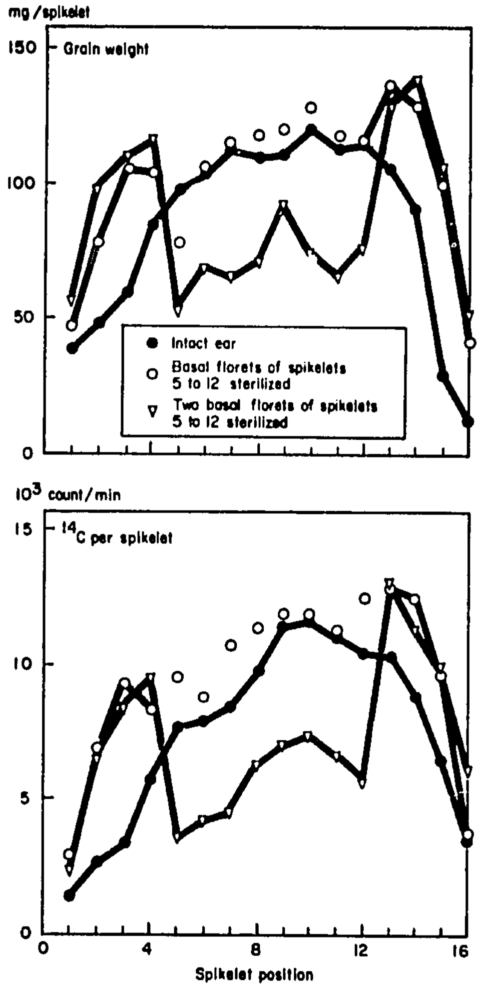
Our experiments with wheat suggest, however, that the adverse effect of low light intensity on grain setting is not through effects on supply of assimilates. At anthesis, and for a few days thereafter, ears are largely self-supporting for assimilates (Evans and Rawson, 1970), and this appears to be a stage of surplus assimilates (Rawson and Hofstra, 1969). Also, although reduced light intensity at anthesis reduced grain set, complete inhibition of ear photosynthesis with DCMU had no effect on it (H. M. Rawson, *unpublished*). It seems more likely, therefore, that grain setting is under correlative or hormonal control. This conclusion is also supported by an unpublished experiment by I. F. Wardlaw who found that injection of chlorocholine chloride, an inhibitor of gibberellin synthesis, near the top of the culm at anthesis considerably increased grain set in wheat even at low light intensity. Thus, endogenous gibberellin levels may mediate the effect of low light intensity on grain setting, as they mediate the effect of plant density on stem growth in barley (Kirby and Faris, 1970).

In experiments with Triple Dirk wheat, main-stem ears with 16 spikelets were either left intact as controls, or the basal one or two florets in each of the eight central spikelets were sterilized before anthesis. These florets are among the first to reach anthesis and usually they set the heaviest grains in the ear. In the control ears no spikelet set more than two grains, but sterilization of the basal florets led to compensatory grain setting in the third and fourth florets of the same spikelets. These distal grains were as large as those they replaced, but grain setting in the fourth florets was incomplete in the ears whose basal florets were both sterilized. Thus, many of the distal florets which normally fail to set grain were capable of doing so. Figure 5 illustrates an unexpected feature of these experiments. Besides the compensatory grain setting within the sterilized spikelets, additional grains were set at the top and bottom of the ear. As a result the grain yield was 20 percent higher in ears in which the basal florets had been sterilized than in the control ears. Clearly, grain set in the distal spikelets was under correlative inhibition by the most advanced central florets. Grain yield per ear in this experiment was apparently limited by storage capacity as determined by grain set rather than by supply of assimilates or by the capacity to translocate assimilates to the more distal parts of the ear. Given increased grain set, increased supply and movement followed.

In further experiments of this kind the same florets were not sterilized, but were emasculated before anthesis, hooded, and pollinated at various times after anthesis. Increases in grain set and yield of up to 30 percent have been obtained in this way. The results suggest that both ovaries and stamens of the more advanced florets play a role in inhibiting grain setting in later florets. The evolutionary progress from *monococcum* to *dicoccum* to modern wheats has presumably involved a progressive reduction in these inhibitory interactions, and their basis deserves further investigation.

Grain volume and weight

In primitive wheats the grains are closely invested by the flowering glumes, whose veins leave parallel marks on the mature grains (Boshnakian, 1918), suggesting that the glumes may physically restrict the growth of the grains, as they do in rice (Matsushima, 1970). The introduction of the gene for loose glumes in wheat may therefore not only have conferred the desirable free-threshing characteristic of modern wheat, but also permitted the great increase



5. Weight and ^{14}C content (after $^{14}CO_2$ assimilation of flag leaves at mid-grain filling) of individual spikelets at various positions (1 = topmost spikelet) for intact Triple Dirk ears, ears in which the first floret of the eight central spikelets were sterilized before anthesis, and ears in which the first and second florets of eight central spikelets were sterilized before anthesis (data of Rawson and Evans, 1970).

in grain size that continues to characterize the evolution of wheat. The search for a comparable gene in rice might be of value since it might amplify the limited varietal differences in grain size.

The evolutionary increase of grain weight in wheat closely parallels that of grain volume (fig. 1), so that grain density has apparently not changed. Matsushima (1970) records that grain density also shows little variation in rice.

Environmental conditions have a pronounced influence on grain size. Many wrinkled and unfilled grains may be found in crops that received poor light or water supply during grain filling. Environmental conditions a week or so following anthesis may also limit the potential size of the grain. With wheat, Wardlaw (1970) found that the temperature during the 10 days after anthesis affected the rate of endosperm cell division but neither the final cell number nor grain size. Reduced light intensity over the same period, on the other hand, not only reduced grain set but also reduced endosperm cell number by 16 percent and final grain size by 76 percent. A comparable reduction in light for 10 days at the stage of rapid grain filling reduced final grain size by 34 percent. This pronounced effect of low light soon after anthesis, like that found by Wang and Yan (1964) with rice, suggests a photomorphogenic or hormonal effect on grain size, rather than a photosynthetic one. Bingham's (1966) demonstration of a paternal effect on grain size in wheat also suggests hormonal influence.

The results of our experiments with partially sterilized wheat ears suggested that storage, rather than photosynthetic capacity, limited grain yields, but this conclusion was difficult to reconcile with the larger size of individual grains in the partly sterilized ears, also found by Bingham (1967). Possibly, the inhibitory effects that the most advanced florets have on grain set in other florets are also found in those developmental processes of the young embryo and endosperm that define the potential size of the grains. Thus, our ability to modify two of the major components of grain storage capacity may hinge on an understanding of these correlative interactions between florets in an inflorescence.

CONCLUSIONS

Undoubtedly poor light conditions often result in crop yield being limited by the supply of assimilates. But the question we asked at the beginning was whether potential grain yield, i.e. yield under favorable conditions of light, temperature, water and nutrient supply, and freedom from pests and diseases, was more likely to be limited by the *capacity* for photosynthesis or by the capacity for storage. There is evidence that storage capacity can limit grain yields of both wheat and rice. It is therefore imperative that we understand the interactions of the yield components and the processes that determine them.

Wheat and rice differ markedly in the number of yield components that may change substantially. The major variables in rice are the number of panicles per unit area and the number of spikelets per panicle. Because there is only one floret per spikelet and because grain size is limited by glume size, storage capacity is essentially determined long before grain filling begins, as Matsushima (1970) has emphasized. Dull light at panicle and spikelet differentiation may therefore limit the capacity of the crop to take advantage of favorable light conditions during grain filling. In wheat, on the other hand, the yield components that are the last to be determined—the number of florets setting grain within each spikelet and grain size itself—vary considerably in response to conditions following anthesis, and they play a major role in yield determination. Thus wheat seems to have more opportunity than rice to increase its storage capacity when conditions during grain filling are favorable. Rice grains are smaller than those of most modern wheats and rice has only one grain per spikelet, but grain number per inflorescence tends to be far higher in rice due to the branched structure of the inflorescence.

In both wheat and rice the major yield components are strongly influenced by light intensity during their determination. Some of these effects are undoubtedly caused by variations in the supply of assimilates, but correlative or hormonal effects appear also to be involved, and these merit much more attention. So too does the role of the processes of floral induction in determining inflorescence structure and spikelet number. In wheat the effect of such processes is large, and it could also be in rice.

Another gap in our understanding of yield development is a lack of insight into the mechanisms that control the partitioning of assimilates, including those by which "sink" organs attract assimilates for storage and modify the rate of photosynthesis in the supply organs. These feedback effects on photosynthesis have often been demonstrated and they pose a major problem in our attempts to determine whether photosynthetic or storage capacity limits grain yield.

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Discussion of papers on maximizing yield potential

General discussion following the papers by Tsunoda, Tanaka, and Evans was led by R. F. Chandler, Jr. The discussions centered on four topics: 1) a comparison of the plant characters of wheat and rice related to yield potential, 2) the relation of photosynthetic efficiency to dry matter production, 3) sink size and filling period, and 4) environmental conditions affecting grain yield.

The discussions revealed that in wheat, the glumes, the rachis, and the leaf sheaths contribute larger proportions of assimilates to the grains than in rice. Also, the flagleaf and the leaf below it intercept a larger proportion of the light in the wheat canopy than in the rice canopy. Although critical evidence is lacking, the inference drawn by wheat workers is that the rather droopy leaves of most wheat varieties have not been a limiting factor in carbon assimilation during the grain-filling period. The question of whether leaf angle affects yielding ability in wheat needs to be studied using isogenic lines differing mainly in leaf angle. On the other hand, leaf angle and leaf arrangement might affect the distribution of growth among tillers of the same plant. It was also pointed out that in the high yielding semidwarf wheats, the thickly packed mesophyll tissues of the leaves might contribute greatly to the nitrogen responsiveness and high yield of the modern wheats, as well as to drought resistance and cold tolerance. There is evidence in rice that erect leaves increase crop photosynthesis and, hence, grain yield. For the continuously irrigated rice varieties, the low photosynthetic rate of thin leaves might be partly compensated for if the leaves are erect.

Though rice varieties show appreciable differences in leaf photosynthetic efficiency (the amount of carbon dioxide fixed per unit leaf area per unit time), the association between the rate and the capacity for dry matter accumulation needs to be established in a canopy under field conditions. On the other hand, to increase grain yield, it is necessary to increase total dry matter accumulation, and it is recognized that any factor that affects plant growth can limit grain yield under a given set of conditions.

In modern bread wheats, one way to obtain high yields is to fill most of the multiple florets within a spikelet. Among wheat varieties, the density of the endosperm material (expressed as test weight) is another contributing factor to grain yield, especially when severe rust epidemics occur. The size of kernel and its filling are related to the length of the ripening period. In rice, an extended ripening period probably would not increase grain size because of the limitations imposed by the hulls. The possibility of developing genotypes with loose hulls was discussed but the approach was considered to have a distinct drawback in losing the protection of the rice hulls against fungi, insects, moisture, and associated biochemical reactions.

One direct contributor to high rice yields is the total number of well-filled spikelets per unit area. In temperate zones, poor grain filling under heavy nitrogen fertilization and adverse environmental conditions appears to be the main limiting factor on grain yield. In tropical areas, the size of the sink could be limiting, if other things are equal. Experiment with CO_2 enrichment indicated that an increase in either spikelet number per unit land area, grain weight, or percent of spikelet filling can raise yields.

The temperature factor was mentioned in relation to plant respiration, the percent of filled spikelets, and the duration of grain filling.

Special problems in rice breeding

Breeding rice for deep-water areas

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Deep-water rice is grown in water from 1 to 5 meters deep on approximately 4 million hectares in East Pakistan and Thailand. It is distinguishable from other varieties by its ability to elongate rapidly under increasing water levels, to produce adventitious roots at the nodes, and to actually float on the surface when uprooted. Until recently, rice breeders concentrated primarily on selection within lowland varieties. In 1964, breeders at the International Rice Research Institute crossed the Thai floating variety Leb Mue Nahng 111 with a semidwarf experimental line from Peta/2 x Taichung Native 1 to obtain lines for possible use in deep water. In Thailand, using locally re-selected semidwarf lines from this cross, breeders have identified progenies that elongate as well as the indigenous deep-water varieties up to a maximum water depth of 150 cm. In further experiments breeders have identified lines that can produce yields at least as well as the traditional deep-water forms and are distinctly superior to the varieties IR8, IR5, and RD1 under most deep-water conditions. Many of these lines have also exhibited excellent flood resistance. The results suggest that varietal improvement in both East Pakistan and Thailand would benefit from a hybridization program involving promising semidwarf and local floating types.

VARIETAL CHARACTERISTICS

The major distinguishing features of floating rice appear to be a semi-prostrate appearance near the base of the plant, even in the early stages of growth under shallow water; the ability to elongate rapidly under rising water conditions (up to 10 cm/day); the formation of adventitious roots at the higher nodes; and a distinct photoperiodic type of flowering behavior. In East Pakistan, M. A. Chowdhury and S. M. H. Zaman (*unpublished*) reported in 1970 that plants are sometimes uprooted by storms and sudden floods. Under such conditions, the plants continue to obtain nutrients through the adventitious roots and when they come in contact with mud, they produce additional tillers from the nodes. Under deep water conditions, the leaves appear to float on the surface. When the water recedes and flowering occurs, a tangled mass of stems results; however, the upper portion of the stem usually

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exhibits phototropism, which reduces the damage to the panicle caused by water and mud and which also facilitates harvesting.

AREAS OF DISTRIBUTION

Deep-water rice varieties are planted on approximately 3 million hectares in East Pakistan and on 1 million hectares in Thailand. R. Seetharaman (*unpublished*) estimated that approximately 1.2 million hectares of deep-water rice exist in India, but probably not more than one seventh of the Indian region is devoted to true floating varieties. Floating rice also reportedly grows in Indonesia, Vietnam, and in Mali and some other areas of Africa.

EAST PAKISTAN VARIETIES AND THEIR CULTURAL PECULIARITIES

In East Pakistan there are more than 600 varieties of deep-water rice. They are grouped into 26 popular classes on the basis of similarities in their characters, such as color and size of spikelets, time of flowering, maturity, and suitability for growth at different water depths. Deep-water varieties of East Pakistan differ considerably in their adaptability to water depth. Success in their cultivation lies in the proper selection of varieties suited to particular water depths. On the basis of adaptability to water depths, varieties fall into one of the following groups: 1) Varieties adapted to water level of up to 2 meters, 2) varieties adapted to water level of 2 to 3 meters, or 3) varieties adapted to water level of 3 to 4 meters.

If the water rise is slow and steady, varieties in the third group can grow even in 6 meters of water.

The most distinguishing feature of deep-water rice is its capacity to grow in rising water. In East Pakistan, the deep-water areas normally flood by the middle of June. If the rice plants are over 6 weeks old by that time and if the water rise is less than 30 cm/day, the plants elongate enough to remain above the water level. By late growth stages the rice plants are long-stemmed. Masses of entangled stems often are uprooted by high wind or strong currents and are carried away to the main streams. Thus at this stage the rice plants really become "floating rice." The uprooted plants draw nutrition from the flood water through adventitious roots that develop from the upper nodes. When the flood water recedes the entangled mass settles to the ground and produces a second flush of tillers from the upper nodes. The yield under such conditions may range from 2 to 2.5 t/ha. A variety under normal conditions may produce about 3 t/ha.

The development of upper nodal tillers and roots in addition to basal tillers and roots is characteristic of all deep-water varieties. Usually there are two flushes of upper tillers.

Deep-water rice varieties have variable photoperiod sensitivity. They are planted from April to May under different soil conditions but a particular variety flowers more or less on the same date even when grown under the varying ecological conditions of East Pakistan.

In East Pakistan, deep-water rice is generally sown broadcast during April or May. Three methods are used. In dry soil, the land is plowed and laddered (smoothed) to a fine tilth and the seeds are sown. The seeds thus sown do not germinate until after the first shower of the monsoon. If the soil has sufficient moisture at planting time, the seeds are sown in the laddered land and then covered with soil. If there is enough moisture to puddle the soil, germinated seeds are sown on puddled land. A great advantage of wet sowing is that it allows aquatic weeds to be controlled easily. Early sowing provides better seedling resistance against floods. The most common weeds are *O. sativa* var. *fatua*, *Echinochloa crusgalli*, *Monochoria* spp., *Scirpus* spp. and *Leersia hexandra*. *E. crusgalli* can completely destroy a rice field.

The flood water usually carries silt and soluble nutrients from which the deep-water rice plants draw nutrients. The soil is also enriched by the annual deposition of silt. Hence, the effect of fertilizer has usually been inconsistent. Nevertheless, plots fertilized with 30 to 40 kg/ha N, 20 to 30 kg/ha P_2O_5, and 20 kg/ha K_2O gave significantly better yield than unfertilized plots.

Early varieties of deep-water rice in East Pakistan are harvested in October in standing water. Because of the difficulty in harvesting this crop, the area under it is limited. Most varieties are harvested during November and December.

WATER DEPTH

Few studies on water depth indicate the water level at which non-floating varieties should be replaced by floating varieties. R. Seetharaman (*unpublished*) stated that non-floating varieties can be grown at water depths ranging from 100 to 200 cm and J. M. Bulaus (*unpublished*) reported that the upper limit in Mali was 60 cm for ordinary rice. In East Pakistan, deep-water varieties are grown in water ranging in depths from 50 to 600 cm, which may persist for periods as long as 6 months. In Thailand, areas near the major rivers and prone to flooding are generally planted to floating rice. Water depths range from 100 to 500 cm, although they average approximately 200 cm.

VARIETIES

Many indigenous varieties have been selected by farmers in areas where deep-water rice is grown. More than 600 varieties of floating rice exist in East Pakistan. R. Seetharaman (*unpublished*) has listed 14 deep-water varieties for specific water levels ranging from 1 to 5 meter depths in India. In Thailand, seven varieties were recommended in recent years after extensive yield tests conducted in both farmers' fields and at experiment stations. Many additional indigenous types are being grown by farmers but there are no reliable estimates of the number of different forms. All recommended Thai varieties have resulted from pure-line selections obtained from local farmers. Reports from researchers in India and East Pakistan also suggest that until recently little hybridization work had been done on deep-water rice.

BREEDING PROBLEMS

Reports from countries where floating rice is grown generally indicate that yields of 2 to 3 t/ha of paddy are obtained under farm conditions. The major breeding problems for floating rice are not well-defined except for the ability to withstand prolonged periods of submergence.

East Pakistan

In East Pakistan, varieties differ in the length of time they can withstand submergence at a depth of 30 cm, up to 21 days. Two varieties, Bedeshi and Dola Aman, continued to elongate until the 20th day of submergence in 30 cm of water. Plants deteriorated rapidly after the 20th day and by the end of 30 days all had died. In East Pakistan, breeding objectives should include good grain quality and resistance to the nematode *Ditylenchus angusta* and stem borers in addition to the ability to rapidly elongate in sudden flooding and to withstand prolonged periods of submergence (at least 1 week). Some damage is caused by the insect pests, *Hispa armigera*, *Pseudaletia unipuncta*, *Leptocorisa acuta*, *Cnaphalocrosis medinalis*, and *Nephotettix impicticeps*. Additional tillering ability is desirable both before and after flooding. All deep-water varieties are highly resistant to bacterial leaf blight and diseases caused by fungi, but some types are susceptible to virus attack.

Other breeding work in East Pakistan is aimed at developing varieties that are quick growing during water rise and able to withstand total submergence for about a week. Crosses have been made among standard and deep-water varieties and some experimental lines from IRRI and India, such as IR532-1-176, IR20, and TKM-6. *O. sativa* var. *fatua*, the common wild rice of East Pakistan, has excellent flood resistance and is being used in breeding work in East Pakistan.

Thailand

In Thailand, the major breeding objectives for deep-water rice include improved grain quality, resistance to the yellow-orange leaf virus (tungro) and bacterial leaf blight, increased tillering capacity, improved plant type, and sensitivity to photoperiod.

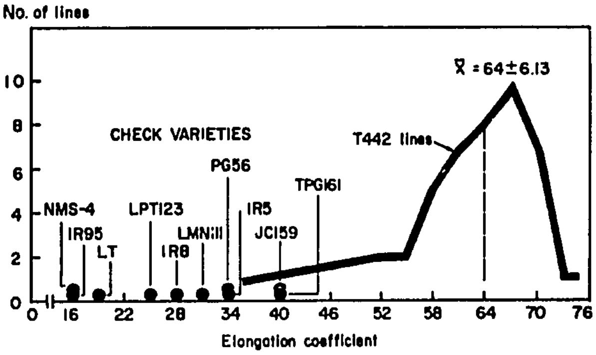
For the past 2 years, researchers have tried to determine whether the ability of floating rice to elongate in deep water could be transferred to semidwarf varieties through breeding and selection. In 1969, 44 semidwarf lines from IR442, a cross between a Thai floating variety (Leb Mue Nahng 111) and a semidwarf experimental line from IRRI (IR95) were tested at the floating rice experiment station (Huntra) near Ayudhaya. These lines (referred to as T442 lines) were a result of selection in 50 cm of water at the Klong Luang rice experiment stations from a F_5 modified bulk population originally obtained from IRRI. Under deep-water conditions, only 99 of 1,000 plants from the original modified bulk population successfully survived for two seasons.

The 1969 experiment involved the 44 semidwarf lines and the following checks: three semidwarf varieties, three tall varieties, two floating varieties, and two semi-floating varieties (tall types which do not float but are capable of limited elongation). It was conducted in a shallow field (5 cm) and in a deep-water (130 cm, maintained until 1 week before harvest) field adjacent to each other. Each site contained single rows of the 54 entries replicated three times in a randomized block design. In the shallow field, the water depth was kept at 5 cm for the entire growing season while in the deep-water field the water level was increased at 3 cm/day beginning 20 days after transplanting until the maximum depth of 130 cm was attained. Plants in all plots were measured for height at the time the increase in water level was begun and again after all plots had completed heading. The experiment was conducted in one dry and one wet season to confirm the reliability of the results.

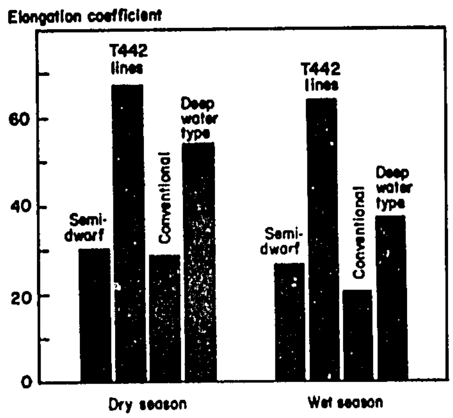
Figure 1 shows the elongation ability of all entries grown during the 1969 wet season. Elongation coefficients were obtained by subtracting the mature height of each line grown in shallow water from that obtained in deep water.

All the T 442lines elongated more than most of the check varieties. Varieties JC 159 and TPG 161 were recommended semifloating varieties and they exhibited the best elongation ability of the check varieties. The wide variability in elongation among the T 442 lines suggests that some lines were superior to others in this characteristic. Although the check varieties, IR8, IR5, and a selection from IR95 died in the deep-water plots, approximate measurements were obtained before they were completely destroyed.

The elongation coefficients of all entries for two seasons are presented in figure 2 where the four types of rice are grouped for simplicity. Results were remarkably consistent for each group for both seasons, with the T 442 population showing the greatest elongation, followed by the deep-water types. The semidwarf and conventional tall varieties showed the least elongation, averaging approximately one-half as much as that of the T 442 lines.



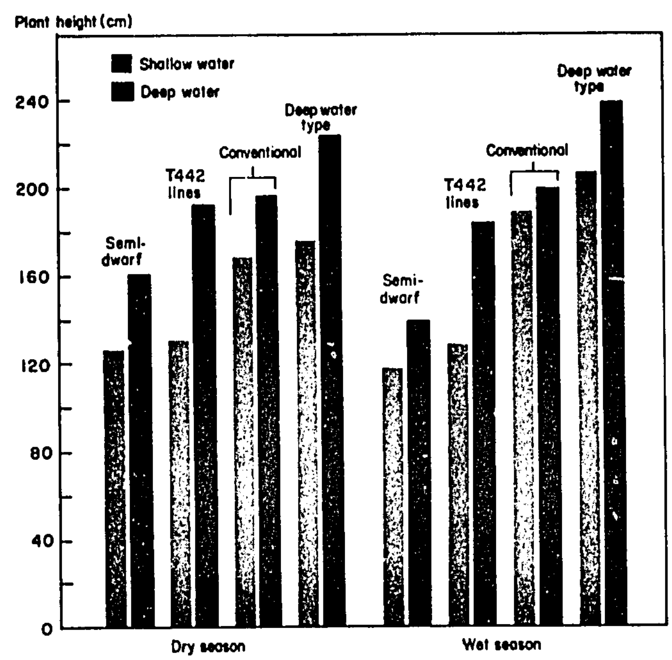
1. Frequency distribution comparing elongation coefficients of T 442 lines and of check varieties exposed to 130 cm of water at the Huntra Rice Experiment Station, 1969 wet season.



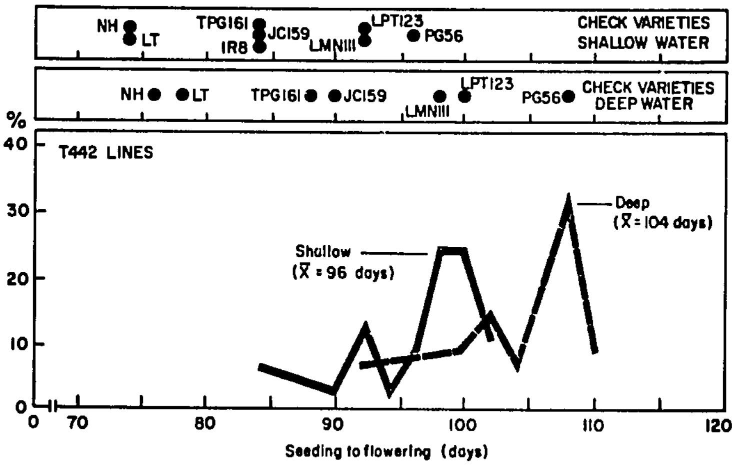
2. Elongation coefficients for four different rice strains grown in two seasons.

In shallow water, the T 442 lines were approximately as tall as the semidwarf varieties (fig. 3), but when exposed to deep water they had approximately the same height as the conventional, tall varieties. The deep-water varieties were extremely tall in both shallow and deep water.

Deep water delayed flowering by approximately 1 week. Most of the T 442 lines matured at the same time as the deep-water varieties. The number of days to flowering are given in figure 4 for the wet season experiment which permitted flowering of the photoperiod-sensitive varieties. All of the T 442



3. Average heights of four different groups of rice grown under deep and shallow water conditions during two seasons.



4. Maturity (days from seeding to flowering) of T 442 population and check varieties grown under deep and shallow water conditions during the 1969 wet season.

lines previously exhibited weak photoperiod sensitivity when grown in the dry season, and they flowered approximately 1 month later than in the wet season. The tall, photoperiod-sensitive check varieties were affected differently by deep water. The check variety Nahng Mon S-4 (NM) showed the least delay in flowering and Leuang Pratew 123 (LPT) showed the most delay.

Yield trials involving promising selections of T 442 were conducted at four locations in 1970 to determine whether any lines could produce yields competitive with those of the deep-water and conventional tall varieties commonly grown in water 50 to 150 cm deep. Table 1 presents the heights and yields of 10 T 442 lines and four check varieties grown at various water depths at the Bangkhen and Huntra rice experiment stations. Under the shallow water conditions at Bangkhen, only a few T 442 lines competed favorably with the check varieties RD1 and Puang Nahk 16; however at the 50-cm water depth at Huntra, many of the lines were superior to the check varieties, RD1, IR8, and Leb Mue Nahng 111. At the 100-cm water depth, both IR8 and RD1 were completely destroyed (fig. 5), but some of the T 442 lines were distinctly superior to the two tall check varieties.

In the experiment where the water depth eventually reached 150 cm and the rate of increase in level depended entirely on natural factors, yields of the T 442 lines were generally lower than under the 100-cm controlled depth, but at least two lines appeared to be as high yielding as the floating variety, Leb Mue Nahng 111. Line T 442-57 appeared quite versatile under all water depths. It produced long, non-chalky grain in most experiments and appeared to be a promising potential variety. Interestingly, the variety Puang Nahk 16, which produced good yields in shallow water, showed a dramatic yield reduction in 100 cm of water and was completely destroyed in the field where the water level reached 150 cm. As might be expected, T 442 lines that were short under shallow water at Bangkhen grew quite tall under 100 cm of water. Line T 442-

Table 1. Height and grain yield of T442 lines and check varieties grown under different water levels at Huntra and Bangkhen experiment stations in the 1970 wet season.

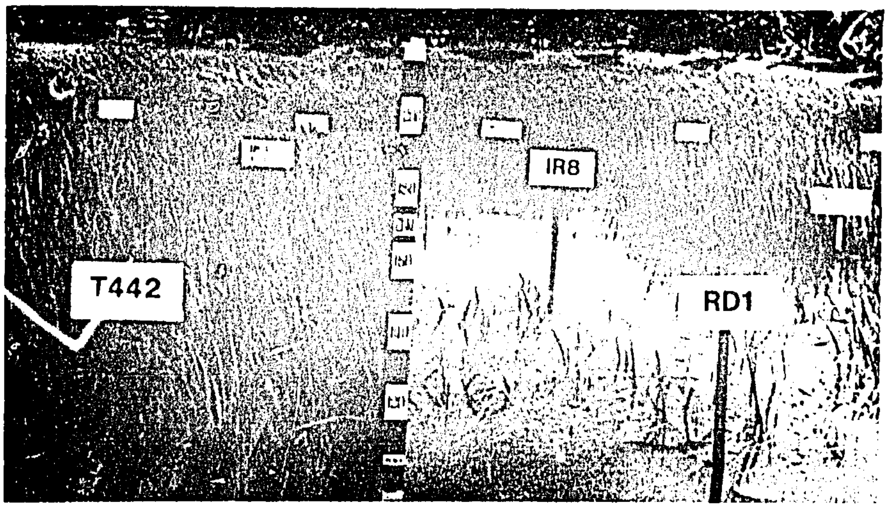
Selection or variety	Bangkhen –5 cm Ht (cm)	Bangkhen –5 cm Yield (t/ha)	Huntra 50 cm Ht (cm)	Huntra 50 cm Yield (t/ha)	Huntra "Flood"[a] Ht (cm)	Huntra "Flood"[a] Yield (t/ha)	Huntra 100 cm Ht (cm)	Huntra 100 cm Yield (t/ha)	Huntra 150 cm Ht (cm)	Huntra 150 cm Yield (t/ha)
T 442-57	117	2.91	139	4.16	145	4.04	187	4.00	176	1.70
-90	120	2.90	136	2.54	150	3.66	181	3.79	172	1.21
-36	118	2.62	157	3.30	138	3.77	181	3.93	174	1.28
-121-24	110	2.60	131	2.16	145	3.70	175	4.89	172	1.31
-38-9	107	2.38	142	1.96	130	3.26	178	3.19	150	0.85
-353-58	110	2.18	146	2.81	144	2.86	184	4.11	169	1.34
-220-43	104	2.03	137	2.12	140	2.84	179	3.64	159	0.46
-429-62	105	1.73	144	1.61	137	2.92	168	2.75	150	0.66
-148-29	108	1.73	140	3.38	140	4.22	151	3.29	162	1.63
-173-35	101	1.61	137	3.56	140	3.65	172	3.89	162	1.18
Leb Mue Nahng 111	213[b]	—	206	2.12	210	5.17	224	2.43	238	1.61
Puang Nahk 16	135	2.86	190	3.73	161	3.73	187	1.34	—	0.00
RD1	100	3.51	119	1.08	109	0.98	—	0.00	—	0.00
IR8	95	3.11	114	0.93	105	0.00	—	0.00	—	0.00
cv (%)		8		21		16		16		28
LSD (5%)		0.31		0.96		0.84		1.05		0.53

[a]Attempts were made to maintain the water level at 5 cm but uncontrollable flooding caused a rapid rise in water level to a maximum of 95 cm for a few days after which the level subsided to about 20 cm. [b]Data from 1969 wet season.

57 increased by 70 cm in height in deep water. Both IR8 and RD1 were taller under 50 cm of water than they were under 5 cm, but they elongated only about half as much as most T 442 lines.

The yield and height data in Table 1 show the performance of T 442 lines and check varieties selected to represent areas which constitute more than 1 million hectares of the Central Plain. Several of the T 442 lines performed consistently well, notably T 442-57, T 442-90, and T 442-148-29. Line T 442-148-29 not only produced comparatively good yields, but also had long, translucent grain and was highly resistant to lodging at both the Klong Luang and Rangsit rice experiment stations (data not shown).

Yield data from the Huntra experiment, designated as "Flood" are especially interesting since the conditions may represent those that commonly occur in many areas of Thailand. A water level of 5 cm throughout the growing season was originally planned for this experiment, but about 7 weeks after seeding, a sudden flood raised the water level in the field at an average rate of 10 cm/day for 7 days. All T 442 lines withstood the flood effects well, as reflected by their relatively high yields. The varieties RD1 and IR8 were unable to cope with the conditions. RD1 gave a low yield and IR8 failed completely. The floating variety, Leb Mue Nahng 111, performed very well. It yielded more than



5. T 442 lines, RD1, and IR8 in yield trials at a water depth of 100 cm at the Huntra Rice Experiment Station, November 1970.

expected, based on other deep-water tests that included T 442 lines. For example, yield data from the deep-water field test at Huntra (Table 1) do not show this variety as being strikingly superior despite the natural quick rise in water level that occurred at approximately the same time that it did in the "Flood" experiment.

The increase in height of the T 442 lines under the flood conditions demonstrates the ability of these lines to elongate rapidly under flooding. The IR8 and RD1 varieties showed only a slight increase from their usual height in shallow water. Actually, the sudden flood conditions caused approximately the same amount of elongation in T 442 lines as that which occurred under a constant depth of 50 cm at the Huntra station, but yields were generally superior.

GENETICS OF FLOATING ABILITY

Ramiah and Ramaswami (1941) reported that two duplicate recessive factors control the floating habit in crosses between floating and non-floating varieties of Indian origin. Their work was primarily based on the classification of F_2 plants grown under shallow water conditions and did not take elongation ability into account. They proposed that a breeding program might combine shorter height, more compact tillering, and tolerance to deep water since there appeared to be no genetic association between floating habit and height or floating habit and compact tillering.

Under laboratory conditions in Japan, Kihara, Katayama, and Tsunewaki (1962) studied the growth habit of floating rice collections obtained from Assam, Thailand, and Africa. They concluded that three factors, designated "a," "b," and "c," were responsible for the survival of deep-water rice.

Factor "a" produced tall height which provided protection against flooding, "b" permitted varieties to elongate at a steady rate corresponding to the increase in water level, and "c" governed the ability to elongate at the maximum rate. Strong floating varieties exhibited high values for the "a," "b," and "c" factors. From the large differences between the various collections Kihara et al. (1962) concluded that floating habit was present in various forms of the species *Oryza glaberrima* and *O. perennis*, as well as *O. sativa*.

Morishima, Hinata, and Oka (1962) speculated that many common rice varieties, particularly the types that have been grown under moderately shallow conditions for many years, have lost most of their tolerance to deep water through evolutionary processes. They hypothesized that there was continuous variation within the floating forms for ability to withstand deep water and several genes were probably involved.

DISCUSSION

Deep-water rice is planted on several million hectares of alluvial soils that are flooded every year. An additional large area subject to periodic flooding borders the deep-water regions where the new improved varieties cannot be grown because of their short height. In Thailand, at least 1 million hectares are thus affected. An area of similar size possibly exists in East Pakistan.

The results of the population study with T 442 reported here and in previous papers (Yantasast, Prechachart, and Jackson, 1970; B. S. Vergara, *unpublished*) strongly suggest that improved plant type, short stature in shallow water, long transluscent grain, and improved yield can be incorporated into deep-water types by transfer of genes from floating rice to semidwarf types. More work is required to determine the maximum water depths such types can withstand and their potential rate of elongation. In East Pakistan varieties that can tolerate submergence for up to 1 week are needed. Selections from the IR442 cross appear promising for relatively minor flooding but they flower too early for practical use. Also the IR442 lines lack a number of important characteristics such as photoperiod sensitivity and resistance to diseases, especially bacterial leaf blight, bacterial leaf streak, and tungro virus.

The Thai deep-water research was conducted to establish whether under actual field conditions, certain selections from the IR442 cross were capable not only of surviving in water depths of up to 150 cm but also of producing yields at least equal to those of ordinary deep-water rice. Undoubtedly, better cross combinations are possible with respect to both the semidwarf and floating parents. Several Thai crosses now undergoing selection appear superior to IR442 in many characteristics, however stable breeding lines have not yet been established. Currently, selected deep-water dwarf lines are being crossed to floating rice. In addition we are attempting to transfer the characteristics of deep-water tolerance into improved varieties that would have "flood resistance" in much the same manner as varieties have resistance to diseases and insects.

If deep-water varieties possess the factors "a," "b," and "c" proposed by Kihara et al. (1962) and if the hypothesis of Morishima et al. (1962) that many common varieties have lost their deep-water tolerance through evolutionary processes of continuous cultivation in shallow water is acceptable, the following points appear to support their findings:

—The T 442 lines contain relatively low values for factor "a," high values for "b," and unknown values for "c" since the experiments were not designed to measure maximum rate of elongation.

—The conventional tall rice varieties of Thailand have high values for factor "a" and low values for "b."

—Indigenous deep-water varieties have relatively high values for both factors "a" and "b."

—Short-statured varieties such as IR8, IR5, and RD1 are essentially lacking in factors "a" and "b" since water depths of 50 cm drastically reduced their productivity, especially at the Huntra Rice Experiment Station, where the 50-cm water level was retained for a prolonged period.

—The possibilities of breeding rice varieties for resistance to deep water and to flooding are sufficiently encouraging to be considered as a major objective in breeding programs in countries where deep-water conditions are present.

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Discussion: Breeding rice for deep-water areas

S. B. Chattopadhyay: The work initiated in Thailand opens up promising lines of investigation. I would like to know how far the work in this direction can be linked up with resistance against flood where there is a sudden rise in water, say more than 30 cm/day, and with capacity of plants to remain submerged and then to resume growth after the flood water recedes. Floods are annual problems in lower Gangetic Delta.

B. R. Jackson: Some of the varieties from Assam and East Pakistan may have the ability to elongate as much as 30 cm per day but I am not familiar with such varieties. East Pakistan researchers have reported that they have identified a few varieties that differ in their ability to withstand submergence.

H. I. Oka: Is floating ability associated with photoperiod sensitivity? Can we have photoperiod-insensitive floating rice?

B. R. Jackson: Ability to elongate is not necessarily associated with photoperiod sensitivity in the T 442 material. This association would be useful in the selection program if such were the case.

B. S. VERGARA: In the areas bordering the deep-water regions where periodic flooding may occur, would you suggest planting a floating variety or a variety that will not elongate but which is resistant to submergence?

B. R. Jackson: I would plant a resistant variety because floating varieties are a last resort.

Tolerance to cool temperatures in Japanese rice varieties

Shiro Okabe, Kunio Toriyama

Rice yields in Japan have recently attained high levels but they have remained unstable under the low temperatures that occur in the growing season. Improved lines with a higher tolerance to cool temperatures should be developed for use in breeding for varieties that combine a high yielding capacity and higher yield stability. Varieties seem to respond in similar ways to cool temperatures at different growth stages, except in delayed heading. Delay in heading is a phenomenon that involves the response of the variety to cool temperature and sensitivity to photoperiod. Rice breeding programs in northern Japan should therefore introduce photoperiod sensitivity more positively.

YIELD INSTABILITY CAUSED BY COOL TEMPERATURE

Despite the great progress that has been achieved in improving varieties and cultural practices, the uncertainty of rice production caused by low temperatures has not been overcome. Rice crops in Hokkaido, the northernmost island of Japan, suffered great decreases in yield in 1954, 1956, 1964, 1965, and 1966 because of cool temperatures in the summer.

Figure 1 depicts the situation in Hokkaido from 1913 to 1970. Generally, the higher the temperature, the better the yield, although the yield levels have gradually increased over the years. It may appear that the cold injuries gradually decreased with time. But, the difference in yield levels between the favorable, or high-temperature years, and the unfavorable, or cool-temperature years, in a recent period, say 1958-70, is not smaller than that in earlier periods, say 1913-37 or 1938-57. Therefore, high yields in recent years are still being decreased by low temperatures to the same degree as in earlier periods. In other words, yielding capacity may have increased recently but yield level has remained unstable because of cool temperature.

A heavy application of nitrogen ensures high yields in warm years. In cool years, however, it may cause a great increase in sterile spikelets or in immature grains. Usually farmers use the maximum amount of fertilizers to raise yield. Thus when new varieties are developed that are highly tolerant of cool temperature under a given cultural condition, the farmers will necessarily have to change their cultural practices to obtain higher yields. The use of

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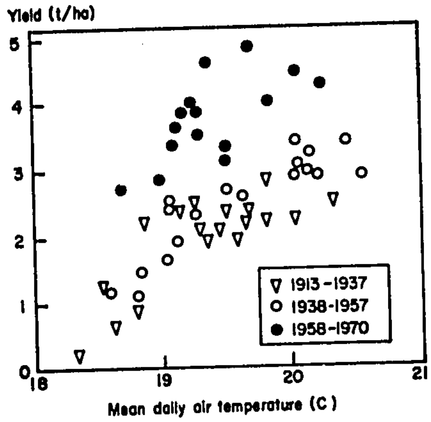

1. The relationship between rice yields and mean daily air temperatures in summer (July-September) in Hokkaido, Japan.

higher rates of nitrogen, for example, may bring about instability of rice yield again. This is a principal reason why the uncertainty in rice production caused by low temperature is difficult to overcome in Japan.

Since most farm holdings are small and the price of rice is high a yield increase is desirable, but the government compensates by paying farmers for the income they lose as a result of natural hazards. So farmers are not eager to be relieved of cool weather damage to their rice crops. For this reason, progress in achieving tolerance to cool temperature in rice plants in farmers' fields may be slow. Improved varieties that are highly tolerant of cool temperature still should be developed to stabilize high yields, however.

PARALLEL VARIETAL RESPONSES TO COOL TEMPERATURE AT DIFFERENT GROWTH STAGES

Injuries to rice plants caused by cool temperature can be classified as the delayed-growth type, sterility type, and delayed-growth and sterility type. The effects of cool temperature on rice plants vary with the plants' growth stages. The effective low temperature, the duration of the effective temperature, the features of plant growth affected by the cool temperature, and the effects on grain yield and quality differ greatly among the different growth stages. Furthermore, the health or nutritional condition of the plants at each growth stage affects their tolerance to cool temperature. The problem therefore is quite complicated. Generally, however, varieties seem to respond similarly to cool temperature at different growth stages, except in delayed heading. Differences in cold injury among varieties in the early growth stage, for example, are fairly similar to those in the germ-cell formation stage.

Rice varieties planted in northern Japan are nearly photoperiod insensitive and their heading dates are governed by their basic vegetative growth period. Heading dates are also greatly affected by cool temperature during the vegetative growth stage. Some varieties, however, show little delay in heading when the temperature is cool during their vegetative growth stage. Their heading behavior is characterized by a short basic vegetative growth period and, in addition, by a special type of photoperiod sensitivity. This delayed heading results from a phenomenon that involves varietal response to cool temperature and varietal photoperiod sensitivity. Photoperiod sensitivity should be introduced more positively in the rice breeding programs of northern Japan to obtain varieties tolerant to cool temperature.

Selection for lines of rice tolerant to low temperature in Korea

M. H. Heu, S. H. Bae

The cooperative japonica x indica breeding program between the Republic of Korea and the International Rice Research Institute has led to the development of IR667-98, which is now being tested throughout Korea. IR667-98 was selected from a cross between IR8 x (Yukara x Taichung Native 1). Breeders are trying to incorporate into this selection the cold tolerance and other desirable characteristics of japonicas. Studies are under way to evaluate the effects of low temperature on breeding lines at different stages of plant growth.

Japonica x *indica* crosses have been used extensively in a cooperative program between the Republic of Korea and IRRI. The major objective of this program is to develop nonlodging, nitrogen-responsive, blast-resistant varieties that are adapted to Korea. IR667-98 (IR8 x [Yukara x TN1]), which was developed in the program, has the desired characteristic. It is now being tested intensively throughout the country.

IR667-98 is not as tolerant to low temperatures as japonica varieties. Breeders are trying to develop lines that have the plant type of IR667-98 plus cold tolerance, resistance to diseases and insects, and the grain shape, appearance, and cooking qualities of japonica varieties.

Before the Korea-IRRI project started, little attention was paid to developing lines tolerant to low temperature since most japonica varieties used as parents possessed adequate levels of cold tolerance for Korea.

The daily maximum, minimum, and mean temperatures at Suwon during the growing season are shown in figure 1. Currently recommended varieties are sown starting in late April by the wet-bed method. Usually if they mature by mid-October no serious leaf discoloration or sterility occurs.

In 1966 most of the japonica x indica lines tested showed distinct seedling discoloration in the seedbed because of low temperatures. Seedlings were stunted after transplanting. In the fall, before killing frost occurred, some lines had wilted, immature plants with discolored leaves.

Since 1967 breeding lines have been sown in late April in semi-upland nursery beds covered with polyethylene sheets. After germination the seedbeds are uncovered during the day for 7 to 10 days before transplanting. In the fall,

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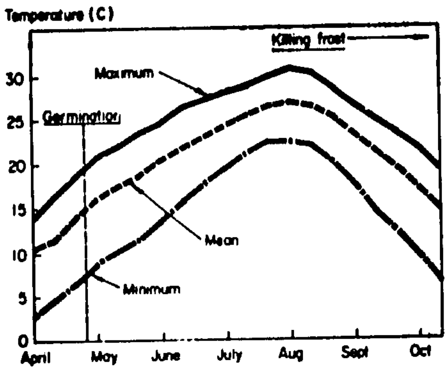

1. Daily air temperature during rice growing season at Suwon, Korea (37°20′ N).

degree of wilting, discoloration, and senescence before maturity are used to determine resistance to low temperature.

Breeders follow this schedule: At seeding in late April, they determine the ability of lines to germinate in polyethylene-covered, semi-upland beds. Shortly before transplanting, they remove the polyethylene and record the degree of discoloration or brown speck. At transplanting in early June, the breeders rate lines for seedling vigor and degree of stunting. Before August 20, they select flowering lines. This allows at least 40 days for maturation before daily mean temperatures drop below 20 C. Near maturity in mid-September, they select lines showing the least discoloration and senescence.

More information about the reactions of seedlings and maturing plants can be obtained by using earlier and later seeding dates. But because weather conditions vary from season to season, evaluation cannot always be precise.

Studies have recently been started with the phytotron to evaluate effects of low temperature at different stages of growth. In a study of the germination of seeds at low temperatures, we found that most local japonica varieties germinate at 13 C when dry seeds are covered with 1 cm of water, but most japonica x indica lines fail to germinate. At 15 C many japonica x indica lines germinate within 7 days and grow like japonica control varieties.

In a study of seedling tolerance to low temperature, the Amamiya method was modified slightly (A. Amamiya, *unpublished*). Seedlings in the three-leaf stage that had been germinated at 25 to 30 C (room temperature), were placed at 10 C for 4 days and then brought back to 25 to 30 C. The wilted seedlings were counted the day after the plants were returned to room temperature. Preliminary results show that some of the seedlings of japonica x indica lines were slightly less tolerant to low temperatures than japonica varieties. Perhaps a longer exposure to low temperature will differentiate the test lines better.

It is evident that screening at any one stage of growth is not sufficient. For example, IR1317-266-2 withstands low temperatures as it nears maturity but it is not tolerant during germination and early seedling growth.

Under field conditions advanced-generation lines are tested at three dates of seeding (scheduled according to early-, ordinary-, and late-season cultures) usually 3 weeks apart. In this way, the test lines are exposed to low temperatures in both the seedling and ripening stages.

Tolerance of rice to cool temperatures—USA

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In California, breeding rices with tolerance to cool temperatures is divided into three phases: tolerance during germination and seedling establishment, stability of period from seeding to heading, and tolerance to sterility induced by low temperature. At cool temperatures, the seedling vigor of California varieties is good, that of tropical short-statured varieties, very poor, and that of the Hungarian varieties, Italica Livorno, Zerowshani and Szegedi Szakallas 28, very good. Methods of screening for seedling tolerance are reviewed. Heritabilities (broad sense) for seedling vigor at low temperatures ranged from 48 to 81 percent. Data from crosses between California varieties and Hungarian varieties suggest a high degree of phenotypic dominance for good seedling vigor. IR8, under the cool California conditions, requires about 50 more days to reach heading than it does in the Philippines. From crosses of IR8 with cold-tolerant California varieties, however, many lines with cold tolerance are readily recovered, some of which have under cool temperatures, a vegetative period that is even shorter than the California parent. Indica varieties, such as sources of the short-stature gene, are more susceptible than California varieties to sterility induced by low temperature. Minimum temperatures at the microsporogenesis stage are most related to this sterility.

INTRODUCTION

Breeding of improved rice varieties with tolerance to cool temperatures is an important objective of the program at the Rice Experiment Station, Biggs, California, USA. We recognize three aspects of the problem; tolerance to cold water during germination and seedling establishment, tolerance as related to stability of growth period from seeding to heading, and tolerance to sterility induced by low temperature.

Practically all rice in California is planted by dropping pre-soaked seed from airplanes into fields flooded to a depth of about 15 cm. Water depth varies within fields because of imperfect levelling, provision for draining the fields, and the drop of about 6 cm between levees. Night air temperature at seeding time in late April or early May sometimes falls to around 5 C. In many areas the irrigation water is from snow-fed sources and its temperature commonly is from 8 to 13 C in the canals at seeding time. Water temperatures in

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the fields are higher depending upon position in the field, hours of sunshine, and air temperature. Seedling tolerance to cold water is especially important because of our method of culture.

The minimum air temperatures at night during the summer are commonly 15 C and in some areas during microsporogenesis and at heading they may drop to 10 C. Maximum day temperatures are commonly 30 to 40 C.

TOLERANCE OF SEEDLINGS TO COLD WATER IN CALIFORNIA

Ormrod and Buntner (1961) found striking differences among rice varieties in seedling height after 28 days at 15.5 C. Five California varieties produced taller seedlings than the 15 other U.S. varieties tested. Caloro for example produced seedlings that were three times as tall as those of Bluebonnet. Only six of 36 introduced varieties produced seedlings as tall as Caloro in their tests. These were Rikuto Kemochi, Takao-Iku No. 3, Kwol Zo, Su Won, and Precoce

Adair (1968) described a technique for evaluating cold water tolerance of rice seedlings. He used seedling height as the criterion at 26 days after seeding in 15 cm of water at 15.5 ± 1 C. Using this test, C. R. Adair (*personal communication*) reported in 1971 that the Hungarian varieties, Italica Livorno, Szegedi Szakallas 28, and Zerowshani, produced seedlings that were 29, 32, and 46 percent taller, respectively than Caloro. In 1967, J. R. Erickson found that these Hungarian varieties also exhibited superior seedling growth at a warm temperature (Table 1).

J. F. Williams. in a 1970 M.S. thesis (*unpublished*) compared Italica Livorno with the California varieties Calrose and Colusa at water temperatures of 15, 18, 21, and 24 C and measured their height at 7, 14, 21, and 28 days. He found a significant interaction between temperatures and varieties for height of seedlings at 7, 14, and 21 days but not at 28 days. After transforming the data to logarithms the interactions were significant for 7-day-old and 21-day-old seedlings. Williams concluded that "by 28 days, seedling cold tolerance differences had disappeared." In addition, he showed that Italica Livorno has

Table 1. Seedling growth of three Hungarian varieties and Caloro at two temperatures.

Variety	Seedling height[a] (cm) at	
	26.7 C	15.5 C
Italica Livorno	14.08	5.26
Zerowshani	13.34	5.54
Szegedi Szakallas 28	9.62	3.86
Caloro	7.13	3.37

[a]Seedlings at 26.7 C were grown in the greenhouse and measured after 14 days, those at 15.5 C were grown in a growth chamber and were measured after 28 days.

Table 2. Height of 28-day-old seedlings of three Hungarian varieties, the mean of three California varieties and of the F_1, F_2, and BC_1 plants from crosses of the three California varieties with each Hungarian variety expressed in percent of the California varieties when grown at 15.5 C.

Parents or cross	Height (% of California varieties)		
	F_1 test	F_2 test	$F_1 \times P_1$ test
California varieties[a] (P_1)	100	100	100
Italica Livorno (P_2)	150	162	125
Zerowshani (P_3)	134	162	151
Szegedi Szakallas 28 (P_4)	117	157	139
$P_1 \times P_2$[b]	92	136	—
$P_1 \times P_3$[b]	123	151	—
$P_1 \times P_4$[b]	109	121	—
$(P_1 \times P_2)P_1$[b]	—	—	139
$(P_1 \times P_3)P_1$[b]	—	—	149
$(P_1 \times P_4)P_1$[b]	—	—	147

[a]Mean of Caloro, Calrose, and Colusa. [b]Mean.

seedling vigor which was mistakenly identified as cold water tolerance in previous tests. From the viewpoint of practical plant breeding we are interested in seedling vigor that is expressed at rather cool temperatures. Rice breeders in the tropics may be less restrictive on the type of seedling vigor to use.

Williams also found a close relationship between α-amylase activity and dry weight of 1- to 12-day-old rice seedlings grown on slant boards in the dark at 30 C. He observed that a strong relationship exists between α-amylase activity and seedling growth regardless of variety. Among 20 varieties tested, however, Williams found that the slope of the regression of α-amylase activity on shoot growth was dissimilar for japonica and indica varieties. The correlations between α-amylase activity and shoot growth were +0.924 for japonicas and +0.965 for indicas, but only +0.601 when the correlation was calculated for all varieties.

Diseases may affect the vigor of the young seedling. Webster et al. (1970) reported that *Achlya klebsiana* and *Pythium* species were pathogenic on young rice seedlings in California. The *Pythium* isolates were most pathogenic at 21.1 C while *Achlya* was equally pathogenic at 21.1 C and 30 C. Their results suggest that varieties with maximum seedling vigor or with resistance to seedling diseases would produce better stands.

The extent to which seedling vigor at 15.5 C is transmitted in crosses is summarized in Table 2. The tests confirmed the superiority of the three Hungarian varieties. The F_1 and backcross data should be used with caution. The seed quality of these two generations may have affected the results since about one-third of the lemma and palea was clipped to emasculate the spikelets. We did not grow parent seeds treated similarly to assess the importance of this variable. The F_2 information, therefore, is the most reliable. It suggests a high degree of phenotypic dominance of seedling vigor at 15.5 C. Both the F_1 and F_2 generations of Zerowshani x Szegedi Szakallas 28 produced seedlings with more vigor than those of the reciprocals. Otherwise, the reciprocal crosses performed similarly.

Heritabilities (broad sense) of seedling vigor at 15.5 C were calculated by subtracting the mean variance of the parents from the F_2 variance and dividing by the F_2 variance. These estimates ranged from 48 to 81 percent on the original data. They suggest that the development of rice varieties with improved seedling vigor or cold tolerance or both is a realistic objective.

P. P. Osterli and M. L. Peterson (*unpublished*) recovered F_4 lines from the cross Italica Livorno x Caloro that ranged in seedling height from 62 to 92 percent of the taller parent at 15 days in water at 18 C. Caloro seedlings were 53 percent as tall as the other parent. These workers believe the slant board technique of Jones and Cobb (1963) is the most efficient method for primary screening. Selected materials are then evaluated in 15 cm of water at 18 C, and finally in the field.

Consequently we have used these sources in crosses with short-statured sources from the tropics to combine short stature with adequate seedling vigor under our climatic conditions. The F_2 and subsequent generations are seeded directly in flooded fields to simulate farm conditions for selection purposes.

T. H. Johnston (*personal communication*) in work in Arkansas noted the development of narrow cross bands of chlorotic tissue on newly emerged seedlings following exposure to minimum temperatures of 4 to 5 C.

STABILITY OF GROWTH DURATION FROM SEEDING TO HEADING

The importance of the effect of cool temperatures on the time from seeding to maturity can be illustrated with the relatively photoperiod-insensitive variety, IR8. In the Philippines IR8 requires about 90 days from seeding to heading. In California it requires about 140 days from seeding to heading, approximately a 50-day difference. From crosses of IR8 with CS-M3, a California variety requiring 110 days to heading, we have some selections showing transgressive segregation. They head in 90 days under our conditions. Therefore, when the segregating generations are grown at low temperatures it is not difficult to recover lines from crosses of this type that are insensitive to cool temperatures.

RESISTANCE TO STERILITY INDUCED BY COOL TEMPERATURE

In California, late-maturing varieties (150 to 155 days from seeding to maturity) are exposed to cool irrigation water or minimum night temperatures of approximately 10 C in several areas. Growers consider Calrose more resistant to sterility under these conditions than Caloro.

In 1971, S. Lin (*unpublished*) at the University of California subjected Caloro rice plants to 7.2 C at night and 15.5 C during the day for 0 to 5 days at the microsporogenesis stage, 5 days before microsporogenesis, and 5 days after microsporogenesis. Treatment at the microsporogenesis stage for 3 to 5 days caused floret sterility of 28.5 to 47.0 percent. Treatment started 5 days before microsporogenesis gave sterility of 25.9 and 44.2 percent after 4 and 5 days of treatment. Plants for which treatment was started 5 days after microsporogenesis had only a slight increase in floret sterility.

Lin also tagged tillers of Calrose rice at their estimated time of microsporogenesis on three dates representing 5-day intervals in a field. Mean minimum temperatures for the three 5-day periods were 14.2, 11.6, and 10.6 C, and 8.3, 12.6, and 24.7 percent sterile florets, respectively, were produced. Mean maximum temperatures were 33 C or higher for each period. Lin's results confirm that minimum temperature at the microsporogenesis stage is critical and that minimum temperature around 10 C can induce sterility in varieties that are more tolerant than many. M. L. Peterson (*personal communication*) indicates that IRRI material is very susceptible to low temperature in the field, especially if IR8 is a parent.

Until refined techniques are developed we will continue to assess resistance to sterility in field plantings. Davis, California has cool nights and a nursery there is used for screening work. We also seed somewhat later than normal to improve the chances of exposing the materials to conditions that cause sterility in the field.

In addition, we grow about 4,000 F_3 panicle-rows of short-statured materials in Hawaii each winter. There sterility induced by cool temperature has occurred on many lines. For example, in one set of F_3 lines, 75.4 percent produced less than 40 g of seed from a 120-cm row, 7 percent produced over 100 g and only 1 percent produced more than 200 g. IR8, Taichung Native 1, and Dee-geo-woo-gen reacted similarly and averaged 34 g of seed per row. Calrose, Earlirose, and three pure-line tall California experimental varieties produced from 238 to 456 g/row.

The distribution of 48 F_5 short-statured lines derived from IR8 x S-8023-3/2 was quite different, suggesting that selection for resistance to sterility had been effective. Among these lines 25 percent produced over 200 g and a similar percentage produced less than 40 g/row. It seems possible that hybrid sterility in early generations may also be accentuated under cool temperatures.

In Arkansas, Wells and Kanarengsa (1970) and T. H. Johnston (*personal communication*) have noted a higher incidence of spikelet sterility on rices seeded later than usual and consequently subjected to cooler temperatures during the early reproductive stages. Johnston also noted that the variety Dawn and selections having Dawn as a parent developed small imperfect florets when plants were exposed to recorded minimum temperatures of about 12.7 C. We also have observed malformed panicles apparently caused by cool temperatures.

Johnston suggests that the report of Wells and Kanarengsa (1970) showing increased spikelet sterility associated with nitrogen topdressing just before panicle initiation may be based on the physiology or nutrition of the plant or its potential yielding ability. It seems possible that inadequate available sugars for translocation to the developing grains could contribute to spikelet sterility.

Better knowledge of the effect of temperature, reduced sunlight, nitrogen nutrition, and other environmental factors that may affect sugar development and translocation could be of value in selecting for resistance to sterility.

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Resistance of japonica x indica breeding lines to low temperatures

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The degree of yellowing of seedling leaves was used as a measure of cold resistance in Korea and in cold-water tanks at the International Rice Research Institute. Seedling vigor was used in California. In East Pakistan low temperatures caused leaf yellowing and stunting in the early tillering stage. In West Pakistan and Nepal suppressed growth and prolonged growth duration were attributed to low temperatures. Degeneration of florets at tips of panicles was attributed to cold injury at IRRI and in Nepal. The relationships between cold resistance and amylose content of the grain, the extent of panicle exsertion, and varietal resistance to green leafhoppers were studied. The different types of cold resistance studied appeared to be inherited independently of each other but further studies are needed. Japonica/2 x indica lines showed higher levels of cold resistance than indica/2 x japonica lines. Thus, the tests used probably are valid since japonica varieties are inherently more resistant to cold than indica varieties. Semidwarf plant types resembling IR8 were observed to have japonica-type levels of cold resistance in some of the lines tested. Cold-resistant varieties from several countries have been brought together for evaluation with the hope of finding highly resistant varieties for use as parents in crosses for improved cold resistance.

INTRODUCTION

Since 1969, IRRI has been conducting cooperative experiments with rice breeders in several countries on the response of rice varieties and breeding lines to low temperatures. These studies are aimed at finding superior sources of cold resistance, transferring cold resistance to semidwarf tropical indica varieties, and developing testing techniques for evaluating varieties and breeding lines for cold resistance.

We have been using japonica and indica varieties and japonica x indica hybrid lines in these studies. Some specific features of cold damage that have been observed are, 1) in Korea, leaf discoloration in the seedling stage and at maturity; 2) in East Pakistan, in the boro season crop, leaf yellowing, stunting of plants in the early vegetative growth stage and blanking or sterility at maturity; 3) in the Swat Valley of Pakistan and in Nepal, stunting and delayed heading; and 4) in California, USA, seedling establishment problems.

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The material tested in 1970 can be divided into two groups: A and B. Group A included japonica varieties and hybrid lines from crosses between japonica x semidwarf indica varieties backcrossed to japonica varieties. Group B was made up of hybrid lines from crosses between japonica x semidwarf indica varieties and one or two backcrosses to semidwarf indica varieties.

Most lines in group A showed good panicle exsertion in the field at IRRI in 1970 and possessed many japonica characteristics. The group B lines had been selected for semidwarf indica plant type and tended to resemble IR8.

A collection of japonica and other cold-resistant varieties and lines from different countries is being assembled at IRRI. From this collection it should be possible to identify superior cold-resistant genotypes at different growth stages.

COLD RESISTANCE AT THE SEEDLING STAGE

Extreme yellowing of all leaves of seedlings of indica varieties frequently occurs when daily mean temperatures are as low as 15 to 20 C. In 1970, 330 IRRI lines were grown in seedbeds at Suwon, Korea, under low temperature. Most lines of group A, in which japonica germ plasm predominated, remained green (S. H. Bae, *unpublished*). Most of the lines showing normal seedling color had low amylose content which is characteristic of the japonica parents. But when we tested 255 F_3 lines from japonica x semidwarf indica (high-amylose) crosses in cold-water tanks at IRRI in 1971 we found no significant relationship between amylose content and seedling color at 13 to 14 C water temperature.

Tests of 614 F_3 lines from six japonica x semidwarf indica crosses showed that there was no association among three characteristics: the extent of panicle exsertion in F_2 plants, seedling color, and resistance to the green leafhopper. In a field planting at IRRI during the 1971 wet season, these same F_3 lines showed no relationship between plant type and seedling color, indicating that the cold resistance of japonica varieties based on seedling color can be transferred to the semidwarf indica plant type. Since most lines in group A, in which japonica genes are predominant, have green seedlings and lines in group B have mostly yellowish seedlings, the cold water tests probably are a good index of cold resistance in the seedling stage.

Amamiya (1971) showed that cold resistance based on differences in seedling color recorded in a growth chamber for 3 days at 5 C was monogenically controlled and that the pattern of soluble proteins in the "Sephadex" analyzer was closely related to the resistance.

Seedling vigor based on height as measured in a cold resistance nursery at Biggs, California (H. L. Carnahan, *unpublished*) showed that lines of group A tended to be more vigorous than those of group B. No lines of group A were graded 1 (very poor) or 2 (poor), while 95 percent of the group B lines were graded between 1 and 3 (medium). As shown in Table 1, the high amylose lines tended to have less seedling vigor than the low amylose lines in both

Table 1. Seedling vigor in the cold-water nursery at Biggs, California, as affected by the amylose content of group A and group B of indica x japonica hybrid selections.

	Number of lines							
	Amylose content (%)							
	27.1 and higher		23.1 to 27.0		23.0 or lower		Total	
Seedling vigor[a]	A	B	A	B	A	B	A	B
1.0	0	26	0	2	0	4	0	32
2.0	0	29	0	1	0	6	0	36
2.5	1	31	0	4	2	26	3	61
3.0	7	33	0	7	11	23	18	63
3.5	7	3	3	1	11	2	17	6
4.0	1	1	4	0	31	4	36	5
4.5	0	0	1	0	9	0	10	0
Mean seedling vigor	3.2	2.1	3.8	2.6	3.8	2.7	3.7	2.4

[a]1, very poor. 2, poor; 3, medium; 4, good; 5, excellent.

groups. Seedling color at Suwon and seedling vigor at Biggs did not show the close relationship expected.

COLD RESISTANCE AT THE TILLERING STAGE

In the boro season in East Pakistan, lower leaves turned yellow after short periods of low temperature. Since low temperatures usually do not occur after panicle initiation, there was no clear relationship between leaf yellowing and grain yield. Some of the japonica x indica lines were highly sensitive to leaf yellowing, but this was not necessarily associated with the seedling discoloration observed in Korea. More precise tests are required but there is an indication that different genes control the two symptoms.

Severely stunted lines were observed in East Pakistan. They were only one-third the normal height, had small stems, and short, narrow, and erect leaves. Tillering was high in some lines and low in others.

Differences in days to heading in the dry and wet seasons at IRRI were related to stunting. The lines that showed delayed heading in the dry season had 2.6 times as many stunted lines as those which showed earlier flowering in the dry season.

The stunted lines showed less sterility than other lines in East Pakistan (M. Chaudhury, *unpublished*). It is possible that stunting caused delayed heading and that the stunted plants escaped the low-temperature period critical for sterility. Stunting and leaf yellowing were observed in the same season and the two characters appeared independent of each other.

Table 2. Effect of low temperature on plant growth of two groups of IRRI lines.

Plant ht at IRRI (cm)[a]	Group	Plant ht at Khumal, Nepal (cm)[b]					
		Under 50	50 to 59	60 to 69	70 to 79	80 to 89	90 to 99
95 or less	A	3	1	1	1	–	–
	B	5	5	–	–	–	–
96 to 100	A	–	–	3	3	-	–
	B	5	15	2	1	–	–
101 to 105	A	–	–	3	7	–	–
	B	14	15	23	9	2	–
106 to 110	A	–	–	–	1	4	1
	B	7	16	20	21	2	-
111 to 115	A	–	–	–	4	5	1
	B	3	6	12	13	2	–
116 to 120	A	–	–	–	3	5	-
	B	1	1	4	4	6	–
121 to 125	A	–	–	–	–	5	1
	B	–	–	1	1	–	–
126 or more	A	–	–	–	–	3	1
	B	–	–	–	1	–	–

[a]At maturity. [b]At maturing stage.

Marked stunting occurred in the 1970 cold nursery in Swat Valley, West Pakistan, where the water temperature was 13 C in seedbeds and from 18 to 21 C throughout the growing season. Almost all of the group B lines failed to flower (G. W. McLean, *unpublished*).

A comparison between plant heights at IRRI and at Khumal, Nepal, showed that the inhibitive effect of low temperatures on plant height was much more pronounced in group B than in group A (Table 2).

COLD RESISTANCE AT THE REPRODUCTIVE STAGE

Degenerated florets on top branches of panicles occur frequently in many countries and sometimes they are caused by low temperatures (Tanaka, 1941; Sato and Masuda, 1956). In the 1970 dry season nursery at IRRI, 8.9 percent of 441 lines exposed to the minimum temperature of 19 C, which occurred about 3 weeks before heading, had degenerated florets. Only 3 percent of the other 3,622 indica lines which headed earlier or later had degenerated florets.

EFFECT OF LOW TEMPERATURE ON GROWTH DURATION

The effect of low temperature on the growth duration of group A lines differed markedly from that in group B in Nepal in 1970 (B. B. Shahi, *unpublished*). In group A, all 57 lines heading in 70 to 90 days at IRRI completed maturation in Nepal. In group B, nine of the 92 lines heading between 71 and 80 days at IRRI, and 64 out of 100 lines heading in 81 to 90 days, failed to flower or mature in Nepal.

Growth durations at IRRI in the two crop seasons were studied to determine how much of the information on heading dates could be useful in predicting the duration in Korea. The difference in accumulated temperatures in the cooler (dry) and the warmer (wet) seasons at IRRI was only slightly correlated with the accumulated temperatures in Korea (0.466 for group A and 0.322 for group B).

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Discussion of papers on tolerance to cool temperatures

B. S. Vergara: Since the darklength during the panicle initiation stage in northern Japan is very long, one has to find a variety whose critical photoperiod is between 14 and 15 hours. In our tests, we have not found such a variety. Does such a variety exist in Japan that can be used as a source for this particular character?

S. Okabe: Yes. Dr. K. [illegible]'s experiments indicated that Somewake, Kokei 2, [illegible] and Tohoku [illegible] responded to different photoperiods in such a manner. They all came from the Tohoku district. Tohoku [illegible] is being used in breeding programs as a source of long critical photoperiod.

D. J. McDonald: Is it true that Hokkaido varieties become less cold tolerant when grown in other environments such as in northern Honshu?

S. Okabe: Such cases have occurred but not frequently. The situation is complicated. On one hand, the extremely early panicle initiation of Hokkaido varieties in northern Honshu may be related to the occurrence of sterility. On the other hand, an excessively high nitrogen content in plants at panicle initiation, which often happens in very early varieties, is apt to increase spikelet sterility under low temperature during that period.

C. Kaneda: Dr. Okabe, you concluded that Japanese varieties seem to respond in similar ways to cool temperatures at different stages. Don't you think this is because japonica varieties have a narrower genetic base than indica varieties?

S. Okabe: Possibly. But since we have no information on indica varieties, more data are needed to clarify this matter.

B. S. Vergara: How is seedling vigor measured in California?

H. L. Carnahan: We equate seedling height to seedling vigor. In the field in our breeding program, we assign a score on a 1 to [illegible] scale at approximately 4 weeks after seeding.

B. B. [illegible]: While scoring height of different varieties in your cold tolerance test, do you keep in mind the genetic background of the varieties?

H. L. Carnahan: In controlled temperature tests the seedling lengths are measured and California varieties are always included as checks. In field tests, short statured breeding lines are usually planted in one nursery and tall lines in another nursery. In each case, however, California varieties and other parents are included as checks for a reference point.

[illegible]: Mr. Kaneda, have you found any correlation between cold tolerance in the seedling stage and cold tolerance at panicle initiation stage?

C. Kaneda: In our materials, lines showing severe yellowing at the seedling stage generally were unable to exsert panicles at a later stage.

A. O. Abifarin: How can one differentiate between the cold symptoms on leaves and lack of nitrogen in a farmer's field without previous knowledge of the temperature and fertility conditions?

C. Kaneda: Comparison with plants grown along the borders of the field will be helpful because the border plants usually receive more nitrogen than plants in the middle of the field. If nitrogen deficiency is the problem, the border plants should have a darker leaf color. If susceptibility to low temperatures is the problem, the border plants will have the same degree of, or more severe, yellowing than those grown in the middle of the field.

DISCUSSION OF TOLERANCE TO COOL TEMPERATURES

S. C. LITZENBERGER: Assuming that favorable response to cool temperatures is genetically controlled and that response to warm weather is, too, it should be possible through population breeding to develop a population insensitive to cool and warm environments. I suggest this method be attempted, using the male-sterile lines or chemisterilants to initiate such a program.

Breeding methods

Mutation breeding in rice improvement

Walton C. Gregory

The objectives and achievements of current mutation breeding programs of rice in Asia are related to the land areas used relative to the requirements of conventional breeding, to the probabilities inherent in mutation breeding work, and to the conditions under which mutation breeding would be advisable. Mutation and conventional breeding work clearly should be integrated irrespective of the amount of mutation breeding work attempted. Mutation breeding is probably being over-emphasized momentarily in the light of the present stage of development of rice breeding by exploitation of natural resources. Although fundamental inquiry in the mutation field may be highly desirable, such inquiry should not be confused with the development of new varieties of rice. Nor should such inquiry be so administered as to be achieved under the guise of rice breeding or at the expense of conventional rice breeding work. Administrative policy at the international level will influence whether or not to implement mutation breeding of rice. Some strictures on the relationship of mutation breeding to basic national programs of rice improvement are brought forward.

INTRODUCTION

Mutation breeding of rice in South and Southeast Asia has taken on prominence since the start of the FAO/IAEA coordinated program of research on the use of induced mutations in rice breeding. This resurgence of activity has raised questions concerning the wisdom of devoting so much talent and so many resources to mutation breeding possibly at the expense of conventional breeding. A part of this concern has arisen from emphasis given mutation breeding by publicizing the activity of FAO/IAEA programs at Vienna and a part of it has come from the relatively expansive effort made in the development of nuclear science in Asian countries. The major source of concern, however, has arisen in the more fundamental area of the effectiveness of the exploitation of natural breeding resources through conventional breeding methods compared with that of mutation breeding, given the present stage of exploitation of natural breeding resources for the improvement of rice.

This paper is based on a trip through various Asian countries to visit plant breeding research centers (Table 1). The trip was made at the request of the International Rice Research Institute (IRRI) for the specific purpose of

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Table 1. Countries and research centers visited (July 31-August 29, 1971).

Pakistan	*Lahore*—Kala Shah Kaku Rice Experiment Station
	Lyallpur—Radiation Genetics Institute
	Tandojam—Atomic Energy Agriculture Research Center
	Moenjodaro—Dokri Rice Station
India	*New Delhi*—Indian Agricultural Research Institute
	Bombay—Bhabha Atomic Energy Institute
	Hyderabad—All-India Coordinated Rice Improvement Project
	Cuttack—Central Rice Research Institute
Thailand	*Bangkok*—Bangkhen Rice Experiment Station, Kasetsart University Atomic Energy Laboratory
	Suphanburi—Rice Experiment Station
Taiwan	*Taipei*—Taiwan Agricultural Research Institute, Botanical Institute of Academia Sinica
	Taichung—Chung-Hsing University, Taichung DAIS
	Chiayi—Chiayi Agricultural Experiment Station
Japan	*Konosu*—Central Agricultural Experiment Station
	Hiratsuka—National Institute of Agricultural Sciences
	Misima—National Institute of Genetics
	Ohmiya—Institute of Radiation Breeding
Philippines	*Los Baños*—The International Rice Research Institute

evaluating the use of induced mutations for the varietal improvement of rice and to suggest improvements in applying the technique.

I attempted to find common ground in the various countries and stations in terms of mutation breeding objectives and mutation breeding achievements, and then to relate these to the proportion of breeding resources committed to mutation breeding and to the expectations of achievement on theoretical and experimental grounds.

Inherent in the charge I received from IRRI was the request for an evaluation of mutation breeding *per se* as well as an evaluation of mutation breeding of rice under the particular conditions of the places visited.

Table 2. Stated objectives of mutation breeding in selected research centers in Asia.

Objective	Research centers (no.)					
	W. Pak.	India	Thailand	Taiwan	Japan	Total
To correct defects in existing varieties	2	2	1	2	0	7
Earliness and short culm	2	1	1	2	2	9
Panicle length, grain/panicle, grain size and quality	1	1	1	0	0	3
To induce disease and insect resistance	0	2	1	1	1	5
Effect of mutagens	1	3	1	0	1	6
To increase protein	0	2	0	1	1	4
To improve grain yield	0	2	0	0	1	2
Fundamental botany and genetics	0	3	0	1	2	6
To achieve directed mutation	0	1	0	0	0	1

The factual material presented below originated in published works, mimeographed reports, and personal conversations with research workers during the survey. The paper is not a review of the known work on mutation breeding of rice, although during the survey I referred to most of the papers published on the subject. Most of the works cited in this paper have appeared since 1965, but the literature cited should not be considered a complete bibiiographic supplement to the reviews by Nayar (1965), and Gustafsson and Gadd (1966). I have taken the statements made to me at their face value with no effort to question their reliability, or general applicability to areas beyond the laboratory where they originated. The information received is summarized in several tables to facilitate comparisons between proposed objectives and claimed achievements against achievements attained and resources used relative to those of conventional breeding.

EXTENT OF MUTATION BREEDING OF RICE IN ASIA

All the objectives and achievements listed below are to my knowledge without positive errors. But, there may be serious deficiencies of both objectives and achievements in this report because of ignorance or oversight on my part. Notwithstanding such possibilities, I feel that the sample data presented are highly representative of the population sampled and meet the requirements of the present evaluation.

In Table 2 the objectives have been collected under nine general classes and the number of research centers in each of five countries listed by class. Table 2 shows a great unanimity of opinion between countries about appropriate objectives for mutation breeding of rice, but also a large duplication of effort within countries. For example, at least nine stations in five countries are working on induction of earliness and short culm—and these are characteristics commonly available from natural sources.

As ambitious as the stated objectives may seem compared with the more modest objectives of conventional breeding programs, they are not without parallel records of achievements. Recorded below (and summarized in Table 3) are some of the reported achievements of mutation breeding of rice in Asia since 1966. If these achievements are in fact realized in stable lines and can be successfully employed in conventional rice breeding programs, there is little doubt that mutation breeding will have contributed to rice improvement in Asia. At present, however, it is difficult to assess the intrinsic worth of the various mutants and impossible to judge whether they were worth the price paid for them compared with similar achievements from natural sources.

PAKISTAN

Tandojam (Miah et al., 1970; Miah and Awan, 1971; A. J. Miah, G. Mustafa, and A. M. Soomro, *unpublished*)

1. IR8 mutants
   —The length-to-width ratio has been increased.

Table 3. Summary of reported achievements of mutation breeding of rice in Asia.

	Pakistan	India	Thailand	Taiwan	Japan
		Grain characters			
Increase in grain size	√	√	—	—	√
Increase in length: width ratio	√	—	—	—	—
Rectify grain defects	√	√	—	—	—
Non-shattering	—	√	—	√	—
Increased yield	—	√	—	√	√
Slow alkali digestion	—	√	—	—	—
Non-glutinous to glutinous	—	—	√	—	—
Increased protein content	—	√	—	√	√
		Plant characters			
Panicle number	√	—	—	—	—
Panicle length	√	—	—	—	√
Shortened culm	√	√	—	√	√
High tillering	√	—	—	—	—
Earliness	√	√	√	√	√
		Disease and insect resistance			
Blast	—	—	√	√	—
Bacterial leaf blight	—	√	—	√	—
Tungro virus	—	—	—	—	—
Grassy stunt virus	—	—	—	—	—
Gall midge	—	—	√	—	—
Stem borer	—	—	—	—	—
Leafhopper	—	—	—	—	—
Planthopper	—	—	—	—	—
		Biological studies			
Increased recombination	—	√	—	—	—
Directed mutation	—	—	—	—	—
		Economics			
Improved variety	—	√	—	—	√

—Mutants 1 to 26 days earlier have been induced.
—Panicle number has been increased.
—Panicle length has been increased by 2 to 5 cm.

2. Kangni 27

Short-culm mutants and early-flowering mutants have been produced. The yields are not good.

3. Dokri Basmati

—Reduction in culm length was accompanied by reduction of panicle length, spikelet fertility, and 100-grain weight and yield.
—Higher tillering, accompanied by reduced yield, has been induced.

4. Jajai

—One-hundred-grain weight varied from 2.2 to 2.6 g; length/width maximum increased from 4.3 to 4.8. Yield was reduced in some mutants and maintained in others.

—Earliness: 26 days maximum improvement was reported.

INDIA

New Delhi (Siddiq, 1968; Siddiq and Swaminathan, 1968*a,b*; Siddiq, Ismail, and Swaminathan, 1969; Swaminathan, 1969; Nerkar, Siddiq, and Puri, 1970; Siddiq et al., 1970; Swaminathan et al., 1970; Swaminathan et al., 1971)

1. Wild type rice was rectified:

—Shattering to partial shattering.

—Dwarfs with normal size panicle and normal grain number were produced.

2. Cross-over frequency in indica x japonica hybrids was enhanced.

3. Resistance to bacterial leaf blight: Some increase in resistance was reported in irradiated indica x japonica hybrids; indica-type grain in mutants from japonica varieties was retained with greater resistance to bacterial leaf blight.

4. Improved varieties were rectified:

—Indica grain type from japonica varieties showed more resistance to alkali digestion.

—Mutants of IR8 with fine grains showed better cooking quality.

5. Protein content

—Mutants with indica-type grain from japonica varieties ranged from 9.1 to 11.2 percent compared to 8.7 percent in the control.

—Hooded mutants of Taichung Native 1 ranged from 9.7 to 11.3 percent compared with 10.2 percent for Taichung Native 1.

—Fertile segregates from 150 semisterile mutants ranged from 8.3 to 13.8 percent compared with 10.2 percent in the control.

Bombay (Rao and Gopal-Ayengar, 1964; Joshua, Rao, and Gopal Ayengar, 1966; Rao and Gopal Ayengar, 1966; Rao et al., 1968; Gopal-Ayengar, Rao, and Joshua, 1969; Narahari, 1969*a,b,c*; A. R. Gopal-Ayengar, N. S. Rao, B. Y. Bhatt, K. B. Mistry, D. C. Joshua, and R. G. Thakare, *unpublished*)

1. Increased protein in IR8 (around 10%): Sixty mutants ranged from 5.6 to 16.5 percent.

2. Induced dwarfs: 0.5 to 2.9 percent of the population were dwarfs.

3. One mutant showed improved yield over Basmati.

Cuttack (Nayak and Padmanabhan, 1970; Nayar and Jachuck, 1968, 1969; Jachuck and Sampath, 1969; Sampath and Jachuck, 1969; Ratho and Jachuck, 1971; Central Rice Research Institute, *unpublished*; R. N. Misra, *unpublished*; P. Nayak, *unpublished*)

1. Mutants from Saturn showed improved yield in both rabi (dry season) and kharif (wet season).

—Rabi: Saturn control, 3,625 kg/ha; Saturn mutant, SM-14, 5,275 kg/ha.

—Kharif: Saturn control, 4,275 kg/ha; Saturn mutant, SM-14, 4,975 kg/ha.

2. Short culms with stiff straw were easily isolated.
—Short culm mutants of Saturn and Tainan 3 gave high yields.
—The dwarfing genes in some of the mutants were different from the one found in Taichung Native 1.
3. Undesirable traits such as awning, shattering, and red pericarp have been removed from "spontanea" rices.
4. Resistance to bacterial leaf blight was increased at each generation of selection through the M_4 generation where lines with a high degree of resistance were found.

THAILAND
(Dasananda and Khambanonda, 1970; Khambanonda, 1971; P. Khambanonda, *unpublished*; T. Kawai, *unpublished*)
1. Lines 23 days earlier than the original variety have been produced but they lodge, yield less, and are more nearly sterile.
2. Blast resistance was induced in a susceptible variety. The original variety scores were near 7 (A blast score of 1 signifies high resistance and a blast score of 7, high susceptibility.) The induced scores were 2 to 3. The induced scores later regressed to 4 to 5. New experimental lines from conventional breeding program were scored 4 to 6.
3. IR5 was changed from nonglutinous to glutinous.
4. Slight improvement in resistance to gall midge was found.

TAIWAN
(Ouang, 1964; Li, Hu, and Woo, 1965, 1966; Huang and Chuang, 1967; Lou and Huang, 1968; Hu, Wu, and Li, 1970; Tong, Chu, and Li, 1970; Li, Hu, and Woo, 1971; S. C. Woo and H. W. Li, *unpublished*)
1. Hybrid selections, using selected high yielding mutants as one parent, have performed well; none has yet exceeded certain other hybrid selections now being produced over most of Taiwan.
2. Semidwarfs occur frequently, but usually carry some defect that is corrected by outcrossing; indica-like semidwarfs have been produced from japonica.
3. Mutants have been found resistant to blast, leaf blight, and other diseases for two seasons.
4. Early mutants have occurred.
5. Protein content of 107 mutants ranged from 5.5 to 13.3 percent; protein content of original varieties ranged from 7.6 to 8.5 percent (a later analysis of total protein in 15 natural strains showed a range of 8.1 to 18.5%).

JAPAN
Hiratsuka (Kawai, 1967, 1968*a*,*b*, 1969; T. Kawai, *unpublished*; Kawai and Sato, 1965, 1969; Sato, 1966)
1. Higher yield (103% of control or more).
2. Short culm and earliness with yield 98 percent of control or more have been isolated.

3. Early heading was found in 1.4 percent of M_2 strains. Grain yield of a few early strains equalled control; many showed shorter culms, and a few showed increases in panicle length, spikelets per panicle, grain weight per panicle, panicle density, and 1,000-grain weight.

4. Frequency of beneficial mutants has been found to be 2.56 to 2.80 percent of spikes for high yielding and 2.80 percent for short culm.

5. Beneficial morphological mutants were found in 3.8 percent of progenies after X-rays and 2.8 percent after neutrons.

6. Improved varieties: "Reimei" (Futsuhara, Toriyama, and Tsunoda, 1967), a mutant of Fujiminori, now a leading variety in northern Honshu, ranked second in acreage in Japan in 1965. In addition to being equal to or better than the original variety, it is more stable over years and places.

Ohmiya (Tanaka, 1969*a,b*, 1971; Tanaka and Sekiguchi, 1966)

Protein content 2.5 times higher than mother line has been recovered in early high yielding mutants. In 545 mutant lines (from Norin 8; brown rice = 6.5%) a range of from 4.2 to 16.3 percent protein was found. In one mutant the stature was shorter; it flowered earlier and had high yielding capacity with protein content of 13 to 15 percent.

Published record of research on mutation breeding of rice

Nayar (1965) reviewed most of the mutation work in rice up to 1965. Gustafsson and Gadd (1966) attempted to relate the breeding characteristics and accomplishments to the work which had been done with rice mutations. These two review papers summarize the contributions to rice mutation work through 1965. At about this time the FAO/IAEA coordinated program of research on the use of induced mutations in rice breeding was started (Sigurbjörnsson, 1968). Reports between 1966 and 1971 emphasized breeding objectives themselves; previously much more effort seems to have been directed toward investigation of mutagens, dosages, mutant types, M_1 effects, segregation in M_2 and M_3, and genetic and cytological characteristics. Nevertheless, Oka, Hayashi, and Shiojiri (1958), Bateman (1959), Kao, Hu, Chang, and Oka (1960), Sakai and Suzuki (1964), Jalil and Yamaguchi (1964), and Miah and Yamaguchi (1965*a,b*) reported studies on quantitative variations from induced mutations in rice, which though not selective breeding, still represented closely allied subject matter. Li et al. (1965, 1966) reported work directed primarily at breeding objectives. None of this early work resulted in much improvement in rice production.

Throughout recent years, both in published papers (Hu et al., 1970; Dasananda and Khambanonda, 1970) and in conversation, explanations have been sought for why, after 20 years of mutation work on rice, so few true genetic advances in rice performance can be attributed to this effort.

Undoubtedly, the explanation is complex. It may be traced to a few important sources. For example, most early work was concentrated on mutagens, M_1 effects, dose, treatment methodology, and, to a slightly lesser degree, on mutation frequency, mutation spectrum, and cytogenetic effects. From 1950 to 1966 over three-fourths of the papers, when multiply listed according to the subjects of investigation reported in each paper, dealt almost exclusively with these areas (Table 4). This concentration was necessary in a field that had been recently revived after World War II and in which many new resources for inducing mutations required evaluation. As shown in Table 4, however, only a small shift in emphasis has occurred since 1966, after the initiation of the FAO/IAEA revival of mutation breeding of rice in 1964. From 1966 to 1971 nearly two-thirds of the subject-paper combinations still dealt with mutagens, M_1 effects, etc. The concentration on subjects more closely related to plant improvement was actually greater than the proportions indicate, however, since the two-thirds result from a larger proportion of papers dealing with "mixed" subject matter, than during the period 1950 to 1966. Nevertheless, it is somewhat surprising that such a large proportion of the research effort should be devoted to these ancillary fields in light of the ambitious breeding objectives summarized in Table 2 and the stated achievements of mutation breeding summarized in Table 3.

Proportion of experimental land area used for mutation breeding

Neither the amount of money expended nor even the number of persons engaged in what has been labeled mutation breeding is a good measure of the relative amount of effort toward rice improvement that can be ascribed to mutation breeding compared with conventional breeding. In the final analysis the resources used in developing a variety, that is, the size and number of experimental plots, the number of nurseries, replications, locations, and years more nearly reflect effort toward plant improvement than other less direct components of the cost function of plant breeding. I therefore feel that the land area devoted to mutation breeding and conventional breeding more

Table 4. Published and unpublished papers on mutation breeding of rice since 1950 listed according to subject matter reported.

Subject	Subject-paper combinations (no.)		
	1950-66	1966-71	Total
Mutagens	20	20	40
Dose and M_1 effects	27	22	49
Treatment methods	24	12	36
Mutation spectrum	21	11	32
Mutation frequency	25	22	47
Cytology, sterility, lethality	34	7	41
Polygene and quantitative effects	18	11	29
Character improvement	7	22	29
Variety development	11	11	22
Genetic segregation	3	7	10
Selection	1	3	4
Probability of detection	2	0	2
Total subject-paper combinations	193	148	341
Total papers	146	55	201

Table 5. Extent of mutation breeding of rice in selected research centers in Asia — areas of land employed.

Country	Centers (no.)	Area (ha) All breeding	Area (ha) Mutation breeding	Ratio[a] (%)
Pakistan	4	21.1	2.2	10.4
India	3	9.7	3.2	33.0
Thailand	2	10.0	1.7	17.0
Taiwan	3	8.5	0.1	1.2
Japan	3	16.5	3.1	18.8
Total	16	65.8	10.3	15.6

[a]Land devoted to mutation breeding in percent of land for all breeding purposes.

nearly reflects the comparative effort being made in these two research areas than any other available data. This assertion presumes that the money, personnel, numbers of experiments, and all other such data categories are highly correlated with the land area that is used for plant breeding. While dilettantism either in ancillary research or in the effective use of personnel will necessarily reduce the correlation coefficients, the core of the relationship will not be eradicated.

Table 5 shows the land area used for mutation breeding and conventional breeding at several research centers in Asia. The data do not necessarily reflect national averages nor should the data be compared from one country to another. It is impressive that in no sample in any country did the area of land devoted to mutation breeding approach in size the areas on the same stations devoted to conventional breeding (Table 5).

In the comparisons made, approximately 30 percent of the research work in mutation breeding has been devoted to practical breeding objectives and only 15 percent of the land area in all rice breeding was devoted to mutation breeding. It is instructive to compare the limited objectives and land area allotted to breeding at IRRI (Tables 6 and 7).

THE NEED FOR AND ADEQUACY OF MUTATION BREEDING OF RICE

Probability of improvement

If one sets up a 95-percent level of assurance that a desired change, say earliness, will be realized and the rate of change is 1:1,000 M_2 plants, then with the highly efficient "einkorn" method, approximately 20,000 M_2 plants would be required. If the magnitude of change is carried to the point where no more than one out of 10 of the recovered mutants yields at least as well as the original variety, approximately 200,000 M_2 plants would be required. If one added to these objectives the still more difficult but equally reasonable

Table 6. Stated objectives of a single conventional rice breeding program (IRRI) in tropical Asia (T. T. Chang, *personal communication*)

Early objectives

- Yield response to nitrogen
- Lodging resistance through use of short, stiff culms
- Plant type to enhance sunlight reception and use
- Early maturity

Current objectives

- Development of disease and insect resistance
- Improvement of milling quality and cooking characteristics
- Protein content
- Cold resistance

one of a high level of resistance to some pathogen, say with an induced mutant expectancy of 1:100,000, an M_2 population of at least 20 billion plants would be required for the simultaneous recovery of earliness, high yield, and disease resistance (Yoshida, 1962; Kawai and Sato, 1969).

This one fact of arithmetic probably explains better than all other considerations why so many successful mutation breeding experiments are reported and why so little improvement in production can be ascribed to mutation breeding. It may even suggest that mutation breeding should quit itself of complex varietal development separate from conventional breeding programs.

Any genetic change, irrespective of its source, which provokes a large phenotypic deviation from the normal adaptive syndrome of characteristics will be unlikely to produce an improvement in adaptation. The understanding of this fundamental principle was greatly enhanced by Fisher (1958, p. 41-44), who in 1929, in his discussion of the nature of adaptation, pointed out that the closeness with which an organism is adapted to its environment includes the degree of conformity to the environment of numerous features of the phenotype. "For the more complex the adaptation, the more numerous the different features of conformity, the more essentially adaptive the situation is recognized to be."

Table 7. Allocation of land areas to rice breeding at the International Rice Research Institute (single season) (H. M. Beachell and G. S. Khush, *personal communication*)

Function	Area (ha)
World collection and genetic studies	1
F_2 and bulk hybrids	1
Pedigree rows	4
Yield trials, nurseries for disease and insect testing, and seed purification	4
Mutation breeding	0
Total	10

Fisher might have gone on to say that the environment presents, not only its external components such as soils, fertilizers, water supply, and sunlight, but also features internal to the organism itself including, in the ultimate, the remaining genes in the nucleus with respect to a given gene. Hence, any change in genetic composition of a nucleus in a crop plant must first conform to the demands of the nuclear environment itself and from these extend further and further outward through the cytoplasm, tissues, organs, and individuals of the species to the complex world of populations, diseases, insect pests, soils, climate, and ultimately to the nutritional, taste, and economic requirements of man.

Fisher likened this situation to the geometric features of the closeness with which a point A approaches a fixed point O, where zero distance between A and O may be conceived as perfect conformity. All possible positions in which A will be closer to O will be enclosed by a sphere passing through A and centered at O. If A is moved any distance, r, in any direction and is carried outside the sphere, it will increase the distance AO and will worsen adaptation. If it is carried into the sphere, it will decrease the distance AO and hence improve adaptation. If r is sufficiently small, the chances of being carried into or out of the sphere are equal, but if r is equal to or greater than the diameter, d, of the sphere, there is no chance whatever for improvement. The probability of improvement in fact is $\frac{1}{2}(1 - r/d)$. Fisher's adaptation sphere was conceived as of many diameters. In fact, "for any degree of adaptation," Fisher said, "there will be a standard magnitude of change represented by $d/\sqrt{n}$," where n = the number of dimensions. "The higher the adaptation, the smaller will this standard be, and consequently the smaller the probability that a change of given magnitude shall effect an improvement." For values of r divided by $d/\sqrt{n}$, the following relationship exists:

$r\sqrt{n}/d$	*Plus effects*	*Minus effects*
(Very small)	1	1.0
1/10	1	1.3
1/2	1	3.5
1	1	13.0
2	1	236.0
3	1	7852.0

Thus if one is dealing with a highly adapted strain and is unable or unwilling to alter the environment, a change of any great magnitude is almost certain to be deleterious in character.

This situation is well illustrated in rice where the use of short, stiff, erect mutants from tall, lax types do extremely poorly in the old environment mixed with the tall plants, but perform well, sometimes exceedingly well, if isolated in pure stands and fertilized with high rates of nitrogen. Kawai and Sato (1969) reported that even with a weak positive correlation of earliness and yield, the latter was seriously reduced in extremely early forms.

The above commonly accepted principle is usually in the back of the mind of every agronomist, but the magnitude of the forces involved is frequently lost sight of. One must be continuously alert to the magnitude of any planned genetic change as well as to existing and forecast changes in the environment of his crop.

The principle is related to mutation breeding through the relationship of mutant frequency and magnitude of change. For example, when M_2 plants of irradiated peanuts (*Arachis hypogaea* L.) were classified in terms of the degree to which they departed morphologically from the norm of the mother variety, the frequency distribution was $y = be^{-ax}$, where y is the frequency, $b = y$ at $x = 0$, $a = \log_e P$, $P = \sum[Y_1/Y_2 \ldots Y_i/Y_{i+1}]/n - 1$, $x =$ magnitude of change, and $Y =$ number of mutant plants in successive classes of x (Gregory, 1965). That is, the frequency of change increased exponentially with decrease in the magnitude of the effect.

Gaul (1963) pointed out that the small mutations of barley were at least 50 times as frequent as the large mutations. Baur (1924) had preceded Gaul in emphasizing the evolutionary importance of the high frequency of small variations, and East (1936) had pointed out the genetic, breeding, and evolutionary significance of numerous small deviations. More recently, Mukai (1964) states that in *Drosophila* the rates of both spontaneous and radiation-induced polygenic mutations are extremely high compared with those of major genes. Whatever the source of these small variations, they are the building blocks of evolutionary change in a changing environment referred to by Darwin and by his successors in the science of genetics.

A more recent discussion of this problem and its relationship to the role of induced mutations in plant improvement can be found in Brock (1971), who cites the calculations of Kimura, experimental data from Mukai, and a number of other authors to the effect that mutation frequencies of small effect are high in natural situations and would perhaps be higher if enzyme-mediated repair systems did not intervene.

For any instance of inducing a mutant, given our present knowledge, the plant breeder may have little or no idea whether the change can occur or, if it can, what the probability of its occurrence is in his material. There are, however, some guidelines which he may follow. If, for example, other members of the genus or even the family with which he is working have produced such a mutant naturally or artificially, or even if some more distantly related plant group has exhibited the mutant, the breeder may have some confidence that the mutant change can occur. He will not know, of course, what the reaction may be in his material, whether the new change will be lethal, sterilizing, or so debilitating as to render it useless for plant breeding. Mutation frequency studies provide some basis for estimation though many of these investigations were characterized by the ease with which the mutant could be counted rather than by the nature of the mutation itself. In the area of mutants of positive interest to plant breeding, some instances may be cited which provide reliable grounds for estimating whether mutant frequency may lie within the scope of a given plant breeding program. Using the standard of chlorophyll mutants in barley, Gustafsson (1965) summarized the rates of production of several useful mutants:

Early work (10,000 roentgens X-rays)	*Approximate order of magnitude*
Proportion of erectoid to chlorophyll	1:7-10
Proportion of erectoid (deleterious) to erectoid which equalled control in production	1:5-6
Therefore the proportion of useful erectoid:chlorophyll	1:50

With regard to their later work reporting rates of mutation in barley (Gustafsson, 1965), additional information was as follows (adjusted to 10,000 rad/10,000 spike progenies):

10,000 total progenies:870 progenies segregating chlorophyll mutants or about 12:1
122 progenies segregating erectoids or about 1 erectoid:7 chlorophyll
23 progenies segregating erectoids equal in productivity to the mother strain or about 1 erectoid: 40 chlorophyll.

Summarizing the occurrence of other favorable mutants along with the 23 erectoids, Gustafsson gave the following:

High-productive erectoids	23
Other high-productive mutant types	13
High-productive homozygous chromosomal types	800
High-productive quantitative mutants	180
Total	1016

or one favorable genetic change:10 at 10,000 rad. Deleterious changes identified in the same population were as follows:

Chlorophyll mutants	870
Poor erectoids	100
Other visible mutants	410
Chromosomal aberrations	200
Viability-decreasing quantitative effects	4320
Sterility mutants	870
Total	6770
Unaccounted for	2214
Grand total	10000

Thus if the breeder were only looking for the erectoid mutation and would not accept a loss in productivity under the conditions described, he could isolate 23 such types from a total of 123 types in 10,000 M_2 plants after 1 year for the M_1 generation, 1 year for M_2, and at least 1 year in replicated trials. If the breeder wished to be even more certain, he might have to invest 3 to 5 years in replicated testing. In highly bred material such as barley in Sweden, he may just have isolated the line giving rise to an improved variety and be ready to place it in the official variety trials. On the other hand, in a less well developed breeding program, he may have only made the equivalent of another plant introduction.

If chlorophyll mutations could be used in rice as Gustafsson has done in barley, it might be of significance to review some of the reports on the frequency of induced chlorophyll mutations reported for rice. Matsuo, Yamaguchi, and Ando (1958) showed that the percentage of chlorophyll mutations rose approximately linearly with increasing dose following irradiation with both X-rays and thermal neutrons to 6 to 7 percent maximum at approximately 30 kR before falling away at higher doses. This compares to 8.7 percent for the barley data mentioned above. Yamaguchi (1962) arrived at similar values in M_2

Table 8. Natural resources known to exist in the world collection of rice (T. T. Chang, *personal communication*).

Characteristic	Natural germ plasm resources				
	Abundant	Less abundant	Moderate	Scarce	Rare
Grain quality	√	—	—	—	—
Earliness	√	—	—	—	—
Short culm	—	—	√	—	—
Blast disease resistance	—	—	—	√	—
Bacterial leaf blight resistance	—	—	—	√	—
Virus disease resistance	—	—	—	—	√
Sheath blight resistance	—	—	—	—	√
Gall midge resistance	—	—	√	—	—
Stem borer resistance	—	—	√	—	—
Leafhopper resistance	—	√	—	—	—

for similar doses of gamma rays. Under the restrictions of post-treatments with water and sodium hydrosulfide, he obtained 6.9 and 8.6 percent, respectively, at 30 kR. Tanaka and Sekiguchi (1966) reported similar values for acute radiation of dried seeds.

Thus the role of mutation breeding in any crop apparently will reach its maximum efficiency only if steady directional selection pressure is applied to the field of numerous small changes in addition to any changes of large effect that occur. Considerably more success may also be expected in the presence of an ingeniously expanded Fisher's adaptation sphere.

Position of mutation breeding in a plant breeding program

The use of mutation research and mutant induction for rice breeding purposes has to do with more complex questions than collecting favorable mutant plants. Ideally, the breeder must balance the priorities of all his factors and operations and order them in terms of their relation to the basic needs of the industry, today, in the near future, and in the far future. In this context, mutation breeding may be completely out of place in the early exploitative years of a breeding program, occupy a similar role to plant introduction at a later stage, but finally come to be the primary source of required modification in a mature or old breeding program.

At any given moment during the development and maturation of a breeding program, the need for induced mutation is related mostly to the genetic wealth of the world collection. In the presence of resources which are as yet largely unexploited, there is little justification for providing additional resources by mutation at the expense of neglecting the ones already in hand (Tables 8 and 9) (Shastry et al., 1971; see also Chang elsewhere in this book).

The philosophy of varietal improvement on an international basis will influence the need to employ induced mutation as a supplement to conventional

Table 9. Distribution of disease and pest resistant varieties from northeast India (Shastry et al., 1971).

			Varieties (no.) found resistant to					
Region	District	Plains/ hills	Blast	Blight	Rice tungro virus	Gall midge	Stem borer	Green leaf-hoppers
NEFA	Subansiri	Hills	–	8	–			
	Siang	Hills	–	5	–		1	
	Luhit	Hills	–	1	–			
	Tirap	Hills	–	1	–			
Assam	Kamrup	Plains	4	–	–	3	4	1
	N. Lakhimpur	Plains	5	–	6	6		
	Sibsagar	Plains	3	–	8[a]	8[b]	3[a]	
	M and NC Hills	Hills	3	–	8	9	1	
Meghalaya	K and J Hills	Hills	6	–	–	5	3	
	Garo Hills	Hills	6	–	–	12	11	6
Nagaland	Mokokchung	Hills	–	1	–			
Total			27	16	22	43	23	7

[a]Includes 5 from RRS, Titabar. [b]All from RRS, Titabar.

breeding. One might conceive of an international program where a central research institute maintains the world collection, devotes all of its effort to uncovering fortunate combinations, and then sends out bulk F_2 or F_3 populations from which the fortunate combinations arose to all of the peripheral local environments for final varietal development. Such a program has much in favor of it: more explicit local adaptation, avoidance of reducing the genetic base of world rice production, and feedback of new, different, but superior, strains to the world collection. Such an output and inflow might largely do away with the need for artificial mutation for a long time to come.

But, if the philosophy of the development of superior varieties at the center prevails, then the genetic base will tend to narrow, the world collection will be a static pool of the collected samples possible at its initiation, and the loosely adapted central developments will be subject to improvement through mutation so artificial mutation breeding will have a definite place in the local breeding programs.

This situation also means that where international or other collaborative breeding development is envisioned, if more than one supporting agency is involved, the separate funds allocated might compete for personnel and space. In mutation breeding of rice, it is of paramount importance to have some basic philosophical and policy agreement at the highest levels. I strongly recommend, at least on the international level, that different supporting agencies come to some common, broadly conceived philosophy of short- and long-term programs of rice improvement and the use of induced mutations in it.

CONCLUSION

I have commented on the extent to which the induction of mutations is being used in Asian countries as a supplementary or alternative technique to conventional rice breeding by hybridization. I have discussed the need for mutation breeding and the adequacy of approach and methodology in mutation breeding. I have presented some of the achievements of current mutation breeding programs.

I have called attention to broad principles operative in connection with mutation breeding and have made some assessment of the chance that a breeder could meet the demands of these principles without making disproportionate inroads on other breeding operations.

There are certain circumstances under which a change in a cultivated species cannot be achieved through conventional breeding. There are others which, though attainable through conventional means, can best be produced by mutation breeding. An example of the latter is the change of red-grained Sonora 64 wheat to white-grained Sharbati Sonora reported by Swaminathan (1969) a small phenotypic change of considerable economic value.

An example of the former occurred in the peppermint oil industry of the United States with respect to resistance to *Verticillium*. This fungus attacked the only economic source of the oil, a strictly vegetative clone susceptible to the wilt. Murray (1969) reported the recovery of seven highly resistant, five moderately resistant, and 50 slightly resistant strains from a total of 6 million substolons which arose from an original irradiated population of 100,000 stolons.

Finally, a situation may arise where a vitally important characteristic exists at a single locus or a few loci thus subjecting the industry to the risk of being invaded by some innovative pathogen.

The gene-for-gene mutation systems of host and parasite described by Flor (1955) in *Linum* indicate the dangers of holding critical single-locus characteristics constant in vast populations of the host. Therefore, if the dwarf, stiff strawed, erect-leaved high-yielding rice varieties have a small multifactorial base in the world collection of rice, there is a present and pressing need for their further induction and incorporation into many superior genetic backgrounds. There is hardly any doubt that this could be accomplished on a grand scale if the experience with the induction of erectoid types of barley may be taken as example. In barley, Swedish plant breeders analyzed 166 erectoid mutations between 1951 and 1960 (MacKey, 1961). Many of these were either repeat mutations or alleles at the same locus, but Hagberg, Gustafsson, and Ehrenberg (1958) showed that 70 of the erectoid mutations represented no fewer than 22 loci. By 1969, Gustafsson (1969) reported that a total of 685 erectoid mutants of barley were then known from 26 different loci. As MacKey (1961) pointed out, most of these erectoids are agronomically poor in their original backgrounds. But, if needed, they would serve as an almost inexhaustible source of the character. The new plant form required of modern rice production exists in more than one collection and indeed has been induced artificially. Until now, however, no such multiplicity of loci has been uncovered in rice as that reported in barley.

In an old or fully matured breeding program, the question arises as to whether the rate of improvement can be raised above that of naturally occurring mutation by further recombination and induced mutation. While at the present stage of rice breeding, this question may seem academic, the search for the answer must be started now, 10 to 30 years in advance of the time for decision. There is no reason to believe that the so-called "green revolution" in rice will repeat itself any more than it has in maize. The programs of improvement will mature and their support will become more conservative, varietal competition more intense, and improvements smaller and more difficult to achieve. It is at this time that we will need a great deal more fundamental information about mutation and its control than the plant breeders possess at present.

SOME SPECIFIC OBSERVATIONS

1. The separation of the plant breeding operations and facilities from mutation breeding denies the mutation breeder the status of a plant breeder and renders him ineffectual while at the same time it segregates mutation breeding from the normal sequence of events of an integrated varietal development program. The physical separation leads to antagonisms and meaningless expensive competition for resources, prestige, and recognition.

2. The confusion of mutation production with the breeding of new varieties (when in fact the mutation breeder has contributed only another entry of questionable need, if not value, to the world collection of rice varieties) leads to the rejection of appropriate use of mutation breeding by the conventional plant breeder.

3. Personal involvement of personnel and prior commitments of funding agencies as well as national commitments to nuclear science lead to overemphasis on the potential of mutation breeding in rice improvement.

4. The expansion of personnel and new facilities in atomic research centers without concomitant expansion in land and conventional breeding facilities coupled with their separation tends to deny the mutation breeder the opportunity to do any real plant breeding. He, more often than not, is required to send a collection of ill-tested materials to a conventional breeding station where he is unable to observe it. If nuclear science establishments insist on staying in the mutation breeding field, they should acquire the customary land and facilities necessary for adequate plant breeding procedure, or better, make budgetary allowances for contractual arrangements with established plant breeding centers for land and facilities or, better still, make common cause with plant breeding centers, assisting them in the expansion in land and facilities required to handle the added work load.

5. The mutation breeder needs to recognize the limits of his function and to abandon the notion of the creation of new varieties as opposed to making

limited improvements in established varieties and adding specific contributions to the world bank of germ plasm resources.

6. Mutation breeding suffers from the fact that the young men engaged are frequently inexperienced in conventional breeding, having gone directly from their graduate training into mutation breeding.

7. Mutation breeding could make a contribution to rice improvement in three areas.

- Mutations for rare or unavailable characteristics.
- Mutations for adaptation to new and potentially useful environments.
- Mutations to alter physiological control processes that evolved to fit the organism to specified survival conditions but no longer are required in modern agriculture (for example, feedback mechanisms that cut off starch accumulation).

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Discussion: Mutation breeding in rice improvement

E. A. Siddiq: I would like to point out a few areas where mutation breeding can assist conventional breeding programs: 1) to combine the "erectoid" type with semidwarf plant type, 2) to obtain dominant and "semi-dominant" dwarfs, 3) to improve physiological efficiency or even to change leaf anatomy, and 4) to improve protein distribution in the grain.

A. O. Abifarin: Would such objectives as earliness and quality improvement mentioned in mutation breeding programs have been achieved earlier by using conventional breeding methods?

W. C. Gregory: The continuous efforts of conventional breeding and the off-and-on history of mutation breeding cannot easily be compared. Undoubtedly, early maturing lines have been developed from conventional breeding programs. The more pertinent point is that these achievements in mutation programs are isolated in separate lines and are not combined in individual varieties. Therefore, the job of combining these characteristics into one variety still lies ahead of the mutation breeder or the conventional breeder who wishes to make use of them.

A. O. Abifarin: In most cases, there has been no mention of the relative performance of these mutant varieties for yield or other traits. What is the correlation between these mutant traits and those agronomically desirable traits such as grain yield?

W. C. Gregory: In most cases of reported mutation induction, the parallel breeding and testing work has not been done. This accounts for the scarcity of data on mutant performance relative to other strains. In general, where tests have been conducted, as the intensity of mutant expression rose, i.e. as the magnitude of change increased, characters such as yield became progressively reduced, following the expectation of Fisher's theory. Gaul (Gaul, H. 1963. Mutationen in der Pflanzenzuchtung. Z. Pflanzenzuecht. 50:194-307) showed this to be true for earliness in barley and Kawai and Sato (Kawai, T., and H. Sato. 1969. Studies on early heading mutations in rice. Bull. Nat. Inst. Agr. Sci. Ser. D, 20:1-33) also studied correlations between heading date and a number of agronomic traits. Some of the significant correlations were as follows: culm length, 0.723; panicles per plant, −0.323; panicle length, −0.438; fertility, 0.460. To the extent that such correlations are forward steps in improvement, the picture I painted concerning multiple selection criteria in mutation breeding is somewhat less bleak.

R. A. Marie: Can you explain why some plant species apparently mutate easier than others?

W. C. Gregory: No, I cannot. There is reason, however, to suspect tandem repeats of genetic information in higher organisms with only a portion of the redundancy operational at a given time. If this is indeed the situation, then one can imagine that different degrees of tandem redundancy would provide easy answers for mutable loci and organisms. The evidence for such an arrangement of genetic information within genes is mostly from the field of molecular genetics and is highly controversial at present. There is also the possible influence of abundance and activity of repair agencies such as DNA polymerase which conceivably vary from species to species.

S. C. HSIEH: Mutation breeding is a tool for creating new genes that might bring about good characters. Although breeding programs at several centers have made good progress in improving yield, disease resistance, and protein, mutation breeding still provides a good chance to induce changes in these characters. The major problem is how to screen for the favorable mutants. We need to pay more attention to the screening part.

T. T. CHANG: At IRRI we find it advantageous to have an objective evaluation of promising genotypes on a systematic scale. For the promising mutants reported by various agencies, we have gathered seeds from the originating stations and grown 54 mutants along with their parents and those hybrids of a similar category in a current field experiment. The results will be summarized in the IRRI Annual Report for 1971.

G. MCLEAN: Judging from the results, I feel that inadequate selection among treated progenies is still a weakness of most mutation breeding programs.

D. S. ATHWAL: Mutation breeding is an additional tool to create variability and can probably be used with advantage to a limited extent or at selected research centers. My major objection is to pursuing this approach at the cost of conventional breeding methods especially by plant breeders in many developing countries.

G. MCLEAN: Are mutation breeding units of atomic energy research centers integrated with the agricultural experimental stations?

W. C. Gregory: Except for Thailand where the two programs are conducted together, all countries had separate atomic institutes from which the "promising mutants" had to be sent to a regular breeding station for evaluation.

G. MCLEAN: It seems to be a defective policy to create agencies that become semi-autonomous structures.

W. C. Gregory: Just as serious, intelligent young men are cut off from the support and collaboration of more experienced staff located in experiment stations.

L. M. ROBERTS: What are the examples of real and significant contributions of mutation breeding in the U.S.?

W. C. Gregory: I know of only one striking achievement of mutation breeding in the United States – the one in which Murray (Murray, M. J. 1969. Successful use of irradiation breeding to obtain *Verticillium*-resistant strains of peppermint, *Mentha piperita* L., p. 345-371. *In* Induced mutations in plants. International Atomic Energy Agency, Vienna.) induced both great vegetative vigor and *Verticillium wilt* resistance in *Mentha piperita* while holding the high quality and yield of oil of the original clone. Another achievement is the work of the late A. T. Wallace and his associates on induced resistance to a strain of *Helminthosporium victoriae* in oats. They also induced resistance to stem rust and crown rust in the variety Floriland. From the strains resistant to stem rust the variety Florad was produced. Selections from Florad x Coker 58-7 resulted in two released varieties, Florida 500, which is resistant to stem rust and Florida 501, which is resistant to crown rust. For a listing of varieties produced with induced mutations or having induced mutations in their background, see Sigurbjörnsson, B., and A. Micke. 1969. Progress in mutation breeding, p. 673-698. *In* Induced mutations in plants. International Atomic Energy Agency, Vienna. Most other achievements in the U.S. listed by Sigurbjörnsson and Micke are either so indirectly related to artificially induced mutation as to make the mutation-breeding contribution uncertain or they involve such characters as straw strength in wheat, etc.

I should comment about the improved yield of peanuts selected from an X-rayed single plant progeny, since many exaggerated statements have been made concerning their performance. About a 10 percent gain in yield was realized in a single cycle of selection following the radiation treatments.

Rice breeding with induced mutations

A. Micke, S. C. Hsieh, B. Sigurbjörnsson

The Food and Agriculture Organization and the International Atomic Energy Agency jointly sponsored a 5-year coordinated program on the use of induced mutations for rice improvement in 10 countries. Approximately 60 indica and japonica rice varieties were treated with physical and chemical mutagens. The participating scientists selected a large number of promising mutants from the mutagen-treated populations. Mutant lines with short stature and lodging resistance, early maturity, increased protein content, increased disease resistance, and high yield were obtained. Some of them are expected to be released directly to farmers as new varieties, others are being used in cross-breeding programs.

INTRODUCTION

Recent advances in rice breeding have dramatically increased yields. At the same time they have drawn attention to a number of shortcomings: resistance against diseases, insect pests, drought, and soil salinity, as well as various quality characters, and adaptation to modern agricultural production techniques, including high levels of fertilization and combine harvesting.

Recognizing the need to further improve the new high-yielding varieties, FAO and the International Atomic Energy Agency (IAEA) jointly organized, a coordinated research program, Rice Breeding with Induced Mutations, in institutes in several countries in Southeast Asia, the Far East, and Latin America. The program was started in 1964 and ran for 5 years. The breeding work and associated research were supported financially under IAEA research contracts. They were coordinated through annual meetings convened at various locations in the regions. IAEA further assisted through mutagenic seed treatment, radiation services, and technical guidance through the staff of the IAEA laboratory.

In addition to conducting research on fundamental aspects of mutagen application and mutagen action on genetic material, the program concentrated on such practical goals as inducing short-statured, more lodging-resistant mutants; inducing early-maturing mutants; improving grain quality; and inducing disease- and pest-resistant mutants from existing productive varieties (IAEA, 1968, 1970, 1971).

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TECHNIQUES

Each cooperating institution was encouraged to choose its own breeding and research goals, methods, and materials but the total program constituted a comprehensive approach to solving rice breeding problems. The leading japonica and indica rice varieties in the geographic locations of the cooperating institutions were used for the irradiation experiment. Some institutions included advanced breeding lines in their programs which had not yet been released as varieties. Approximately 60 varieties were treated with mutagens by the cooperators. Examples of mutagen and doses used are shown in Table 1. Details of the experimental methods of each research contractor can be found in IAEA publications (IAEA, 1968, 1970, 1971).

The optimal dose ranges of X- and gamma-irradiation were 15 to 30 krads for indica varieties and 15 to 25 krads for japonica varieties. The dose range of fast neutrons suitable for rice was approximat [illegible] tenth the gamma dose. Ethylmethane sulphonate was the main chemical mutagen used for seed treatments. The seeds were usually presoaked in distilled water before mutagen treatments. This reduced the treatment time and the physiological damage caused to the M_1 plants. Usually, the mutagen solutions were not buffered, but after treatment the seeds were washed in running water.

The handling of mutagen-treated material in successive generations varied somewhat, depending on the objectives of the individual breeding programs. At the annual research coordination meetings, however, common practices for selecting mutants of economic importance were recommended.

At least 200 to 300 seeds were used in each treatment, and about 3,000 to 5,000 seeds per M_1 generation were used. The treated seeds were sown in a nursery or in seeding boxes and later transplanted into the field. The size of the M_1 population in the field depended, of course, on the breeding objectives, but in general a minimum of 1.000 to 3,000 seeds were grown. If the material was not planted in isolation, usually three panicles were bagged to prevent out-crossing. From each M_1 panicle, 15 to 25 seeds were planted in rows for identifying mutants on a single-plant basis in the M_2 generation. The M_3

Table 1. Examples of mutagens and doses used in rice mutation breeding programs.

Mutagens	Doses
Gamma rays	5 to 60 krad
Fast neutrons	1 to 3.5 krad
Thermal neutrons	5 to 40 (10^{12} N/cm^2)
X-rays	20 to 25 KR
EMS	0.1 to 2%
MMS	0.02 to 0.15%
EO	0.15%
EI	0.05%
DES	0.01 to 0.2%
PMS	0.4 to 1.0%

generation was again grown in progeny rows and again checked for mutants. Routine tests for disease resistance were made often. Each row that appeared promising and uniform was harvested in bulk. In the M_4 generation, promising and true-breeding lines were harvested in bulk as lines. These lines, together with the checks, were subjected to the preliminary yield trial. In later generations trials for yields and disease resistance were repeated for final evaluation of promising material.

RESULTS

The cooperating scientists succeeded in inducing and selecting a number of mutants of economic importance. In addition, valuable observations were made regarding mutation spectrum, mutation frequency, genetics of induced mutations, and other related problems.

Development of short-statured, lodging-resistant lines

Short-statured plants usually have better lodging resistance and thus remain erect on heavily fertilized soil. Four promising short-statured, indica-type mutant lines have been obtained in Taiwan. Three mutant lines, KT20-74, SH30-21, and YH 1, gave better yield than the variety Taichung Native 1 in regional trials at six locations during 1964-66. At a demonstration farm at Chiayi, YH 1 gave grain yields of 7.1 t/ha in the second crop of 1967 and 8.5 t/ha in the first crop of 1968, or about 20 percent more than the yield of Taichung Native 1 (Li, Hu, and Wu, 1968; Hu, Wu, and Li, 1970). YH 1 is becoming popular among farmers in the central part of Taiwan.

A high-yielding mutant line, M1-273(m), with short culm and an erect growth habit, has been selected in Ceylon after gamma-irradiation of the variety H 4. This mutant line outyields its parent by 50 percent. It yields about 10 percent less than IR8 in dry zones, but 10 percent more than IR8 in wet zones in the yala season. In the maha season, yields were equal to those of IR8 (Ganashan, 1971).

In Guyana, Pawar selected mutants which resist lodging, mature very early, and give high yield. Mutant line M643-4 gave a yield of 5.6 t/ha as compared with 2.9 t/ha of the mother variety, B.G. 79, the most popular variety in Guyana. The increase in yield was mainly due to its resistance to lodging. Farmers were supplied with seeds of this mutant for advanced testing in 1970 (Pawar, 1971).

Other short-statured, lodging-resistant mutant lines were selected from variety Khao Dawk Mali 105 in Thailand (Khambanonda, 1971) and from variety Kangni-27 in West Pakistan (Miah et al., 1970). In East Pakistan, short-statured mutants have been selected from the local variety Dular. Some of them produced twice the yield of the mother variety (Haq et al., 1970). In Korea, Ree (1971) selected 30 short-culmed promising mutant lines from the japonica variety, Palkweng, and he expects that high-yielding varieties can be developed from them for practical cultivation.

Induction of mutants with improved grain quality

A serious shortcoming of modern high-yielding varieties has been their frequently unsatisfactory grain quality. Improvement through induction of mutations seems possible. The induction of indica-type grain characteristics in japonica-type rice has been reported at the Indian Agricultural Research Institute (Swaminathan, Siddiq, Singh, and Pai, 1970). Mutants with glutinous endosperm have been selected from Khao-Tah-Haeng 17, Khao Dawk Mali 105, IR8, and C4-63 in Thailand (Dasananda and Khambanonda, 1970).

Other important aspects of grain quality, protein content, protein quality, and protein localization in the grain have been included in the research program. Although the protein content of rice is strongly affected by different environmental factors there is no doubt that it is genetically controlled (Tong, Chu, and Li, 1970). Of the many genes involved some major ones can strongly influence protein content and protein composition, for example, the opaque-2 and floury-2 corn. Therefore, an attempt to induce mutations for high protein content and good amino acid composition seems worthwhile.

In Japan, Tanaka and Takagi (1970) analyzed 545 mutants derived from the rice variety Norin 8 and reported that the protein content varied between 4.2 and 16.5 percent. The protein content of the mother variety is about 6.5 percent. They also reported a significant negative correlation between the growth duration of early mutants and their protein content. In late-maturing mutants the opposite correlation was found. High protein content was also positively correlated with small single-grain weight and relatively long culms.

Similar results have been obtained in Korea. Protein content of 809 rice mutants from six varieties varied from 68 to 168 percent relative to their respective mother varieties. Protein content and culm length were negatively correlated. Dense planting increased protein content, the actual increment being mutant-specific (C. Harn, J. L. Won, C. K. Park, and S. Y. Yoon, *unpublished*).

Scientists at the Indian Agricultural Research Institute succeeded in developing mutants whose protein was more evenly distributed throughout the grain endosperm than the normal situation in which the protein is concentrated in the outer grain layers and therefore is partially lost during milling (Kaul, Dhar, and Swaminathan, 1970). Four mutants having indica type of grains were induced in the japonica variety Taichung 65. They had protein contents between 9.1 and 11.2 percent as compared with 8.7 percent protein content of the mother variety (Swaminathan, Naik, Kaul, and Austin, 1970). Hooded strains frequently have a higher protein content. In Guyana, 21 mutants with 10 to 12 percent protein content have been selected. The protein content of the mother variety, B. G. 79, was 9.3 percent (Pawar, 1971).

These results support the view that mutation breeding offers an additional chance for improving the grain quality of rice, including protein content.

Development of high-yielding mutant lines with early maturity

In multiple cropping systems, which often include rice, early maturity is important. Early maturity reduces the time during which a crop is exposed to hazards of diseases or pests, and it facilitates more intensive use of crop land.

In the Philippines, 13 high-yielding lines that mature 2 to 16 days earlier than the mother variety, Peta, have been selected after gamma irradiation (Viado et al., 1970; Escuro et al., 1971). Grain yields of these early maturing lines were between 4.7 and 5.6 t/ha. These yields were significantly higher than the yield of their mother variety (3.4 t/ha). Besides being early maturing, the lines were also more resistant to lodging. Two mutant lines from IR8 appear to be distinct improvements over IR8 with regard to earliness, culm length, and cooking quality. These lines are now reportedly undergoing intensive field testing and are expected to be released to farmers soon.

In Hungary, in cooperative research with the IAEA laboratory at Seibersdorf, a mutant line, Early Cesariot, which matures 2 to 3 weeks earlier than the mother variety, Cesariot, has been selected. The mutant line retains the mother variety's resistance to lodging and blast disease. This early mutant line yielded as well as the highest yielding variety in Hungary according to official yield trials conducted in 1970. This mutant can be used directly as a new variety in Hungary (Mikaelsen, Saja, and Simon, 1971).

In Japan, extremely early mutant lines have been selected from Norin 8. These lines showed the same or higher productivity than the mother variety in a 3-year trial (Tanaka, 1969). In East Pakistan, four mutant lines were selected that ripened 10 to 25 days earlier than the mother variety, IR8. In spite of the much shorter vegetative period they still give yields comparable to IR8 under local conditions (Haq et al., 1971). Similar early ripening mutant lines have been selected from varieties Jajai-77 and IR8 (30 to 35 days earlier) in West Pakistan (Miah and Awan, 1971). In Thailand, four early-maturing, high-yielding mutant lines have also been selected from varieties Nahng-Mon S-4 and Khao-Tah-Haeng 17. These lines were reported to be in the final stages of yield testing (Khambanonda, 1971).

Selection for disease- and pest-resistant lines

Disease resistance is a key factor in increasing yields and stabilizing crop production. The development of resistant varieties was therefore included in the objectives of the coordinated research program.

The variety Norin 8, which is susceptible to all races of the blast fungus in Japan, was treated with mutagens. A number of the mutant lines showed improved resistant reactions to blast disease. The frequency of induced blast-resistant mutants following gamma-irradiation of the seed was about 0.1 percent of the M_2 strains (Yamasaki and Kawai, 1968).

In Thailand, many mutants with increased blast resistance have been obtained from varieties Nahng-Mon S-4, Khao-Tah-Haeng 17, and Nangh-Phaya 132. One mutant line from Muey-Nawng 62N showed better gall midge resistance (Khambanonda, 1971). In Korea, mutants that resist blast disease while retaining high yielding ability have been selected from the leading japonica variety Palkweng (Ree, 1971). In Ceylon, two mutant lines that have higher resistance to bacterial leaf blight than the mother variety have been selected from IR8 (Gunawardena, Navaratne, and Ganashan, 1971). In India mutants selected for indica-grain type had better resistance to bacterial leaf blight than the japonica mother variety (M. S. Swaminathan, *unpublished*).

Table 2. Rice varieties from which mutants of economic importance have been isolated.

Type of mutants	Mother variety	Investigator
Dwarf stature, lodging resistance	Khao-Dawk-Mali 105	Dasananda and Khambanonda, 1970. (Thailand)
	Dular	Haq et al., 1970. (East Pakistan)
	I-kung-bau, Ketze, Shung-chiang	Li et al., 1968; Hu et al., 1970. (China)
	Kang-ni 27	Miah et al., 1970. (West Pakistan)
	B.G.79	Pawar, 1971. (Guyana)
	Palkweng	Ree, 1971. (South Korea)
	H4	Ganashan, 1971. (Ceylon)
High protein content	IR8, Dular	Haq et al., 1971. (East Pakistan)
	Paltal, Kwanok, Jaekeun, Palkweng, Hokwang, Baikna 18	C. Harn, J. L. Won, C. K. Park, and J. Y. Yoon, *unpublished*. (South Korea)
	B.G.79	Pawar, 1971. (Guyana)
	Taichung 65	Swaminathan, Naik, Kaul, and Austin, 1970. (India)
	Norin 8	Tanaka and Takagi, 1970. (Japan)
Early maturity	Peta, IR8	Escuro et al., 1971. (Philippines)
	IR8	Haq et al., 1970, 1971. (East Pakistan)
	Nahng-Mon S-4, Khao-Tah-Haeng 17	Khambanonda, 1971. (Thailand)
	Jajai 77	Miah and Awan, 1971. (West Pakistan)
	Cesariot	Mikaelsen et al., 1971. (IAEA, Austria)
	Norin 8	Tanaka, 1969. (Japan)
Disease and pest resistance	IR8	Gunawardena et al., 1971. (Ceylon)
	Nahng-Mon-S4, Khao-Tah-Haeng, Nahng-Phaya 132, Muey-Nawng 62M	Khambanonda, 1971. (Thailand)
	Palkweng	Ree, 1971. (Korea)
	Norin 8	Yamasaki and Kawai, 1968. (Japan)

Rice varieties from which mutants of economic importance have been isolated are listed in Table 2. The mutant lines from the various countries are all undergoing advanced yield testing. Some are being tested in yield trials by IRRI and other organizations.

CONCLUSION

The induction of genetic variability by radiation and chemical mutagens has become a quite useful tool in modern plant breeding. Even with the present mutation breeding techniques which may be far from optimal, it is obviously possible to induce genetical changes in desired directions. Today's problems of mutation breeding seem to originate more from the lack of adequate mass screening methods for particular desired characters than from difficulties in inducing desired genetic changes. A breeder must realize that a population derived from a mutagen-treated variety requires a selection scheme quite different from that used for a population derived from hybridization. This is particularly true if the desired changes cannot easily be recognized on a single-plant basis by simple inspection. The good results reported most frequently from mutation breeding—short straw, earliness, resistance against leaf diseases—are easily recognizable characters. The reports dealing with improvements in non-visible characters are more rare, but they definitely prove that such mutations are induced and can be found if appropriate methods are used.

Future joint programs of FAO and IAEA will give priority to the development of new screening techniques for protein quantity and quality as well as to the development of reliable and early mass selection methods for disease resistance, particularly of the "unspecific" or "horizontal" type.

The use of haploid plants in future plant breeding is receiving much publicity. Techniques for anther culture will most likely be improved to make mass production of haploids from any crop plant possible. Induced mutations would express themselves in the M_1 generation. Consequently, it would be unnecessary to go through the time-consuming selfing procedure for detecting recessive mutations. But too little is known about phenotypic expression in the diploid stage of characters selected in the haploid stage. Data from Tanaka (1970) indicate that drastic mutations induced in haploid plants may not be transmitted to the next generation. On the other hand, drastic mutations were found in the diploid M_2 generation which were not observed in the haploid M_1 plants and probably originated during or after chromosome duplication.

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Breeding wheat for high yield, wide adaptation, and disease resistance

Norman E. Borlaug

Greater food production can be achieved through the coordination of the total efforts of the agricultural researchers, government policymakers and farmers. The improved crop varieties and the package of new technological practices can only be meaningful if the governmental economic policy encourages farmers to use them. Farmers, especially the small ones, must have access to credit; inputs must be made available at prices they can afford; and they must be convinced that the new varieties are good for them. Development of improved wheat varieties in Mexico was done through a program involving a broad range of genetic material and disease testing at many geographic locations. In the beginning, scientists worked in 67 locations to produce the desired varieties in a short time. The researchers soon observed that by moving the breeding materials from one region to the other, wide adaptability could be built in. Cooperation not only among researchers in the country but also in other countries has helped tremendously in the development of wheat varieties with wide adaptability and stable yield. On-farm testing was an essential feature. The one-variety system—whether it be wheat, rice, or cotton—is dangerous because of the possibility of epidemics. Only a dynamic national breeding program where researchers keep producing and releasing varieties with different sources of resistance can cope with the problem. Insects and disease organisms are capable of genetic changes, too, so that scientists must continually search for and incorporate more sources of resistance.

AGRICULTURAL CHANGE

As we look at the overall picture of food production in the world, I think we are all convinced that varietal improvement in itself is no cure for stagnant agricultural production. If we are to push things ahead from this standpoint—as we must—we fully realize that we must manipulate and handle simultaneously, in a harmonious way, three groups of production factors. This is especially true in a developing country where the land has been cultivated for a long time, where the production levels are stagnant, where the essential plant nutrients are exhausted and production is limited—irrespective of crop variety or losses from diseases and insects. I am convinced that in all programs, whether in developing countries or affluent countries, the key to changing food production is a coordinated national effort. I am against fragmentation and local efforts.

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They fail to mobilize the experience and technological know-how that bear on the overall aspects of food production.

On the question of production, we must consider three groups of factors that are to be manipulated simultaneously and harmoniously, if programs are to be successful. These include a new package of technological practices which, in turn, comprise improved varieties, fertilizer practices, control of pests and weeds, and moisture management. Moisture management has to do with irrigation, or how you conserve moisture, especially in areas where moisture is likely to be limiting in certain parts of the crop season.

But even with this vital package—one that produces a big change in yields per hectare—change in food production does not come automatically. The governmental economic policy of the country must be hitched to the wagon. Unless this is accomplished, there is no possibility of provoking change—especially in those lower economic currents of the society, made up of the very large numbers of small farmers who have lived on the outside of the economy under subsistence agriculture.

This calls for a whole series of devices put together in a certain way by the government of the host country. It has to do with pricing of the grain, it has to do with the price and availability of such inputs as fertilizers, weed killers and pesticides, and especially credit for the small farmer so that he can begin to participate. Remember that the farmer has never had this opportunity before and, unless all these factors are combined in the national production campaign, there will be no change. I repeat, irrespective of how good the variety, the fertilizer recommendation and the pest control, no change will be forthcoming. Then, of course, one can have both of these factors under control but, unless these changes are spectacularly demonstrated by showing what is possible, one cannot put the change across to the farmers. Demonstration must be done in the farmer's field. In too many parts of the world in which I have worked, too much of the research, especially demonstration work, is being done on government experiment stations where they then try to bring the farmers to see the results. We are deceiving ourselves if we think we are going to promote a change in crop production practices with this kind of approach. Remember that the small farmer, in particular, is suspicious of all the things he sees being done on a government experiment station. He will always say that the government has all sorts of money; "They have my taxes and they can do things that I cannot do," and besides he is not so sure of how much is science and how much is "hokus-pokus." But if he sees the demonstration installed on his own farm or on a neighbor's farm, in his own village, he or his neighbor becomes the most effective extension agent in the whole countryside. It is up to us then, as extension workers and research scientists, to hitch these people together and spread the word. It is amazing, however, that even without this effort, the word spreads rapidly if the research is viable and the economic ingredients are brought together in the right way.

Now, having all of these, there is one more item which to me is the most important in making a national program work. This is the team spirit which can surmount problems in the midst of a whirlwind. The defeatist spirit is the greatest enemy of progress and it persists and is too widespread among scientists. If constructive change is to be provoked, there is no place for defeatism in the ranks of leadership or among the scientists charged with the responsibility.

WHEAT BREEDING IN MEXICO

I would like to turn now to consider the history of the wheat breeding program in Mexico as it is related to what has happened in wheat production in this last 4 to 5 years in many other parts of the world. In the early years, there were no government stations and it has only been in recent years that such stations were established and adequately equipped. From the outset, the development of high yielding varieties was our primary concern; the second most important consideration was the efficient use of irrigation water since this was limiting and most of the wheat was grown during the winter or non-rainy season. We were interested also in speeding up the plant breeding process from the time the cross was made to the emergence of a new variety.

Essentially all of the varieties being grown when our program started were mixed types, some of them probably dating back to early colonial times. It was not uncommon to see 15 or 20 types of wheat growing as mixtures in the field. This was not as common in the state of Sonora which had been influenced by the wheat breeding program in the state of California, but for the rest of the country, I am certain many of these mixtures date back perhaps 100 years. We were concerned also that the new varieties should carry a broad spectrum of disease resistance and that they should have broad adaptability.

To produce a variety in a short time to meet the needs, we decided we should grow two generations per year and, to accomplish this, we worked at 67 locations. After a short period of testing, we found that the same result could be obtained by growing our main breeding nursery in the winter in the state of Sonora, at about 28°N and at only a few meters elevation above sea level, and in the summer at a high elevation where diseases could be fostered and the wheat would grow adequately, because of cool temperatures. The first location represented, and still does, the main wheat growing region of Mexico. The second generation, summer season location was found near Mexico City, in the Valley of Mexico at an elevation of about 2200 meters and also in Toluca Valley nearby, at about 2600 meters. Here the heavy rainfall during the summer season provided good conditions for the development of epidemics to screen the materials. Different diseases were found to be important in these two locations. On the coast, for example, stem rust was the greatest enemy while in the high Valley of Toluca, stripe rust was important. Leaf rust and stem rust occurred in both places. By moving the breeding materials from one region to the other it soon became apparent that wide adaptability could be built in. We wanted this adaptability because Mexico is a mountainous country and varieties should be able to fit both the slopes and plains. This would simplify seed production problems. As these new varieties were moved from the coastal plains to the high valleys—from low elevation to high elevation—we began to find varieties that were well adapted to both conditions.

We also found why the Canadian varieties and the northern U.S. spring wheat varieties were so poorly adapted under Mexican conditions. This observation later proved to be the same throughout Asia, South Asia and the Near and Middle East. They were not adapted to the short days of the lower latitudes. But it was not only the total hours of daylight that was involved. Tremendous differences in plant response occurred depending on whether the days changed from long to short or short to long as the season advanced, even with the same number of hours of light. This was vividly illustrated at Chapingo, in the early years of our work. Normally, we planted our yield nurseries there in the last week of November, about 1 month before the shortest day of the year. Thus, the days were getting shorter in the early period of growth and becoming longer as the plant moved toward maturity. This added a new scientific dimension to the work. The next generation was sown just across the road, about the last week of May—again about a month before the longest day of the year—when the days were becoming longer. There was about 35 percent difference in yield, withou' any disease factors or soil fertility factors involved. It was evident that the total number of hours of light was not the principal factor but that, in this kind of variety, the conditions at Chapingo in the summer are similar to the life pattern for which they were selected in the northern U.S. and Canada.

YIELD STABILITY

I would like now to consider yield stability or broad adaptability, which now is one of the most important factors affecting whether we wish to use a new line as a commercial variety.

What is yield stability?

No one can define this fully because we do not know how many factors, other than hours of light and temperatures, are involved. There are obviously many others, but we have found these to be among the principal contributors to broad adaptability of a variety under commercial conditions. In addition, our method of selection under widely different environments—as mentioned previously—provided an opportunity to select types suitable to both.

I would like to say a few words about what has happened in the use of some of these varieties developed in Mexico. I am not going to refer to a particular variety, but to the group of varieties. Many of these were introduced based on initial experimental testing dating back to 1963 and 1964 in India and Pakistan and a number of other Middle East countries. It would seem on the surface that this was taking a long chance to move varieties so far from Mexico. But, after 2 years of widespread testing, it became evident that these varieties were very much at home and that the disease pattern was more or less similar to that present in Mexico. It was possible, therefore, to sort out which varieties were adapted and then develop a set of agronomic practices which would fit best in cultivation. This was done in India by a well organized national coordinated program. Based on Mexican experience, modifications were made in soil fertility manipulation, fertilizer, and cultural practices to fit local needs.

I am not going into details, but essentially the same was done in West Pakistan. Similar adaptive changes were made in certain low elevation agricultural areas of Turkey, in certain valleys of Afghanistan and Iraq and, more recently, in the rainfed areas of North Africa.

The important thing is that breadth of genetic adaptation was incorporated into these semi-dwarf varieties through earlier work that was done in Mexico, even though we did not recognize at that time that this characteristic had been incorporated to the degree that permitted this flexibility. We did have some earlier indication through our cooperative testing in Latin America. We also knew that we could breed for adaptability to high and low elevations for the latitudes involved in Mexico, but the number of locations for yield testing had been quite limited.

The first move made to increase the scope of yield testing was made at the Latin American Plant Breeders Meeting in Chile, in 1958, where a committee decided that it would be interesting to set up an Inter-American Yield Test. We agreed to coordinate this and it was decided that we would grow the seeds and select representative commercial varieties from all American countries, for inclusion in the test. The materials were then grown in all of the countries under a wide range of conditions. Immediately the varieties separated themselves. Some were specific in adaptation. The Canadian varieties were unable to function economically below 39°N latitude. This prevents them from being used in the tropics and subtropics and even in Argentina, where the main commercial area is in the region between 35°S to 36°S. We learned much in this test.

About a year or so later, when we began working in a training program in the Middle East with the Food and Agriculture Organization, there was interest among the students to set up a Middle East-Mexican-Colombian varietal program including daylength-insensitive varieties. This was set up and again we got some interesting data in about 3 or 4 years. Now, we make up 90 sets and these are sent around the world to many scientific collaborators. From this, data come in, and reports are made up which go back to the collaborators. There is an opportunity for any plant breeder who has a selection that is in the advanced stages of testing to submit it for test. We ask for 200 grams of seed, which we multiply. Those selected are incorporated into this yield test. By following this practice, a man can obtain more data in one year than he would get in 20 years on the breadth of adaptability and stability of yield. I refer to stability of yield in the broad sense, as it relates to adaptability when diseases are not limiting. But you can see also in which locations diseases limit a variety or new line that is under test.

The magnitude of change in total wheat production in a country such as India has been fantastic. Production rose from the high of 12.3 million metric tons before the green revolution to that of the present year, 23.2 million. Most of this gain has been achieved through increasing yield per unit of cultivated area and much less through expansion of cultivated area. This has changed the whole technology of wheat production as it relates to fertilizer and improved cultural practices.

There are many people who failed to comprehend some of the implications. Time and again economists write that we are making the rich richer and the poor poorer. That just is not so. Recent studies made both by India and Pakistan have shown that the little farmer, the one with 1 or 2 hectares, is participating and benefiting greatly. You will also hear many people say that these varieties require much more irrigation water and are very demanding. This is not true either, for you will find that they may require one extra irrigation, but if you calculate the water requirement per kilo of grain produced, you will find they are much more efficient producers than any of the previous varieties. After all, producing grain is the name of the game. You will find the same critics saying that they have to be babied and they have to have heavy fertilization. Of course they do, if we are to capitalize on their maximum potential. But, on the other hand, even at low fertility and on dryland, they do surprisingly well, displaying their efficiency even though they were developed under irrigation.

Again you always hear of their poor quality. This criticism is given not only by laymen but by scientists. Generally this can be considered scientific bias. Some of the people who have been most vocal about this, have been blindfolded and given the Chapati test. Often they put the Mexican varieties in the first place, so you see how bias voiced loudly in high places can tangle up the truth. All of these things you must contend with. The grain merchant all along the line wants to feature this difference so he can make more money. He has been found to buy grain of large-seeded dwarf varieties or screen out large seeds of other Mexican varieties which he can buy at a lower price, and mix them with indigenous grain to be sold at the higher price which these have traditionally commanded. This is market manipulation at its worst. Thus, you see one has to be a little careful when provoking change to avoid these types of confusion.

It is said repeatedly that the high yielding wheat and rice varieties are less resistant to diseases than the old land-race indigenous varieties. I think this depends on what basis you are using for comparison. If you define this on the basis of the microclimate it is true given both varieties being susceptible. Under unfertilized condition with plants widely spaced in order for them to extract from this depleted soil enough nutrients to produce some grains, there is little opportunity for the disease organism to produce an epidemic. But, under unusually favorable climatic conditions a rust epidemic can become established as I have seen happen in Mexico with these kinds of varieties, resulting in devastation of the crop. But once you start fertilizing the old varieties, even at intermediate level, epidemics are the rule and you have a true picture of its susceptibility. On the other hand, the new varieties are actually highly resistant, covering most of the races of the disease and certainly in all cases they are superior to the old land-races.

This does not mean that they are going to remain resistant very long and this change in the ecological balance because of the improved cultural practices, calls for a higher degree of resistance in the variety unless you are prepared to take chances on loss. We must, therefore, maintain a dynamic national breeding program to back up any initial effort that may have come out of the international scenery, like CIMMYT in this case, or IRRI in the case of rice.

My fundamental belief is that the backbone of continued progress in whatever you want to call this change in cereal production, let us say the green revolution, hinges on the dynamic national program. It is this program that will produce the diversification and make the multiplication of the varieties needed to cover up changing situations such as resistance to the principal diseases and I dare say insects. For wheat, not many insect problems exist. There is, however, one great danger and it is a built-in danger of success that comes with one variety. I'm glad to say that in India, at least, we have passed the vulnerable position created by the widespread use of varieties re-selected from cross 8156. Dr. D. S. Athwal made one of the selections, Kalyansona, and sister selections were made in Pakistan and in Turkey. These probably covered 10 million hectares a year ago. Fortunately, it is very well adapted and is high yielding and has many things going for it, but it is fortunate also that now large areas of three other dwarf varieties selected in India have been distributed and multiplied, so they are beginning to get diversification.

I am opposed to the one-variety system, whether it be in cotton, wheat, or rice. They are all the same. It is dangerous because of the epidemics that can start. It is only with a dynamic national breeding program where you keep producing and releasing varieties with different kinds of resistance, that you can cope with this problem.

Unfortunately, if the new varieties do not yield as well as former ones, they will not be grown long because it has been my experience that the farmers in 2 or 3 years' time will distinguish yield differences of 10 percent. Even though a new variety is the most disease resistant of all of the group, if it yields 10 percent below the present varieties, it will be out of operation in about 4 years. The farmer can spot this difference. He has paid the same price for his grain; he has not experienced losses to diseases as yet and he is going to take a chance on the higher yielding one. The only way to beat this is to keep turning out new ones that are at least better than the commercial varieties for several characteristics.

I would like to have been born a maize breeder, because people in rice and in wheat are among the most vulnerable in the world to changes in races of disease organisms. We are dealing with self-pollinated crops, so we develop inbred lines. We select for resistance to diseases and insects in the area in which we work at a given time. One of these is successful and suddenly the variety is out, like Kalyansona and Mexipak on thousands or millions of hectares. We have an explosive situation. If a race of rust changes, an epidemic can sweep all the gains away. Our only recourse is to diversify varieties. For maize, however, we are dealing with a cross-pollinated crop. In its native home it has been in harmony and balance with the organisms parasitic on it, except when some poor scientist messes it up. From the beginning of time, two species of rust, *Puccinia sorghi* and *P. polysora*, have been present, but they never caused appreciable damage. They were always there, but every plant in that open-pollinated variety is distinctly different and epidemics could not build up. An equilibrium was established. The only way to build up an epidemic is to take one of the high altitude populations to a low elevation or vice versa, where races favored by low or high temperature are present.

The maize variety in its new location is faced with a race that could not survive in its native place. There was no selection pressure and the variety is now susceptible and an epidemic can develop. The equilibrium has swung in favor of the parasite. However, hybrids involving resistance at both locations offer a tremendous advantage provided the inbred lines entering the cross have been properly screened. This brings up one other point which we tend to forget: In the tropics with tropical crops, the organisms live throughout the year and are not eliminated by cold as they are in the higher latitudes. Whether it is corn rust or wheat rust, the inoculum arrives late, giving the plant a definite advantage.

To fully appreciate how resistance can persist over long periods of time, in spite of the absence of the disease organism capable of attacking the population one has but to look at corn and corn rust in West Africa since the early fifties.

Apparently when maize was taken from the Americas to West Africa in the early colonial period, the rust that went with it (based on the early herbaria collections—which of course do not go back 400 years, but nevertheless were collected early in the period) was *Puccinia sorghi* which does not thrive at high temperatures, but only at low temperatures. It just did not find a happy home in that part of Africa. It managed to survive, but caused no damage. It was only after maize began to be grown in the highlands of East Africa that temperatures were favorable. The disease flared up and caused havoc in corn production. As a sequel about 1948 or 1949 the high temperature organism *Puccinia polysora* was introduced to West Africa. It immediately spread to the entire population of corn in that part of the continent and yields fell drastically. Scientists were called in and worked vigorously to produce resistant varieties, but before they were released, the epidemics subsided. Apparently the peasant farmers had selected resistant plants for seed stocks, which contained genes for resistance that had persisted in the population over the 400 or so years since it was introduced as a crop from the Americas. While this can also occur in close-pollinated crops, its likelihood is much greater in open-pollinated species, where the genes for resistance are passed around at random within the population in each generation.

Even more amazing is the case of the white pine blister rust in western white pines, which was introduced about 1900 into America. It was found that one in 20,000 trees was resistant. This disease, which was endemic in the Orient, had developed a high level of resistance in pines of Siberia, Japan, China, and extending into the Himalayas. The naturally resistant trees in America had apparently received these genes across the land bridge from Siberia thousands, or possibly hundreds of thousands, of years ago, when the ancestors of present species could still interbreed. They had persisted in the population and were only exposed when the organism was introduced and became epidemic. Recent fossil finds in Siberia indicate that types similar to the American species did exist in that area in the past.

I want to say one thing concerning my fears on the advisability of continuous cropping of the same crop species. I feel there is a moral obligation to say that if we continue this practice without breaking the cycle of the disease organism, the longevity of resistance can be expected to be short in dealing with one such as

Piricularia sp. in rice, where variability is well established. The question I pose is how long will resistance remain functional with two or more crops of the same species grown each year. There is bound to be more inoculum and, therefore, greater opportunity for the fungus to mutate to new forms which will attack the resistance.

In a similar vein we speak of resistance to insects. This also is transitory. Insects are capable of mutation too and we must continually search for and incorporate more sources of resistance. It is my advice that you keep the germplasm pool broad and make use of double crosses, top crosses, and other forms of multiple crosses with a continuous inflow of new variation.

We have found in wheat that single crosses made between tall varieties and dwarfs produce few dwarf plants and there is insufficient variation within this type to sample the variation present from the cross. Using multiple crosses of F_1 by F_1 and including three dwarf parents, the yield of dwarfs is high and our chances of selecting superior genotypes in the framework of the dwarf type are infinitely enhanced.

CONCLUSION

Before I close, I would like to say that we have to fight on another front, in this part of the world: The environmentalists are developing a real chaos in the United States. They think we are all going to die from poison. These fat-bellied philosophers who have never been hungry and who have tremendous power in the legislatures, would like to be called ecologists. I will never give them that satisfaction. They are environmentalists who are off balance. You have seen what they have done to DDT. There is little evidence that any single human has been harmed by DDT and plenty of evidence that control of malaria has saved millions. I happen to have worked in wild life in my early professional career and know about some of the other factors that are involved in the reduction in population of wild life. They have pointed their finger to three or four species that have been reduced by DDT and it isn't so. These species were on their way out for a long time before DDT had come into the picture. The excellent analyses that we have now in gas chromatography are involved in confusing the issue.

Before World War II we had difficulty in measuring one part per million in most chemicals; now one part per billion or several parts per trillion are easily identified by means of gas chromatography. This can be compared to the accuracy of putting astronauts on the moon and bringing them back after 800,000 miles or more to within a mile of the ship dispatched to pick them up.

If we throw common sense out of the window in this kind of thing and let these fat-bellied philosophers dictate our future, we are going to be in real trouble, particularly in the case of compounds like DDT, which has brought control of malaria to the world. There is no comparable substitute, according to the World Health Organization, so we better not throw it away until we have it.

Now they are speaking against chemical fertilizers. If they pass legislation to deny us the use of these, our efforts in agricultural research will have very little significance.

Discussion: Breeding wheat for high yield, wide adaptation, and disease resistance

V. A. JOHNSON: You mentioned the genetic isolation associated with self-pollination or inbreeding in crops like rice and wheat. In wheat we now have one or more chemical gametocides to induce male sterility. Is it time to put such a chemical to work in an organized manner?

N. E. Borlaug: I am for any means that would put more variability into the population that we can grow well commercially. I don't know how to reverse evolution and change the pollination system in wheat and rice, but perhaps we can manipulate it chemically. I continue to have an interest in the multilineal variety. In cooperation with national programs, we are building a series of phenotypically similar lines at two levels of plant height to have both wide adaptation and broad disease resistance. The multilineal complex will hold back a disease epidemic and they will provide a certain degree of protection. But it takes time to develop multilineal lines.

R. F. CHANDLER: How intense is your crossing program and how much effort should be put in the selection program in relation to the number of crosses being made?

N. E. Borlaug: We make a large number of crosses. We look through all of the international nurseries and early screening nurseries, which are made up of early generation lines sent around the world, and watch the large number of lines carefully as new parental lines. Then through the literature and the USDA-coordinated international rust nurseries, we search for those new types and cross them widely in our programs. Many of the crosses were discarded because of their tallness and photoperiod sensitivity. We threw away the single crosses but we use their pollen for backcrossing. More commonly, we make double crosses of these F_1 plants. By growing a reasonably large number of such populations, we expect to find combinations carrying the particular disease resistance. Meanwhile, our pathologists convert the unusually good lines to dwarfness and insensitivity and try to retain the disease resistance. So we work from several different sides. We probably make about 2,000 to 2,500 crosses and grow two generations in a year. But we do not grow all of the crosses. For the F_2 populations, we plant a minimum of 2,000 seeds each for about 600 crosses at our central stations. In addition, we send collaborating national programs about 50 sets of F_2 seeds each. We would like to grow more of these but we have to stop at about 250,000 plants. To get epidemics of rust, we inoculate the plants with mixtures of races to spread the rusts.

R. F. CHANDLER: With such large numbers, once in a while you may miss some promising plants.

N. E. Borlaug: Yes, but somebody else will catch the progeny. Our whole philosophy in plant breeding is to look everywhere for sources of resistance, to make many crosses, and to subject them to epidemic conditions in a wide range of environments to take care of the physiologic specialization of the pathogens in different parts of the world. This calls for international cooperation and growing large populations.

R. F. CHANDLER: Have you done any mutation breeding?

N. E. Borlaug: Not to any appreciable extent yet. We are considering using this technique to improve the shrivelled grains in one *Triticale* line. This line has disease resistance, insensitivity, semi-dwarfism, and high nutritive value.

H. L. CARNAHAN: What is the effect of photoperiod sensitivity on wheat performance other than adaptability?

N. E. Borlaug: I am not sure. But at high latitudes, the insensitive Mexican wheats can suffer badly from drought in the early spring. For northern areas, sensitivity may be advantageous.

L. M. ROBERTS: Do disease problems become more serious in the semidwarf wheats?

N. E. Borlaug: I don't think so, but when you make such a big jump, you may not have all of the disease resistance built into the varieties.

L. M. ROBERTS: How about insect problems?

N. E. Borlaug: We have not worked long enough in areas which have insect problems. In heavily infested areas such as Morocco and Tunisia, there is evidence of great diversity in an insect species. That would complicate and lengthen the breeding work.

H. E. KAUFFMAN: Please comment on the need for rice workers to move rapidly into a broad international testing program for diseases and insects like you have in wheat.

N. E. Borlaug: I think it is of tremendous importance to develop such international programs. For instance, we can obtain information quickly on a certain disease from a cooperating country, such as Tunisia, on *Septoria*, incorporate resistance into our new lines, and send the material to Tunisia and other countries for broad screening a few generations later. These steps can add long-time protection to a breeding program. I am particularly concerned about continuous cropping in rice because of the tremendous build-up and turn-over of inoculum.

R. F. CHANDLER: Could you or Dr. Johnson tell us about the Russian variety which yielded well at high latitudes in Turkey in the international winter wheat trials?

V. A. JOHNSON: This winter wheat, Bezostaia, has been the highest yielding variety in the international winter wheat performance nurseries since the project was established in 1969. It is in a performance class by itself and it has wide adaptability. Morphologically, it is similar to the CIMMYT wheats.

N. E. Borlaug: Although this variety was developed in a local program, it has tremendous yield stability built into it. The Russians also have an impressive spring wheat, 8156. There was an element of luck in breeding the 8156 complex which resulted in resistance to powdery mildew and immunity to loose smut.

T. T. CHANG: What are your views on genetic conservation?

N. E. Borlaug: I am concerned about it. Although the USDA world wheat collection has 17,000 accessions, it is still questionable if it is representative of all types. I understand a Rockefeller Foundation meeting will soon review the situation in wheat, rice, maize, sorghum, and millets and discuss ways to broaden the base for collection.

D. S. ATHWAL: I agree that a new variety may have to be replaced every 3 to 5 years because of the dynamic disease and insect situations. It will be a continuous struggle between plant breeding and the pests. We have to keep ahead of the diseases and insects by developing varieties with new sources of resistance before the disease or insect changes and causes serious damage. But I am concerned about the limited sources of resistance available to us. Shall we one day run out of resistant genes for one disease or one insect? What is the situation in wheat? Can you build up a higher level of resistance from lower levels by breeding? Or, are other means available?

N. E. Borlaug: I have to be optimistic. I think there are more resistant genes around. Some genes probably have a low level of protection individually, but we can bring them together and part of this is related to field resistance. With corn rust in West Africa or with rust on western white pines, these genes have long ago dispersed in a few varieties or trees and when they are brought together, they still function. I think that in rice you are in a better position because you can multiply rice seeds faster than wheat. We need a more efficient seed multiplication system so that we can have enough seeds of several promising selections before making a final decision on what to release and thus, to save a year or so. If we can move fast on seed multiplication, we may stay ahead of the disease or insect.

T. T. CHANG: I would like to point out a genetic mechanism that could provide sources of resistance in addition to mutation or cumulative action of weaker genes. Some varieties probably are phenotypically susceptible or moderately resistant because the resistant gene is masked by inhibitors. When you cross such a variety with the right parent, which may be a susceptible variety, the inhibiting effect is removed and resistant progeny may appear. As we learn more about inhibitors, it is clear that their presence in existing germ plasm is more widespread than we used to think.

G. SATARI: In Indonesia, we have several tungro-resistant rice varieties that are still resistant and high yielding 20 years after their release though we grow rice twice a year. What is your idea on this long-term resistance?

N. E. Borlaug: I do not pretend to understand it. I have mentioned cases of persistent functional resistance. But, more often than not, it does not last too long. Be thankful if you can make it last. But, I am worried, especially as we provide a more favorable environment for the insects and diseases by thick planting and fertilization that the whole ecology is changing. The plants become more palatable.

H. I. OKA: In rice, insensitivity to photoperiod is important to wide adaptability. I understand that you have the winter habit in wheat. Has the degree of winter habit been a limiting factor in the adaptation of the Mexican wheats?

N. E. Borlaug: No, most or all of the Mexican wheats are spring wheats. But in a cooperative program, one CIMMYT researcher is inter-crossing the winter and spring wheats to provide genetic material for the high plateaus in the Middle East and the Near East.

W. H. FREEMAN: You mentioned *Triticale*, a man-made species. Are there other possibilities?

N. E. Borlaug: It is incredible, looking back at the history of agriculture, that scientific man has not come up with a major cereal. All we are doing is putting the polish on what was done very well by Neolithic men. I think we can do better with all of the new techniques at our disposal. Despite the crossing or sterility barriers between the tetraploid wheats and rye, we are intercrossing *Triticales* made from different species of wheat to obtain new variability. We should go to all other sources. The original crosses were made from a handful of plants. When we work with wide crosses, we need to work with large populations.

L. M. ROBERTS: Broad crosses could be facilitated by using cell and tissue cultures. Protoplast fusion between cells of different species has been obtained. The problem is to have the regeneration of the cell wall. I believe that new hybrids can be made by such techniques.

Hybrid wheat breeding

James A. Wilson

The genetic basis for economically significant heterosis in wheat is probably similar to that in the established hybrid cereal crops. For increasing efficiency of selection for plant vigor, genetic stress may be employed in self-pollinated crops by fixing depressant characters that are separate from the quantitatively controlled effects of inbreeding depression. The wheat plant is adaptable to cross pollination. Large fields give relatively high pollen saturation in the air and adequate hybrid seed set. Excellent commercial seed fields have been established and harvested in hybrid-blend production involving female-to-male ratios of 8:1. Several cytoplasms and a large number of restoring genes are now available for hybrid wheat breeding. The cytoplasm and restoring genes coming from *Triticum timopheevi* have been used extensively. Additional sources of genes that restore fertility to Timopheevi steriles have been identified. Some of these are found on chromosomes that do not carry the Timopheevi-restoring genes. Although three restoring genes from Timopheevi appear adequate in most environments and genetic backgrounds, four or more may eventually be used under conditions requiring additional levels of restoration. Although single-cross restored grain hybrids have not yet proven superior to commercial varieties, improvement of restorer lines and progress in forage hybrid breeding justifies an optimistic view of wheat hybrid development. Early hand-crossed hybrids in certain wheat classes have shown very promising hybrid vigor. Restored grain hybrids have equalled in yield the best commercial varieties. Lack of superiority in the hybrid has stemmed from agronomic weaknesses and from restorer-line testers with mediocre yield potential. Yield tests in 1971 indicated that restorer-lines have now been developed that equal the check varieties in grain yield. The progress made in hybrid forage breeding with chromosome-addition types, warrants continued effort in this area with grain types.

INTRODUCTION

In the past decade much breeding work has been concentrated on converting the highly self-pollinated wheat species into a cross-breeding organism for producing hybrid seed. In advanced agricultural economies the belief that hybrid crops are the most efficient forms available has strongly motivated various research programs. The knowledge that breeding improvements can

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be built into a plant type which allows a control over seed production and marketing has also generated interest in hybrids.

BREEDING CONCEPTS

When the first attempts were being made to produce hybrid maize, breeders generally believed that it was impossible to produce seed corn by detasseling and cross-pollinating low yielding inbreds, but they recognized that varietal crosses were potentially economical. The startling recovery of vigor in the hybrid of crossed inbred lines suggested that inbred stocks were necessary for obtaining maximum heterosis. The discovery of the double-cross technique for producing improved maize seed was a dramatic way to combine in the hybrid the desired heterotic effects of the single crosses. The emphasis on pure double-cross for economical seed production has declined because new inbreeding concepts now require less intensive levels of inbreeding and allow the use of partial inbreds as seed parents. Also, the greater phenotypic uniformity achieved with single crosses results in more efficient plant populations and harvest. In some instances, pure single-cross hybrids are made on highly improved seed-producing females that are extremely high yielding compared with the earliest inbreds available. Currently, hybrid maize concepts being formulated in some areas seek to eliminate intentional inbreeding of parental stock. These concepts emphasize the selection of the necessary characteristics in open-pollinated "broad lines" for the production of hybrids (Stringfield, 1964). The pure hybrid crosses, involving varieties or inbreds, have not reached some maize-growing areas of the world, and, because of seed distribution problems, synthetic varieties are often considered first.

Although most of the theory and impetus for hybrid breeding originates from workers dealing with naturally cross-breeding species, significant hybrid breeding work has been conducted on grain sorghum, wheat, and barley species that have a high level of inbreeding.

It is generally believed that inbreeding depression occurs only when inbreeding involves cross-breeding species. But, a range of inbred lines that have different yield levels is the normal result of working with germ plasm of wheat. The variation in the yielding ability of inbred lines of wheat suggests that this crop also expresses inbreeding depression.

The inbreeding depression effect in maize seems greater than that in wheat. This difference has often been explained by the many deleterious recessive mutations that are retained in the maize population. A crop like wheat retains relatively few deleterious genes during continuous inbreeding. Although additive gene action and favorable epistatic gene combinations may cause yield to vary among inbred lines from inbreeding species, it seems reasonable to expect that certain combinations of favorable dominant growth factors and deleterious recessive mutant genes would likewise be present since deleterious recessive characters have been identified in these crops. The occurrence of deleterious recessive mutants in a highly inbred organism like wheat may further support the concept that favorable dominance is predominant in the heterotic effects of maize.

The lack of prominent inbreeding depression in wheat could in part be due to its polyploid nature which may have allowed the duplication of several genes that have the same function. Yet, certain gene pairs among the duplications could have a homozygous recessive and deleterious effect. If we assume that vigor effects increase through the accumulation of favorable dominant genes of different loci in maize, we may make a similar assumption for wheat regarding the accumulations of favorable genes that have the same ancestral locus. If one dominant gene is adequate for fulfilling a function and the fitness of a given genotype, the duplicated genetic material at certain loci in the homeologous chromosomes could undergo mutation or deletion, causing gradual loss of duplicated genetic materials. Cytological evidence obtained by Kerber (1964) by reducing hexaploid wheats to tetraploid wheats suggests that two genomes depend heavily on the remaining genome for viability and vigor. Either a new epistatic gene balance has evolved in the hexaploid, which conditions vigor, or the duplication of favorable growth factors having common loci is essential for vigor. Probably both these and other genetic actions are involved. Nevertheless, the hexaploid wheat in this genome elimination experiment behaves like a diploid that has lost genetic material.

Artificial intensive inbreeding in maize apparently allowed a natural biological pressure system to express itself and this resulted in highly efficient selection for plant vigor. The breeder of self-pollinated crops normally devises various environmentally induced pressure systems to increase selection efficiency, but he gives little or no thought to developing pressure systems within the species that could be important in selecting for plant vigor. Although various types of gene action are apparently involved in vigorous inbred lines of maize, the cumulative effect of favorable dominant growth factors may be operating and the vigorous lines isolated at the inbred level are most likely to produce favorable dominant effects in the hybrid. Thus, significant progress for hybrid effect may be accomplished at the inbred level through visual selection and yield testing. A more intense inbreeding depression in self-pollinated crops might vastly improve the efficiency of visual selection for vigor and favorable dominant growth factors. Since the inbreeding depression of self-pollinated crops does not appear promising for increasing the efficiency of visual selection for vigor, other simple plant characters might be used to increase selection efficiency. In developing a biological selection pressure system, the character used must be recessive and not expressable in the hybrid. The use of a selection pressure system other than that of inbreeding depression may be an additional, but generally unrecognized, principle applicable to hybrid breeding.

Although cross-pollinated and self-pollinated crops differ considerably in response to certain breeding methods, a common system of gene action should exist in all species of grasses and organisms. It therefore appears illogical to say that economically significant heterotic gene action exists in maize but not in sorghum, wheat, barley, or rice. If the economic significance of heterosis is questionable, the question does not apply to self-pollinated crops only.

CROSS POLLINATION

The opening of the flowering glumes in wheat is generally a normal expression, but it is influenced considerably by certain genetic traits and environmental effects. Varieties that have lax heads and relatively thin glumes, lemmas, and paleas are more effective pollen donors and recipients than varieties that have compact heads or deeply concave glumes, lemmas, and paleas. Moderate temperatures and humidity seem most favorable for pollination while high temperature and drought stress strongly inhibit flower opening. Very low temperatures for a time likewise may limit anther and pollen development greatly. Low temperature however does not appear to restrict stigma development or open flowering.

Wheat varieties of a given class have been observed to differ significantly in seed set. Within the wheat regions of the U.S., the most erratic results of pollination have been obtained with the hard red spring type. The problem is partly caused by environmental conditions that produce pollen sterility. Varieties that tend to have consistently high pollen fertility are needed as background germ plasm for wheat hybrids in the northern U.S. No selection has yet been identified in hard red spring wheat that does not have a potentially serious sterility problem in that region. Although winter varieties differ in ease of cross pollination, their pollen sterility seems more predictable from one year to the next. Hot, dry winds can cause variation in seed setting of male-sterile winter lines, however.

Cross pollination potential increases as grain yield levels increase possibly because more pollen is produced per unit area and the plants have large flowers that have relatively large stigmatic surface areas.

The pollen of wheat is quite buoyant and may move long distances to effect seed set. It retains a high level of germination for several minutes after dehiscence, which is a sufficient time for it to blow a long distance. Under identical test conditions, D'Souza (1970) found that wheat pollen moved about 50 meters and to a height of 0.9 meters while rye pollen was carried 120 meters and to a height of 1.3 meters. Since rye pollen is smaller than wheat pollen (which is smaller than maize pollen) rye is believed to be the most efficient cereal grain in cross pollination.

While increasing male-sterile lines, cross pollination potential, as measured by the yield of the A-line versus the B-line, increases as the pollen donor area increases. Therefore, as the sterile-increase fields become larger, the seed-set percentage increases.

The earliest data available on seed-set potential with male-sterile lines indicated that around 70 percent seed set could be obtained in crossing blocks having planting ratios of 1:1. As crossing blocks have increased in size, there has been a tendency to change the ratio to 3:1 with the reduction being made in the male lines. Nevertheless, the seed setting potential on the female line has remained about the same. Therefore, somewhat higher seed set might be expected, on the average, with large crossing blocks and 1:1 ratios, but currently it seems more economical to choose a lower seed set and a higher proportion of females in the planting. Seed sets on a field basis have run as high as 90 percent. For some reason, it is difficult to obtain seed set above 90 percent.

A commercial forage hybrid currently being distributed in the southwestern U.S. by DeKalb AgResearch, Inc. is produced on a female-male ratio of 8:1. This wide ratio is obtained by using an unusually good pollen-shedding male line and close planting of female and male lines in grain-drill rows. Because the lines are close together a hybrid blend is harvested but the resulting seed content averages about 95 percent hybrid. In 1971, the hybrid seed production fields averaged over 3 t/ha of seed at a number of locations.

Unpollinated flowers of male-sterile wheats remain open and viable up to 7 days if temperatures are not extreme. The tendency of unpollinated flowers to remain open until fertilized increases the crop's chances of being infected by loose smut and ergot. Rapid build-up of loose smut has been found in male-sterile lines susceptible to loose smut. Ergot is a serious problem on male-sterile stocks in the hard red spring areas of the U.S. Early flowering male-sterile stocks are less infected than those that flower later and are grown under higher daily temperature.

Because exposed stigmas predispose the crop to disease infection, it may be more profitable in some areas to increase the outcross potential of inbreds by developing more efficient pollinating parents. But in wheat areas where diseases are no problem the outcross potential might be increased markedly by developing wheats with stigmas that extend beyond the floral bracts, as in grain sorghum. Much genetic variation exists and improvements are forthcoming without intensive effort since R-line (restorer-line) selections that have large and well-extruded anthers can be easily identified in populations segregating for various degrees of sterility. In some genetic backgrounds, however, extruded anthers are associated with an undesirable shattering character.

CYTOPLASMIC MALE STERILITY AND POLLEN RESTORATION

Cytoplasm found in several *Triticum* and *Aegilops* species contributes to male sterility in the cultivated species of wheat: *A. caudata* (Kihara, 1951), *A. ovata* (Fukasawa, 1953), *T. timopheevi* (Wilson and Ross, 1962), *T. boeoticum* (Maan and Lucken, 1967), and *A. speltoides* (Maan and Lucken, 1971). Several workers have indicated that several species closely related to Timopheevi also carry sterile cytoplasm. Comparisons are being made which should determine whether other members of the Timopheevi complex carry superior or inferior characteristics relative to hybrid wheat breeding. Maan and Lucken (1971) suggested that *A. speltoides* has contributed cytoplasm to the species in the Timopheevi complex.

Many fertility factors have been identified that restore fertility to the various sterile cytoplasms. Generally, the species that contributes the sterile cytoplasm also is a source of pollen-restoring genes. A fertility factor may not be effective for all cytoplasms. Some fertility factors which are effective in at least two cytoplasms have been identified.

Since *T. timopheevi* was the first species identified as having no obvious adverse side effects, it has been used extensively in hybrid wheat breeding. The first efforts to develop pollen-restoring lines of wheat with Timopheevi cytoplasm were directed toward transferring restorer genes directly from Timopheevi (Wilson, 1962) and screening Timopheevi-derived lines that had been developed earlier for disease resistance (Schmidt, Johnson, and Maan, 1962). These procedures contributed to solving the problem of pollen restoration.

Several important sources of restoration for Timopheevi cytoplasm have been found in addition to those from Timopheevi. These other sources are *T. spelta* var. duhamelianum (Kihara and Tsunewaki, 1967), *T. dicoccoides* var. Kotschyanum (Wilson, 1968*a*), French *T. aestium* varieties (Oehler and Ingold, 1966), and Indian *T. aestium* varieties (Miri, Amawate, and Jain, 1970). A large number of hexaploid varieties have weak fertility genes.

Although three restorer genes have been found in some hexaploid Timopheevi derivatives (Wilson, 1968*b*), recent information on monosomic analyses indicate that at least three additional genes are available from various other sources. Fertility factors in several Timopheevi derivatives have been located on chromosomes 1A, 6B, and 7D (Robertson and Curtis, 1967; E. H. Talaat, *unpublished*). The location of the fertility genes in the DeKalb three-gene lines is not known at this time. Duhamelianum has a fertility gene on chromosome 1B (Tahir and Tsunewaki, 1969). Primepi, a pollen-restoring French variety, carries fertility factors on 1B and 5D (P. N. Bahl, *unpublished*). A *T. zhukovskyi* hexaploid derivative was reported as having a fertility factor on chromosome 7B (P. N. Bahl, *unpublished*). All restoring stocks have not been studied for the location of their restoring factors, and some may have fertility factors on other chromosomes.

The fertility factors are not consistently equal or unequal in their effect (P. N. Bahl, *unpublished*). Apparently, genetic background has a strong influence on which gene is the strongest in expression. The gene on chromosome 1A appears to have a relatively strong expression. Also, the gene from *T. spelta* on chromosome 1B appears to be relatively strong.

The genes studied in the Timopheevi derivatives have cumulative effect. Whether the newer gene sources will be additive when combined with Timopheevi restoring genes is not known.

The two-gene Timopheevi restorer and the two-gene Primepi restorer have given complete field restoration in central Kansas. The three-gene Timopheevi-restored hybrids have surplus restoration in some areas of the world and appear completely adequate throughout the winter wheat region of North America.

Significant genetic and environmental modifying effects are generally present to influence the expression of male sterility and pollen restoration. If genetic and environmental effects are both negative in regard to pollen restoration, three or more fertility genes from *T. timopheevi* may be necessary to allow normal pollen formation. Certain female lines that normally have excellent pollen production cannot be restored with two-gene Timopheevi restorers in central Kansas. This indicates that modifier genes are acting as inhibitors or sterilizers. Early maturity backgrounds also have negative effects on pollen restoration. Temperatures that are not optimum also contribute to male sterility; relatively cool temperatures have consistently produced sterility effects. The northern hard red spring wheats have the strongest restoration requirement in North America, and in some years a fourth gene may be necessary to ensure normal pollen development.

HYBRIDS AND R-LINES

Briggle (1963) reviewed studies of the level of heterosis in various wheat crosses. All the reports in his review deal with small plots and low planting rates. Both positive and negative results on heterosis were noted. Although hand-crossed seed and small plots were involved, Livers and Heyne (1968) studied hybrid vigor in hard red winter wheat planted at normal seeding rates over a 4-year period in Kansas. They found that 36 wheat hybrids produced yields 32 percent higher than nine parental types. The best hybrid yielded 31 percent more than the best variety.

We have conducted extensive yield tests with two pollen-restored single-cross wheat hybrids. Data in our tests support data compiled in the U.S. Department of Agriculture Southern Regional Performance Nursery Report of 1970 (*unpublished*), from which Table 1 was developed. The grain yields of these preliminary hybrids appear equal to the yields of the commercial varieties. Pollen restoration was generally adequate in both hybrids except that tip sterility occurred at some locations with the two-gene hybrid, A 235. The three-gene hybrid, A 227, has been fully restored in every location tested. Maturity, height, and shattering are below optimum in the hybrids and may be partly responsible for lack of hybrid superiority.

From studies of these and other pollen-restored hybrids and their parents, the yield levels contributed by the R-lines do not seem adequately high to produce superior grain yield in hybrids. The yields of the R-line parents of

Table 1. Comparative yields of two DeKalb wheat hybrids and two commercial varieties grown during 1969 and 1970.

Variety or hybrid	Yield (t/ha)
Commercial varieties	
Scout 66	2.86
Triumph	2.47
Mean	2.67
DeKalb hybrids	
DeKalb A227	2.65
DeKalb A235	2.62
Mean	2.63

Table 2. Mean yields of selected R-lines and check varieties grown at Wichita, Kansas in 1971 in a three-replication, randomized-block field test[a].

Variety or line	Yield (t/ha)
Check varieties	
Scout	4.16
Satanta	4.81
Mean	4.48
R-lines	
RE30	4.96
RE31	5.04
Mean	5.00

[a]Plot size = 2.97 sq m, LSD (5%) = 185 kg, c.v. = 7.8%.

A 235 and A 227 are about 10 percent less than the yields of the commercial varieties. It is doubtful that superior hybrids can be recovered if poor yielding R-line testers are employed.

Recurrent improvement of R-lines is now the focus of our breeding work. Data from preliminary R-line yield trials in 1971 (Table 2) indicate that the yield level of the best commercial varieties has now been reached. The performance of these R-lines in Timopheevi cytoplasm further supports the theory that the alien cytoplasm has no serious adverse side effect.

No problems have been encountered in pursuing the quality objectives. Most quality properties are intermediate in the hybrid. Lines not suitable for quality can often be combined with other lines for satisfactory hybrid flour quality.

The single-cross and blended combinations of single cross and pollinator seed stock are being tested. The hybrid is first evaluated as a single-cross entity before it is tested in combination with the pollinator. Various pollinator percentages may be considered, but to qualify under a hybrid seed label, a hybrid must have at least 75 percent hybrid seed in the blend, as required by U.S. law.

The F_2 hybrids from restored single crosses have yielded around 10 percent less than the commercial check varieties. Only one F_2 hybrid has equalled the yield of the commercial varieties. F_2 types may be possible, but considerable selection effort would be required to identify the proper parental lines.

Much progress has been made in developing hybrid forage wheats for the western Great Plains of the U.S. Hybrid vigor, drought tolerance, and resistance to wheat streak mosaic have been combined in a 49-chromosome forage hybrid for use solely as a pasture plant. Seven chromosomes from *Agropyron elongatum* are used in the forage wheat hybrid with a 56-chromosome *Agrotricum* as the male parent. The hybrid, though produced in a blend, is approximately 95 percent pure since the male stock yields less than the female and is largely eliminated in harvesting because its kernels are not readily separated from the glumes upon threshing. The 1971 harvest will produce sufficient seed to plant about 25.000 hectares of land.

The use of additional lines in hybrid development has been proposed earlier (Wilson, 1968*a*) as an efficient way to use desirable genes for disease and insect resistance from other species. Breeding materials that involve a number of desirable characters found in *Secale* and *Agropyron* species are being developed. Much has yet to be learned about the number of chromosomes that can be added from these exotic sources without adverse side effects on grain yield or quality.

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Discussion: Hybrid wheat breeding

B. R. JACKSON: Did you obtain the 70 percent seed set at Wichita?

J. A. Wilson: We have obtained 70 percent seed set at Wichita with a number of female lines.

B. R. JACKSON: What factors influence cross pollination?

J. A. Wilson: We may not know all the factors influencing cross pollination, but high yield levels and environmental conditions that favor open flowering are the prerequisites for satisfactory seed production on male-sterile wheats. Females that flower ahead of the males is an additional factor quite important to good seed production.

B. R. JACKSON: What are the chances of using radiation on male-steriles to obtain a stable restorer?

J. A. Wilson: Irradiation is one possible technique in developing restorers. We have sent sterile seed stock to C. F. Konzak at Washington State University for this type of study. We are not working in this area, but are relying on gene sources already identified.

S. S. VIRMANI: In rice, partially pollen-fertile plants with about 50 percent fertility have been reported to have normal seed set in the absence of ovule sterility. What are the factors that make incompletely restored pollen-fertile plants of wheat have seed set below the normal level?

J. A. Wilson: The incomplete fertility in partially fertile wheat hybrids is due to the segmental sterility on the wheat spike. The basal florets having 50 percent stainable pollen can set seed quite well, but the florets at the tip of the head have no fertile pollen. Seed set in this section must be through cross-pollination. The sterile tips of wheat heads generally flower later than the fertile section which reinforces the sterility condition, since less pollen is in the air at the time when the tip florets are receptive.

S. S. VIRMANI: What is the time interval between the opening of floret and dehiscence of the anther in wheat?

J. A. Wilson: The wheat floret can open and close its lemma and palea within a few minutes. If the flower is not pollinated, it may stay open for several days if environmental conditions are moderate.

E. A. SIDDIQ: What is the mechanism of glume opening in the male-sterile parent?

J. A. Wilson: Lodicules adjacent to the base of the ovary swell with water uptake, forcing the lemma and palea apart.

E. A. SIDDIQ: Is there any gene associated with the male-sterile gene or genes to provide stability in the degree of sterility?

J. A. Wilson: I have only limited experience with genetic male sterility, but the types I have seen lack stability of sterility. However, a broad section of wheat germ plasm is quite stable in sterility when placed in Timopheevi cytoplasm.

T. T. CHANG: Could you relate the superior yield performance in some of the hybrids to a better developed root system?

J. A. Wilson: We have no information on that yet.

Outlook for hybrid rice in the USA

H. L. Carnahan, J. R. Erickson, S. T. Tseng, J. N. Rutger

The rice variety Bir-Co (PI279120) and three *Oryza glaberrima* accessions were found to possess male-sterile cytoplasm and restorer genes. California japonica rices, however, have neither. Cross pollination in the field to produce seed set on male-sterile rice plants was only 16 percent for Bir-Co derivatives and 24 percent for *O. glaberrima* derivatives, even though the male steriles were surrounded by pollinators. In spaced plantings 17 out of 19 hybrids yielded more than the higher yielding parent. The best hybrid yielded more than twice as much as the higher yielding parent. The number of panicles and number of seeds per panicle were primarily responsible for the yield heterosis. Crosses between japonica and indica varieties gave low yield because of F_1 sterility.

INTRODUCTION

Jones (1926) in California was one of the first to report hybrid vigor in rice. He studied only one to six F_1 plants of four crosses and compared them at spacings of 30 x 90 cm with five seedlings of each parent. The parents were all adapted to California conditions. The hybrids were taller, had more culms, and yielded, on the average, 69 percent more than their higher yielding parent.

Since cultivated rice rarely outcrosses, an understanding of the flowering process and of genetic variation in floral morphology among genotypes is relevant to the development of hybrid rice. Jones (1924) in California reported that approximately three-fourths of the florets opened between noon and 2 PM. The remaining florets opened primarily during a 2-hour period before or after the main flowering period. Three indica varieties showed a slight tendency to start flowering earlier in the day than three Japonica varieties he observed.

CYTOPLASMIC MALE STERILITY IN RICE

Erickson (1969) was the first U.S. researcher to report male sterility conditioned by the interaction of the cytoplasm and genes in rice. When Bir-Co (PI279120) was used as the maternal parent in crosses with California varieties in 1967, the F_1 plants were almost completely sterile while the reciprocal crosses

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Table 1. Differential seed set of reciprocal F_1 hybrids, reciprocal backcrosses, and F_2 plants of reciprocals.

Cross	Generation	Plants (no.)	Steriles (%)	Seed set of fertiles (%)
California varieties x Bir-Co	F_1	102	0.0	30 to 70
Bir-Co x California varieties	F_1	89	100.0	—
California varieties x Bir-Co/2	BC_1	6	0.0	90 to 100
Bir-Co x California varieties/2	BC_1	42	85.7	20 to 30
Bir-Co x California varieties/3	BC_2	108	93.1	20 to 40
Bir-Co x California varieties/4	BC_3	68	100.0	—
California varieties x Bir-Co	F_2	104	24.0	20 to 100
Bir-Co x California varieties	F_2	64	81.3	20 to 60
California varieties x Bir-Co/2	BC_1F_2	82	12.2	30 to 100
Bir-Co x California varieties/2	BC_1F_2	135	79.3	20 to 100

produced about 50 percent seed set. The reciprocal backcrosses confirmed the effects of the cytoplasm (Table 1). The three California varieties, Caloro, Calrose, and Colusa, when crossed with Bir-Co, always gave higher sterility in the Bir-Co cytoplasm than in their own. The sterility increased with succeeding backcrosses of California varieties into Bir-Co cytoplasm.

The F_1, BC_1, and BC_2 plants from crosses between Colusa, Caloro, and Earlirose, and three accessions (PI231195, PI232853, and PI269630) of *O. glaberrima*, Steud., as maternal parents, all failed to set any seed upon natural selfing.

If Bir-Co is fertile and it possesses male-sterility cytoplasm, it must possess restorer genes. F_3 lines from eight F_2 plants from crosses of Bir-Co x japonica varieties were classified for seed fertility. The F_2 parent plants set seed in about 50 percent of the florets. Considering 20 to 100 percent seed set as indicative of fertility, from 19 to 85 percent of the F_3 plants in the respective lines were fertile. Overall, 44.9 percent of the F_3 plants were fertile. Sterility of the type common in japonica x indica crosses is confounded with the sterility caused by cytoplasm-genic interaction in the present crosses. Therefore, the ease or difficulty of recovering the gene or genes for fertility restoration is not readily apparent. In retrospect, we believe that an assessment of the percentage of good pollen on partial steriles would have been worthwhile. In addition such a study might have revealed whether the cytoplasm also may affect female fertility as reported by Grun (1970) in interspecific *Solanum* crosses.

HETEROSIS FOR YIELD AND YIELD COMPONENTS

The yield and yield components for 19 F_1 hybrids, expressed as percentages of the high parent, are listed in Table 2. The parents and the F_1 plants were seeded in the greenhouse and transplanted to the field 30 cm apart in rows 45 cm apart with each F_1 row flanked by its parents. Data for each cross

Table 2. Index numbers of yield and yield components of 19 F_1 bybrids.

Hybrid and reciprocal[a]	Index number (high yielding parent = 100) Yield	Panicles (no.)	Grain wt	Seeds/ panicle
		Reciprocals		
Calrose x Ku jung do	123	97[b]	102	103
Calrose x Isao Mochi	106	114	107	79[b]
Calrose x Kitaminori	104	106	101	90[b]
Caloro x Ku jung do	115	93[c]	101	105
Caloro x Isao Mochi	124	114	107	93[b]
Caloro x Kitaminori	109	119	105	101
Colusa x *Ku jung do*	122	108	94[b]	118
Colusa x Isao Mochi	117	111	101	112
Colusa x Kitaminori	55[b]	133	98[b]	55[c]
		Hybrids		
Calrose x *Taichung 122*	116	116	101	85[c]
Calrose x Taichung 150	154	111	93[b]	121
Caloro x Taichung 122	117	115	100	103
Colusa x *Norin 8*	131	105	75[c]	123
Colusa x *Taichung 122*	153	110	88[c]	144
Colusa x Taichung 150	210	109	103	142
Colusa x Tedori-wase	185	126	89[c]	136
Earlirose x Eiko	87	132	97[b]	68[b]
Earlirose x *Norin 20*	107	90[b]	103	97[b]
Earlirose x *Norin 48*	103	90[b]	96[b]	104

[a]The parent in italics was the higher yielder. [b]The F_1 value was higher than the mid-parent value. [c]The F_1 value was lower than the mid-parent value.

represent the mean of two or three replications, each containing from seven to 10 plants. These data show that heterosis for yield and for each of the components of yield is common though not universal. Eight of the 19 hybrids produced from 122 to 210 percent of the yield of the better parent. The five hybrids that showed the most heterosis for yield also showed the most heterosis for number of seeds per panicle. The two hybrids that yielded less than the high parent also had noticeably fewer seeds per panicle than the high parent. Panicle number and number of seeds per panicle were the two components most related to heterosis for yield. Of the 19 crosses, 15 showed heterosis for panicle number, three showed partial dominance for high panicle number, and one had slightly fewer panicles than the mean of the parents. For number of seeds per panicle, 12 crosses were heterotic, five showed partial dominance for high number, and two had a lower number than the mean of the parents. Grain weight of F_1 hybrids ranged from 75.3 to 107.2 percent of the better yielding parent. Since the differences in grain weight among parents usually were not great, this component character did not contribute much heterosis for hybrid yield.

The heterosis noted in these experiments is exciting. An important question, however, is how much of the heterosis expressed by spaced plants will be expressed in the dense stand common in commercial fields.

All hybrids from crosses between japonica and indica varieties gave inferior yields primarily because of the common occurrence of F_1 hybrid sterility.

McDonald, Gilmore, and Stansel (1971) studied rates of photosynthesis in several rice varieties and five F_1 hybrids. They reported heterosis for rate of gross photosynthesis. At maximum light and at temperatures of 30 to 40 C, the best two F_1 hybrids, Kulu x Taichung Native 1 and Kulu x Belle Patna, had photosynthetic rates of 44 and 41 percent above those of their respective high parents.

OPEN-POLLINATED SEED SET ON MALE STERILES

To make hybrid rice a commercial reality it must be possible to obtain cross-pollinated seed on male-sterile lines. The low percentage of outcrossing reported for male-fertile rice does not necessarily indicate the amount of crossing that will occur to produce seed set on male steriles. To explore this problem we alternated male-sterile and pollinator plants at 15-cm spacings within a center row and planted a border row of pollinators on each side 30 cm away. This resulted in a 5:1 ratio of pollinator to male-sterile plants. Seed set was determined on both bagged and unbagged panicles. Sixteen male-sterile plants derived from *O. glaberrima* backcrossed four times to California varieties gave from 0 to 5 percent selfed seed set under bag pollination (mean: 1.2%), set from 0.5 to 44 percent seed under open pollination (mean: 24%). In contrast, nine male-sterile plants from Bir-Co backcrossed four times to California varieties produced from 0 to 4 percent selfed seed set (mean: 1.2%) and set from 6 to 31 percent (mean: 16.2%) under open pollination. Seed set of the male fertile was reduced from 96 percent under open pollination to 74.5 percent under bags, but varieties appeared to respond differently to bagging.

These results suggest that limited seed production on male-sterile rice is a major problem that needs additional research. B. J. Hoff (*personal communication*) in Louisiana and we think that selecting for larger anthers might provide more abundant pollen to increase cross pollination. *Oryza perennis* Moench and some indica varieties are possible sources of this character. Other floral characteristics such as the length of time the florets remain open might be associated with increased cross pollination.

OTHER CONSIDERATIONS

Other requirements for developing F_1 hybrid seeds are that the pollinator parent have seed shape, cooking quality, and maturity characteristics very much like those of the F_1 hybrids so that the hybrid seed does not have to be harvested separately from the pollinator and that desired agronomic characteristics be combined with cytoplasmic male sterility and genetic fertility restoration systems to obtain parents that will produce superior hybrids. The possibility of using F_2 and F_3 generations commercially, rather than the F_1 generation, should not be overlooked completely. Such advanced generations might have stop-gap value in a critical situation where rare, simply inherited dominant resistance to a devastating disease or insect is not available in an adapted variety.

We should all be aware of the possible association of characters other than male sterility with a given cytoplasm such as has been reported by Villareal and Lantican (1965) in corn. We should identify and maintain diverse sources of cytoplasmic male steriles in rice.

Shinjyo (1969) reported only 50 percent good pollen in F_1 hybrids heterozygous for the restorer gene or genes. We do not yet know the extent to which our cytoplasmic male steriles may be restored by the restorer in the heterozygote. Incomplete restoration could be a serious problem in temperate climatic areas.

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Outlook for hybrid rice in India

M. S. Swaminathan, E. A. Siddiq, S. D. Sharma

Commercial exploitation of heterosis in maize, sorghum, and pearl millet in India shows that heterosis results not only in substantial yield increases but also in stability of performance, particularly under environmental stress. The potential of high yielding dwarf varieties under irrigated conditions has not been fully exploited, but the development of commercial hybrids from high yielding dwarf varieties of rice might improve and stabilize the production levels of upland rice that is dependent on monsoon rainfall and which makes up most of the rice area of India. An analysis of the prospects for developing commercial rice hybrids in the light of available information shows that although dominant genes for resistance to major rice diseases are a distinct advantage, the male and female parents should be carefully chosen to ensure desirable grain quality in the F_1 hybrid. A commercial rice hybrid could be developed with cytoplasm from the West African rice variety, Sakotira-55, and the restorer systems from varieties like Basmati-370. Some ancillary characters in the rice germ plasm may also be useful in developing commercial hybrids.

EXPLOITATION OF HETEROSIS IN GRAIN CROPS IN INDIA

The widespread commercial exploitation of hybrid vigor in India has been confined to *Zea mays* L., *Sorghum bicolor* (L.) Moench, and *Pennisetum typhoides* Staff ex Hubbard. Our experience with these crops has shown:

—Heterosis offers hope for attaining large increases in yield.

—Heterosis gives the crop considerable resiliency in response to fluctuations in the environment, probably through early seedling vigor, a characteristic particularly advantageous under dry farming conditions. For example, the sorghum hybrid CSH-1 and the pearl millet hybrids, H.B.2, H.B.3, and H.B.4, have consistently yielded more than the local varieties during seasons characterized by drought and unfavorable weather.

—By appropriate reconstruction of plant morphology and developmental rhythm and by exploiting additive gene action through suitable population improvement programs, composites or varieties whose yield potentials are as good as those of hybrids can be developed. Examples of such composites or varieties are the Swarna variety of sorghum and composites of maize, Jawahar, Kisan, Vikram, Ambar, and Vijay (Rao et al., 1969; Swaminathan et al., 1970).

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Table 1. Manifestation of heterosis in some intervarietal crosses in indica rice.[a]

Cross (P_1 x P_2)	Height (cm)			Panicle length (cm)			Tillers (no./plant)			Grains (no./panicle)			1,000-grain wt (g)		
	P_1	P_2	F_1	P_1	P_2	F_1	P_1	P_2	F_1	P_1	P_2	F_1	P_1	P_2	F_1
DGWG x RS II	95	128	136	24.7	26.4	31.5	7	5	14	119	239	277	24.0	24.0	26.5
IARI 5901 x RS II	86	128	136	21.7	26.4	28.9	7	5	10	138	239	196	24.5	24.0	[illegible]
IARI 10560 x RS II	101	128	139	23.8	26.4	31.1	7	5	8	133	239	277	22.0	24.0	25.0
IARI 10561 x RS II	101	128	145	24.2	26.4	30.7	7	5	8	135	239	329	22.0	24.0	23.5
DGWG x NP 130	95	138	117	24.7	27.5	25.9	7	4	15	119	135	169	24.0	18.5	22.5
IARI 5901-2 x NP 130	91	138	127	25.8	27.5	27.6	8	4	12	172	135	189	22.0	18.5	21.5
IARI 5980 x NP 130	89	138	125	26.7	27.5	24.0	5	4	18	146	135	139	21.5	18.5	20.5
IARI 5995 x NP 130	82	138	108	19.0	27.5	19.2	5	4	10	105	135	92	26.0	18.5	23.0
IARI 10560 x NP 130	101	138	111	23.8	27.5	26.1	7	4	13	133	135	222	22.0	18.5	21.0
IR8 x RS I	97	126	137	28.5	27.5	36.1	8	5	36	175	237	296	28.0	24.0	26.6
IR127-80-1 x RS I	130	126	164	29.0	27.5	38.4	4	5	48	375	237	290	20.0	24.0	18.3
S.55 x B.370	80	151	161	20.5	29.5	29.6	6	4	46	106	135	215	25.0	19.5	23.6
S.55 x AC 5636	80	135	189	20.5	28.0	32.2	6	5	55	106	137	329	25.0	20.5	23.8
IR127-80-1 x B.370	130	151	169	29.0	29.5	29.2	4	4	35	375	135	265	20.0	19.5	21.0

[a]F_1 population size ranges from 15 to 20; plants grown at 100-40-40 fertilizer level; plants spaced at 23 x 15 cm in the field; one replication per population.

—Dependence on a single source of male sterility is dangerous if the male-sterile parent carries dominant genes for susceptibility to important diseases, e.g., to ergot, downy mildew, and grain smut, as does CMS 23A of *Pennisetum typhoides*, or poor grain quality, as does MS Kafir-60 grain sorghum which has a chalky endosperm.

SCOPE AND NEED FOR HYBRID RICE

Different estimates show that for hybrid vigor in a self-pollinated plant to be economically advantageous, it must give 25 percent more yield than the best commercial variety. This level of increase can be achieved with several rice crosses (Table 1).

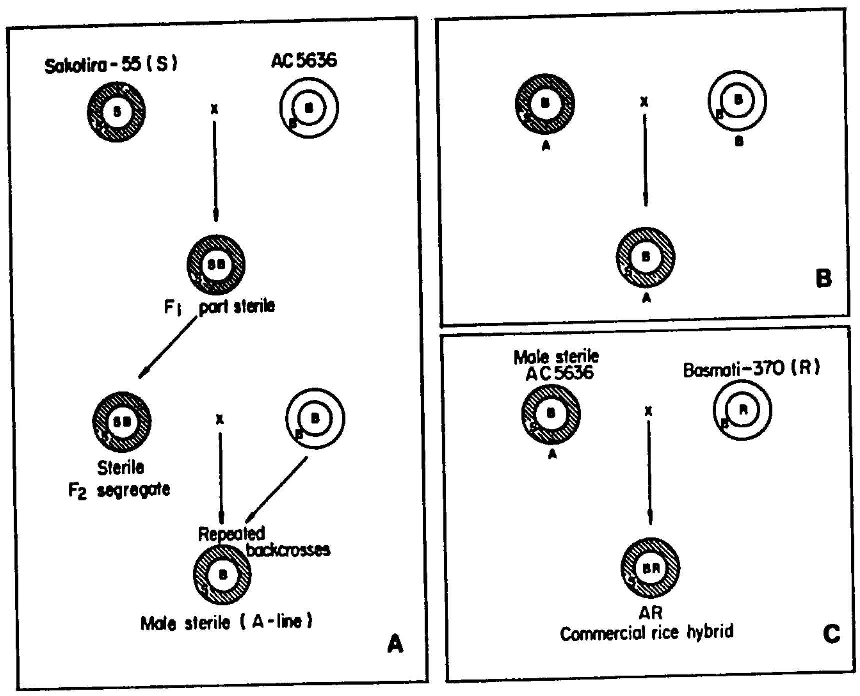
If hybrid vigor in rice will give the same degree of protection against the extremes of weather, as it has in sorghum (Rao and Harinarayana, 1969), research on hybrid rice may be worthwhile in India since over 20 of the 35 million hectares planted to rice depend on rainfall. On the other hand, in the regions that are irrigated or where rainfall is abundant, the dwarf varieties have not fully attained their yield potential because of inadequacies in water management, agronomic practices, pest control, and post-harvest technology. In these areas, therefore, even if yields can be raised through hybrid rice, such increased yields may not be of immediate practical value. If production of upland rice that is dependent on monsoon rainfall can be made more stable, however, fluctuations in food grain production in India will be less violent.

ADVANTAGES AND DISADVANTAGES OF THE RICE PLANT FOR EXPLOITING HETEROSIS

Ratooning and vegetative propagation (Nair and Sahadevan, 1961; Richharia, 1962) would make hybrid seed production much less expensive in rice than in crops like wheat. Dominant genes for resistance to some diseases and pests are known (Ramiah and Ramaswami, 1936; Venkataswamy, 1963; S. V. S. Shastry and D. V. Seshu, *unpublished*) and other desirable characters, such as early flowering (Sampath and Seshu, 1961), seed dormancy (Shanmugasundaram, 1953; Narayanan Namboodiri and Ponnaiya, 1963), and dense panicle (U.S. Department of Agriculture, 1963), have been reported as dominant and hence easily incorporated in the hybrid rice. Considerations of quality, however, strongly affect the price of rice in Indian markets. The F_2 grains may vary in amylose content and gelatinization temperature and this may affect the milling and cooking qualities. Hybrid rice, unless of parents carefully chosen for their high-quality grain may face an adverse price discrimination.

PROSPECTS FOR DEVELOPING COMMERCIAL HYBRIDS

The major prerequisites for developing hybrid rice are a usable form of male sterility; floral characters, such as a long period of glume opening, a protruding stigma, a long period of stigma receptivity, and abundant pollen; and avail-



1. A. Development of male-sterile lines. B. Maintenance of male-sterile lines. C. Development of commercial hybrid. If restoration is easily obtained, as it is for sorghum, and if diverse restorers are available, testing for fertility restoration and agronomic desirability can be undertaken simultaneously. If fertility restoration presents difficulties, as it does for wheat, development of suitable restorer lines would be an additional step.

ability of dominant genes for resistance to the major pests and diseases; and quality features. No systematic exploration of the prospects for developing hybrid rice for commercial cultivation has so far been undertaken in India. Some observations relevant to starting such a program can be made, however.

Usable form of male sterility

Since an early record by Ramanujam (1935) there have been sporadic reports on the incidence of male sterility in rice. Jachuck and Sampath (1966) found self-sterility in *O. barthii* Cheval. The genetic mechanisms underlying such self-sterility have yet to be clarified. No case of cytoplasmic male sterility and fertility-restoring genes has been found in India.

Recently, different degrees of fertility and sterility have been found at the Indian Agricultural Research Institute in crosses involving a rice variety from West Africa, Sakotira-55. Some F_1 hybrids (e.g. Sakotira-55 x AC 5636) showed over 70 percent sterility. The reciprocal crosses showed enhanced fertility. The lines are being studied to determine if the sterility arises from specific interaction between the Sakotira cytoplasm and gene or genes of the pollen parent (fig. 1). Basmati 370 appeared to carry the restorer gene or genes.

Environmental stability in the expression of male sterility will also be tested. No work has so far been done on the chemical induction of male sterility.

Availability of other desirable genes

In the Assam rice collection being maintained at the Indian Agricultural Research Institute, sufficient variation has been observed in the size of anther and stigma and in the duration of glume opening. Some features that favor cross pollination are a large feathery stigma protruding from the spikelet even after anthesis, large anthers bearing abundant pollen, and a longer period of glume opening. These features could be exploited profitably.

PROSPECTS

It is premature to express definite views on the outlook for hybrid rice in India. Practically no scientific effort has been expended in this field except for the recording of useful traits. We think that hybrid rice will have value in increasing yield and stabilizing production in upland areas if it will respond to fluctuations in rainfall as have sorghum and pearl millet hybrids. Before much further work on hybrids is done, data must be gathered on the performance of several F_1 hybrids under upland conditions.

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Cytoplasmic male sterility and hybrid breeding in rice

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The development of commercial hybrids in self-pollinated crops has some inherent difficulties. Cytoplasmic male-sterility as well as fertility-restoring genes are present in rice but the male steriles do not produce a satisfactory seed set on outcrossing. Spikelet sterility is greatly influenced by environments but some sterile lines are more stable than others. The semidwarf rice variety, Taichung Native 1, has been found to be a source of sterile cytoplasm and fertility-restoring genes. Another variety, Pankhari 203, acts as a maintainer. Completely male-sterile progeny were obtained by backcrossing Pankhari twice to Taichung Native 1 x Pankhari. A review of studies on heterosis is presented. Some evidence of variation in floral morphology and outcrossing potential in *Oryza* was found.

INTRODUCTION

The commercial use of F_1 hybrids in maize (*Zea mays* L.), sorghum (*Sorghum bicolor* Moench), and pearl millet (*Pennisetum typhoides* Staff and Hubbard), is a well-recognized achievement of modern plant breeding. Both maize and pearl millet are predominantly cross-pollinated species. Although sorghum is often self-pollinated, it shows on the average about 6 percent outcrossing (Rao and Rachie, 1965). Pollen-sterile lines of sorghum produce nearly normal seed set by open pollination. In maize, hybrid seed was first produced by detasseling or removal of male inflorescence of the seed parent, while in sorghum and pearl millet, the development of hybrids depended entirely upon the availability of cytoplasmic male-sterile lines and fertility-restoring pollinators.

PROBLEMS OF HYBRID DEVELOPMENT IN SELF-POLLINATED CROPS

The development of hybrids in strictly self-fertilized species, like wheat (*Triticum aestivum* L.) and rice, is relatively difficult. The essential prerequisites to a successful hybrid breeding program are the presence of hybrid vigor, availability of efficient cytoplasmic male-sterile lines and fertility-restorers, and ability of male-sterile lines to show satisfactory seed set through cross pollination. About a decade ago, the successful isolation of cytoplasmic male-sterile lines of bread wheat and their fertility restorers generated trem-

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endous enthusiasm among wheat breeders for the development of hybrids. Until now, this remains one of the important objectives of major wheat breeding centers. But commercial use of hybrid wheat is taking longer than was originally anticipated. Although wheat shows considerable heterosis, several problems have been encountered in hybrid breeding (Wilson, 1968).

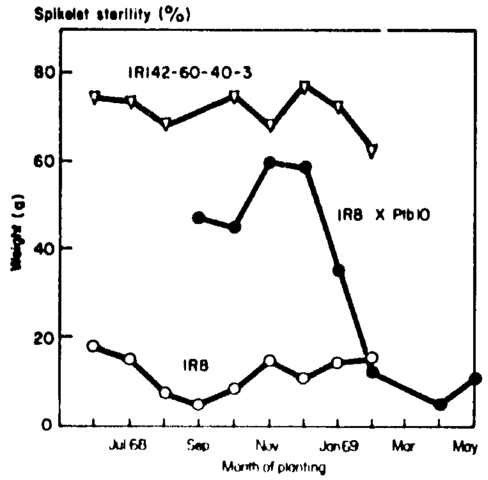
The basic difficulty in the development of hybrids of self-pollinated species is that their floral structures are not well adapted to cross-pollination. Natural outcrossing in both wheat and rice is normally less than 1 percent. The seed set on pollen-sterile plants of wheat was reported by Kherde et al. (1967) to range from 2 to 61 percent. Stansel and Craigmiles (1966) obtained up to 28 percent crossing in semi-sterile rice. In our preliminary investigations, we observed a maximum outcrossing of 13 percent in male-sterile rice. A poor cross-pollination potential of male-sterile lines will make seed production uneconomical. Incomplete restoration of pollen fertility in hybrids can be another problem, but it will be less of a handicap if male-sterile florets of commercial hybrids have the ability to cross pollinate.

CYTOPLASMIC MALE STERILITY IN RICE

There are two recent reports of the existence of cytoplasmic male sterility in rice. Shinjyo and Omura (1966) and Shinjyo (1969) demonstrated that the indica variety, Chinsurah Boro II, possesses a sterile cytoplasm and a fertility-restoring system while the ponlai variety, Taichung 65, acts as a maintainer. Erickson (1969) reported that another indica variety, PI279120 (Bir-Co), is a source of sterile cytoplasm and fertility-restoring genes.

In 1967, we selected many partially sterile plants from IRRI breeding material. By screening for spikelet and pollen sterility for several generations in the progeny of these plants, we isolated two male-sterile lines, D320 from B581A6-545/2 x 81B-25, and D388 from IR400-28-45 x Pankhari 203. An examination of their meiotic behavior showed that no apparent chromosomal aberration was involved in producing male sterility (IRRI, 1970, p. 96-97). D320 and D388 produce normal seed set on hand pollination. While bagged heads produce less than 5 percent seed set, unbagged heads may give 5 to 15 percent seed set. Our current studies indicate that male sterility of D388 can be maintained by using Pankhari 203 as the pollinator. Another variety, Peta, restores fertility to D388.

We observed that spikelet sterility in rice is greatly influenced by environment (IRRI, 1970, p. 96-97). Figure 1 shows spikelet sterility of three different lines in monthly plantings. The spikelet sterility of IR8 x Ptb 10 F_1 plants ranged from about 60 percent in plantings in November and December 1968 to about 6 percent in a planting in April 1969. IR8, a standard variety, and IR142-60-40-3, a pure breeding, partially sterile line, did not show any strong influence of planting time on spikelet sterility. The results indicate that developing male-sterile lines that are relatively insensitive to environmental influences may be possible.



1. Effect of planting time on the spikelet sterility of three lines.

In searching for cytoplasmic male sterility, we studied many crosses among indica varieties and found that crosses of the semidwarf varieties, IR8 and Taichung Native 1, with Pankhari, B581A6-545, Basmati 370, Nahng Mon S4, and CO 22 give highly sterile F_1 progeny (IRRI, 1970, p. 96-97). The F_2 generation of crosses showed no definite pattern of segregation. In our initial work, we ignored small differences in spikelet sterility among reciprocal crosses and assumed that sterility was not influenced by cytoplasm. We now realize that it is necessary to study backcrosses to establish the role of cytoplasm because "gametic-development genes" (Oka, 1964*a*) or other genetic factors probably influence hybrid sterility and obscure the effect of cytoplasm.

We selected crosses that showed some reciprocal differences in pollen sterility for backcrossing and further studies. The results obtained from the Taichung Native 1 x Pankhari cross, on which we have adequate data, are summarized in Table 1. The hybrid material planted in December showed higher pollen sterility than the same material planted in April but the general trend in the two planting seasons was similar. The mean pollen sterility of Taichung Native 1 x Pankhari F_1 ranged from 47.4 to 93.6 percent in the two planting seasons. Its reciprocal cross showed about 12 percent lower pollen sterility. The differences between the reciprocal crosses increased to about 20 percent in the F_2 generation. The backcross of Taichung Native 1 x Pankhari to Pankhari produced more than 33 percent higher pollen sterility compared with its backcross to Taichung Native 1. Continuous backcrossing of selected sterile plants to Pankhari progressively increased the pollen sterility of the progeny. In the second backcross, most of the progeny were nearly 100 percent pollen sterile. On the other hand, backcrossing to Taichung Native 1 gradually restored fertility. Spikelet sterility showed a trend similar to pollen sterility.

The results indicate that the semidwarf variety, Taichung Native 1, is a source of both male-sterile cytoplasm and fertility-restoring genes, and that Pankhari 203 has a normal cytoplasm and acts as a maintainer of sterility.

Table 1. Pollen and spikelet sterility of parents, F_1, F_2, and backcrosses of Taichung Native 1 x Pankhari 203.

Material	April 1970 seeding				December 1970 seeding			
	No. of plants	Pollen sterility (%) Range	Pollen sterility (%) Mean	Spikelet sterility (%)	No. of plants	Pollen sterility (%) Range	Pollen sterility (%) Mean	Spikelet sterility (%)
Taichung Native 1 (T)	5	1.5 to 6.2	3.5	20.1	9	1.6 to 5.0	2.8	6.4
Pankhari 203 (P)	5	2.6 to 4.9	4.0	29.7	10	4.3 to 9.9	7.0	4.6
T x P F_1	4	42.4 to 47.9	47.4	70.8	8	90.2 to 96.6	93.6	96.1
P x T F_1	4	34.4 to 37.1	35.8	58.5	9	68.1 to 97.1	80.4	92.1
T x P F_2	51	3.4 to 58.2	21.0	34.5	50	6.4 to 100	66.0	64.2
P x T F_2	—	—	—	—	56	5.7 to 100	47.8	58.3
(T x P) x T F_1	37	3.7 to 63.6	21.6	39.3	17	5.2 to 95.1	41.0	41.1
(T x P) x P F_1	30	15.1 to 97.5	55.7	63.1	23	9.9 to 100	78.8	79.3
(T x P) x T_2	—	—	—	—	13	7.6 to 73.1	29.9	25.5
(T x P) x P_2	—	—	—	—	21	86.8 to 100	96.2	95.4
(T x P) x P_2	—	—	—	—	72[a]	30.7 to 100	88.8	96.6

[a]October 1970 seeding.

Pankhari is not agronomically desirable; it is tall and photoperiod sensitive, and it has high sterility in crosses with most varieties. We are attempting to develop maintainer and male-sterile lines with improved plant type and other desirable characteristics. By crossing several Pankhari x Taichung Native 1 F_3 plants with male-sterile Taichung Native 1 x Pankhari/3, we were able to identify at least one dwarf and photoperiod-insensitive F_3 plant which is homozygous as maintainer of sterility.

Our preliminary results indicate that there are other indica varieties which behave like Taichung Native 1. On the basis of information available from our work and that of Shinjyo (1969), it may be speculated that many indica varieties have a sterile cytoplasm and a fertility-restoring system while most japonica varieties possess a normal cytoplasm.

OUTLOOK FOR HYBRID RICE

Rice has some advantages over wheat in hybrid development. Rice can be transplanted, ratooned, and propagated by tiller separation and its seed rate is lower.

The heterosis for grain yield and yield component characters has been reported by several rice workers (Kadam, Patil, and Patankar, 1937; Brown, 1953; Alim and Sen, 1957; Pillai, 1961; Rao, 1965; IRRI, 1970, p. 96-97). Usually, however, the experiments were not conducted under commercial planting conditions and the results are of limited practical value. The studies carried out by Jennings (1967) showed that F_1 hybrids are superior to the parents in vegetative growth but they fail to maintain the superiority during

Table 2. Anther length, stigma length, and stigma exsertion in two wild species of rice and IR8 (mean of 15 plants).

Name	Length (mm)		Degree of stigma exsertion (%)
	Anther	Stigma	
"*O. perennis* subsp. *balunga*" (Acc. 101173)	4.5 ± 0.06	1.6 ± 0.03	91.8 ± 1.25
"*O. sativa* f. *spontanea*" (Acc. 100183)	4.1 ± 0.08	2.2 ± 0.06	92.1 ± 1.40
IR8	1.8 ± 0.03	1.7 ± 0.03	6.5 ± 1.30

grain production due to excessive vegetative growth. Although tall hybrids may show superiority over traditional varieties under various conditions of environmental stress, it will be necessary to develop semidwarf hybrids for high productivity. More studies need to be carried out to determine to what extent the hybrids with improved plant type are superior to their parents. It should be possible to improve the magnitude of heterosis by reconstituting inbred strains by a recurrent selection program (Athwal and Borlaug, 1967).

Hybrid breeding offers a method for using non-additive genetic variation. McDonald, Gilmore, and Stansel (1971) reported that two F_1 hybrids of rice had a 40 percent higher rate of gross photosynthesis than their respective high parents. The speed and ease with which favorable dominant genes for disease and insect resistance, photosynthetic efficiency, and other important characters can be combined in the F_1 generation offer a major advantage for the development of commercial hybrids. If a dominant gene for semidwarfing is discovered, it will facilitate development of hybrids with high yield potential.

Several problems in hybrid breeding require solution. The presence of widespread hybrid sterility in rice will interfere with fertility restoration. We need more information regarding the effect of genetic and environmental factors on male sterility and fertility restoration. Perhaps the most important problem is that of modifying the floral structure of male-sterile rice to increase its outcrossing potential. Asian forms of "*Oryza perennis*" which are cross-compatible with *O. sativa* show 20 to 45 percent outcrossing (Oka, 1964*b*). We have identified some accessions of "*O. perennis*" and "*O. sativa* f. *spontanea*" with large anther and extruding stigma (Table 2). They show also longer duration of spikelet opening, and greater interval between spikelet opening and anther dehiscence. Whether the characters responsible for high rate of outcrossing can be transferred to cultivated rice remains to be explored.

Although most of the genetic tools required for developing rice hybrids are now available, much more research must be done before we can tell whether hybrid rice can be commercially successful.

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Discussion of papers on hybrid rice

S. D. SHARMA: U.S. farmers practice direct seeding. What do you visualize for hybrid rice: direct seeding or transplanting?

H. L. Carnahan: Direct seeding.

W. L. CHANG: Have you observed the performance of F_1 hybrids under stressed and non-stressed environments?

H. L. Carnahan: No.

W. L. CHANG: Dr. Carnahan, are the high parents in Table 2 leading commercial varieties in California? If not, what will be the yield advantage of the hybrids over the leading commercial varieties?

H. L. Carnahan: The higher yielding parent is in italics. Calrose, Caloro, Colusa, and Earlirose are commercial varieties in California. In 13 of the 19 comparisons, the California varieties yielded more than the other parent, even under the spaced planting employed in this experiment.

K. KAWANO: I understand that heterosis exists in rice mainly in vegetative vigor. Under spaced planting, hybrids would be able to have higher dry matter production than the parents without simultaneous reduction in grain-straw ratio. But some varieties such as Peta yield well under spaced conditions but not under close spacing at high levels of nitrogen application. Don't you think it is difficult to extend the promising results of hybrids obtained under spaced planting to a practical field condition?

H. L. Carnahan: In this study we used spaced planting simply because of the limited number of F_1 seeds. Your point is well taken. Generally, the number of tillers per plant and number of seeds per panicle become less as stand density increases. Additional research will be required to establish the level of heterosis expressed in dense stands. It appears to me that the environment in lowland rice culture is less likely to limit the expression of heterosis than is the case for many other crops.

P. R. JENNINGS: Who would wish to defend the position that increased height and vegetative vigor, typical of F_1 plants, will result in increased field yields?

E. A. Siddiq: F_1 plants manifest hybrid vigor not only in mere vegetative growth and height but also in some of the yield components. From yield estimation made on a limited number of F_1 hybrids, projection on the increased field yields of hybrid populations cannot be expressed without adequate data. But increased yields at field level has been demonstrated in other cereals. The ideal plant height for rainfed conditions would be, in my opinion, semi-tallness which under moisture stress might not lead to lodging.

T. T. CHANG: Dr. Siddiq mentioned the use of F_1 hybrids for upland areas. I doubt that the cost of hybrid seed production would pay for the low yield levels of upland fields.

D. S. ATHWAL: I also doubt if the benefit will pay for the seed cost. Upland rice requires higher seeding rates than irrigated rice.

W. L. CHANG: What are the possibilities of developing gene pools by using cytosteriles as one parent?

E. A. Siddiq: Although theoretically possible in specific cases like checking gene erosion, I do not know how practical developing composites for resistance to different races of major pests and diseases by the use of cytosteriles will be.

Improving upland rice

Upland rice improvement in West Africa

A. O. Abifarin, R. Chabrolin, M. Jacquot,
R. Marie, J. C. Moomaw

The species of rice cultivated in West Africa are *Oryza glaberrima* and *Oryza sativa*. The former originated in Central Niger River Delta (Mali) and the latter was first introduced by the Arab traders in the 13th century. Upland rice which makes up about 75 percent of total rice production in West Africa is found under different types of climatic, ecological, and soil conditions. Many institutions are involved in research on upland rice both in francophone and anglophone countries. General research has been delegated to the International Institute of Tropical Agriculture in Nigeria and to the Institut de Recherches Agronomiques Tropicales in Ivory Coast. Present breeding objectives include the development of shorter plant height, short, narrow leaves, non-lodging culm, seedling vigor, medium panicle number, high number of grains per panicle, medium to high grain weight, wide adaptability, pest and disease resistance, responsiveness to fertilizers, high yielding ability, early maturity, drought resistance, and long, white, cylindrical and translucent grains that cook dry. Varieties released include OS 6, Anethoda, Moroberekan, Iguape Cateto, 63-83, and Tunsart. Traditional cultural practices limit yields in farmers' fields. Major problems to be solved are breeding for a good upland type that is drought tolerant, disease and pest resistant, and high yielding, and improvement of cultural practices of the farmers.

INTRODUCTION

Two species of rice are cultivated in West Africa. An indigenous species, *Oryza glaberrima* (Steudel), seems to have originated in the Central Niger River Delta (Mali) and was grown there long before the Christian era (Portères, 1956). The species has weak stems, has an easy-shattering, red grain with a long dormancy, is susceptible to disease, and is low yielding. It is no longer widely planted, having been largely replaced by *O. sativa*, L.

O. sativa, the cultivated rice of Asia, was probably introduced into central West Africa by Arab traders coming overland in about the 13th century. The Portuguese were responsible for many introductions along the coast in the

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15th and 16th centuries (Food and Agriculture Organization, *unpublished*). Systematic introductions of varieties from India and Ceylon were made in Nigeria as early as 1890.

Although upland rice cultivation is limited to the wet part of West Africa, it is a major part of the total area under rice (about 75% according to FAO). Upland rice yields are generally low and annual rice production is deficient, although imports vary widely. Average yields, including yields of swamp and flooded rice, are about 1 t/ha while upland rice yields are about half as much. High yields have been reported from experimental sources, however: in Ghana, 2.6 t/ha (A. N. Aryeetey and E. J. A. Khan, *unpublished*), in Sierra Leone, 2.5 t/ha (H. Will, *unpublished*), in Nigeria, 5.4 t/ha (Federal Republic of Nigeria, *unpublished*), and in Senegal, 4.4 t/ha (IRAT, 1971).

Since the importation of rice adversely affects payment balances, efforts are being made to expand rice production on a large scale. The prospect is bright for the development of upland rice cultivation. Upland rice cultivation does not require the large investment in hydraulic structures and land levelling that is involved in irrigated rice schemes. Furthermore, upland rice is relatively easy to mechanize with conventional grain-farming equipment to take advantage of the large areas of under-used land in many places in West Africa.

Recently consumption of rice has increased sharply, mainly because of the development of urban communities and because of the higher value attributed to rice as a food, compared with the more traditional dishes, sorghum, millet, yams, and cassava.

ECOLOGY OF RICE PRODUCTION IN WEST AFRICA

Rainfall has a marked seasonal rhythm in West Africa. In the north of the area there is only one short rainy season. Its duration increases southward. Further south, rains are interrupted in late summer and a short dry season separates two rainy periods. The two rainy seasons usually are too short to allow the rice plant to achieve successful growth.

The north therefore requires early maturing varieties, while longer duration varieties can be grown in the south. Furthermore, as daylength increases in summer from south to north, the duration of photoperiod-sensitive rice varieties is lengthened. Thus varieties that have a short basic vegetative period and insensitivity to photoperiod are needed.

The rainfall pattern in the driest zones of western Africa is highly variable, especially at the beginning and the end of the wet season. Thus choosing the date for sowing is a gamble. Early sowing is usually more successful, however.

The water requirements of the rice plant can be considered as a fraction of measured or calculated potential evapotranspiration (one-half at the beginning and the end of the life cycle, one in the active growth period), and hence the length of the useful moist period is computed from rainfall data. This task has been performed by Cocheme (1971) and a map showing annual rainfall, its variability, and the length of the moist period has been published. Generally, however, upland rice requires about 60 mm of rain per 10-day period.

Rainfed paddy cultivation is most successful on soils with a high water retention capacity. Fine texture is a favorable characteristic of soil, as is the presence of an impervious lower horizon and even the presence of bedrock or iron pan at a lower level. Rainfed rice is often found on such soils.

A number of level, fine-textured soil series have been classed as particularly suitable for rice culture in West Africa. Among many soil groups, the gleyic Cambisols, humic Gleysols, and eutric Fluvisols have been planted to rice (Riquier, 1971) when they occur in a suitable climatic zone. Many riverine and coastal soils (vertisols, Fluvisols, and Ferralsols) are used in mangrove swamps, if salinity is low, "Fadamas," and inland swamps and poorly drained grasslands ("Bolilands" in Sierra Leone). Rice tolerates moderate levels of salinity, but low base saturation (less than 50%) may create nutritional disorders in the plants. The Niger Delta and the Lake Chad border have high potential for upland rice and for flooded rice culture if water control is developed.

INSTITUTIONS

Early national research efforts were primarily directed towards cash crops. Food crops were neglected. Even when rice became a major component in research programs, upland rice was considered to be such a poor-yielding, and even dangerous, crop that it was consistently neglected.

Rice research in Nigeria, Ghana, and Sierra Leone began in a small way in the 1920's with the Moor Plantation in Ibadan as the main center. Research on flooded rice was the principal objective of the Rice Research Station at Rokupr, Sierra Leone, established in 1934, but it included upland rice from the beginning. The Rokupr station was expanded in 1953 to serve all the anglophone West African countries. The West African Rice Research Station became the Sierra Leone national station in 1962 when the association of these states was terminated by independence. Upland rice research was carried on by the Food Research Institute in Kumasi, Ghana, and to some extent by the Agricultural Research Station, Kpong, Ghana.

After World War II, a large peanut cultivation scheme was started in Casamance (Senegal). It soon became clear that it was not advisable to grow one crop of peanuts after another and that some kind of rotation was required. Upland rice was selected as a convenient rotation crop because it could be mechanized. A research station was created at Sefa, which was later (1961) assigned to the Institut Recherches de Agronomiques Tropicales et des Cultures Vivrieres (IRAT) with the aim of selecting suitable varieties of short duration and determining sound growing methods for mechanical cultivation.

Ivory Coast, in 1966, requested that IRAT undertake research on rice, particularly upland rice, which represents more than 90 percent of the rice area of the country. The main research station is at Bouaké.

IRAT agencies in Dahomey, Cameroun, Mali, Upper Volta, and Madagascar are also concerned with aspects of upland rice cultivation (Chabrolin, 1969).

In 1971, the newly formed West African Rice Development Association decided that the Bouaké research station and the International Institute of

Tropical Agriculture (IITA) in Nigeria would be in charge of general research on upland rice cultivation.

Before 1960, Institut National d'Etudes Agronomique du Congo conducted extensive research on upland rice at Yangambi (Congo-Kinshasa). Research included the breeding of a number of successful varieties: the OS and R series.

OBJECTIVES OF BREEDING PROGRAMS

Upland rice, here, means rice whose water requirements are met only by the rain that falls directly on the rice field. It excludes rice grown on run-off water or from a watertable supply.

Upland rice plants in West Africa are tall, 130 cm or more, moderate tillering, have long and broad leaves. These varieties (e.g. Moroberekan, OS 6, Iguape Cateto) tolerate some drought periods, and are moderately resistant to fungus diseases, particularly blast. The quality of their grain is satisfactory by local standards. Their potential yield, however, is less than 5 t/ha, their grain-to-straw ratio is low, and they lodge badly and do not respond to nitrogen fertilizer. A few *Oryza glaberrima* varieties have good seedling vigor and drought resistance but are susceptible to blast, lodge easily and early, and shatter as soon as they mature.

In upland conditions, the short, improved varieties, such as Taichung Native 1, IR8, and I-Kung-Pao, possess high yield potential, but their yield is reduced under moisture stress, and they frequently suffer from blast and Helminthosporium leaf spots.

Past breeding programs have been mainly aimed at developing varieties adapted to specific ecological conditions in which rice was found growing: upland, fresh-water swamp, deep water, and saline (mangrove) swamp. In addition, in most programs the introduced varieties from which selections were being made were too few to result in rapid progress. Only since about 1955 have hybridization, pedigree selection, and backcrossing methods been used. Some selection is now being made from introduced materials or from crosses having morphological characters that produce an improved plant type. In these countries, recent attention has turned to short-statured plants, about 100 cm tall, with short, narrow leaves, stiff, non-lodging culms, high seedling vigor, medium panicle number, high number of grains per panicle, and medium to high grain weight. Except in one or two stations, little work is done on most of these traits though they are frequently found in the program objectives.

The search for widely adaptable and reliable varieties receives major emphasis in the breeding program in West African countries. Several varieties have been included in yield trials at various sites within the countries to determine their adaptability and consistency. H. Will (*unpublished*) in Sierra Leone reported that Tikiri Samba was the most outstanding variety at the three trial sites.

Yielding ability, of course, is an important objective. The absolute yield capacity can only be assessed under optimum conditions in the field, but these conditions, especially climatic ones, are beyond the control of the breeder. In fact upland rice will be judged over a long period for both yield potential, and perhaps more important, yield regularity. A comparison of a variety's yield under upland and flooded culture gives a useful measure of the variety's yield capacity.

Resistance to diseases and pests must be sought. Preliminary observations indicate that disease resistance is closely associated with drought resistance. The main diseases are blast, Helminthosporium leaf spot, and brown leaf spot.

Blast investigation already has a prominent place in most breeding programs in West Africa. In Sierra Leone, H. Will (*unpublished*) reported that an upland variety possessing more blast resistance than the recommended variety, Anethoda, was identified from crosses between Faya, a lowland rice, and Tikiri Samba. In Nigeria, in 1968, three high-yielding upland varieties were crossed with the blast-resistant swamp variety, Tjina, to produce blast-resistant upland varieties. From these crosses, 97 blast-resistant, long-grain, short-duration progeny were selected for further observations at F_4. In the IITA rice improvement program, experiments for blast investigations include screening varieties for resistance under local conditions in the International Blast Nursery which has been grown at eight West African locations. Twenty local varieties are added to the 350 test varieties supplied by IRRI for this blast nursery.

Relatively little attention has been given to resistance to stem borers in the breeding programs of most countries because these insects have little economic importance. Other major rice pests are absent or have low incidence.

Another objective is growth duration of the variety which should be synchronized with the moist period of the location in which it is grown; early maturity generally must be emphasized.

Moderate tillering ability is needed to enable the field population to balance the adverse effects of a poor stand. Experiments show that thin sowing increases the drought resistance of the established seedlings, but low seeding rates carry inherent risks of too low plant populations.

Root systems and their development in upland rice require a particularly detailed study. Roughly speaking there are two types of rooting morphology. Varieties such as IR8 and Taichung Native 1 have an abundant, fibrous, thin root system that does not penetrate the soil deeply. It provides an abundant nutrient supply to the plant, but because it is shallow, the plant is susceptible to drought. On the other hand varieties like OS 6 and Iguape Cateto, have coarse roots that penetrate deeply into the soil but have few ramifications. Such a system enables the roots to get water from the lower horizons of the soil when short drought periods dry the surface soil layers. The optimum root system must still be defined but it probably will retain the advantages of each of the two types.

The erect habit of the plant is a favorable feature in irrigated rice because it prevents mutual shading. But where weed competition is an important factor, upland rice probably should have a more spreading habit, particularly in the early stages of growth.

Seedling vigor, which enables the plant to establish its root system as quickly as possible, is required.

Short stature (100 cm or less) is now recognized as necessary for reducing lodging, allowing heavy nitrogenous application thus improving yield.

Some improvement may be sought in physiological factors that influence resistance to moisture stress, such as leaf curling, cell sap osmotic concentration, stomatal opening and distribution, and root density. These factors require basic research studies.

Until now, grain quality has not attracted much attention in breeding programs. The grain of the local or recommended varieties is generally suitable for the farmer's consumption or for local markets. Breeders have aimed at obtaining a plant type adapted to intensive cultivation, with quality a secondary consideration. Nevertheless, they have selected lines with long, white, cylindrical, and translucent grain which are now replacing varieties with bold and red grain. Other characters, such as chalkiness, translucency, protein content and quality, amylose content, and gelatinization temperature have not been considered in any detail.

Except for a report from Sierra Leone (H. Will, *unpublished*) no consideration has been given to storage quality after cooking.

GERM PLASM SOURCES AND CROSSING PROGRAMS

Some progress has been achieved in the screening of introduced germ plasm for more promising materials. In Ghana (A. N. Aryeetey, *unpublished*), many lines have been screened under upland conditions for yield and other traits. Currently C4-63, Palawan, C 21, 617A, Milpal 17, M2-2 HB Da2, Soavina, C 18, C 2, Inacaba, and Azucena are being studied further. In Sierra Leone, A. J. Carpenter and H. Will (*unpublished*) screened 59 varieties in observational trials under upland conditions. In Nigeria, Beck and Hardcastle (1965) reported 89 accessions in their collection. IITA has recently begun a program for developing upland varieties. In 1970, 874 accessions were planted in an upland nursery for comparative evaluation. Several lines have been identified for further detailed evaluations, and 378 have been selected for observational yield trials.

The plant material gathered at Bouaké is composed of more than 250 varieties from Ivory Coast, Congo-Kinshasa, Senegal, Madagascar, Brazil, Taiwan, Pakistan, and Vietnam and from IRRI.

In addition to the screening of local and introduced materials, various programs of crossing and subsequent selection are under way. In Sierra Leone, A. J. Carpenter (*unpublished*) and H. Will (*unpublished*) made crosses between promising varieties, such as Azucena x Faya, Anethoda x S.R. 26, Tikiri Samba x Faya. Anethoda is the recommended upland variety. It has red grain and it is an indica type. Tikiri Samba is an upland variety and S. R. 26 is a swamp variety said to be resistant to salt. At IITA, crosses have been made between local and introduced varieties or lines. Some of these are OS 6 x IR400-5-12, OS 6 x IR20, OS 6 x IR22, and OS 6 x IR154-61-1. F_2 seeds are being planted for bulk and pedigree selections. Crosses in the Ivory Coast have been made to combine the desirable features of short-statured lines (local or imported) and good yielding and drought-resistant, taller ones. The principal parents of these crosses have been described (IRAT, 1971). Miro-Miro is a Senegalese variety with short straw, profuse tillering, and a small grain. Its grain may be improved by crossing with medium- or long-grain indica rice. R 67, from Yangambi has a medium tillering ability, stiff straw, high stature. It has low susceptibility to blast. Among the early maturing progeny selected from this cross, which are now at F_8, No. 8a, short statured, is kept as a possible parent for new crosses. Bavot and Bokolon tiller profusely and are susceptible to shattering. They are very similar. Bokolon is a local strain; the origin of Bavot is not precisely established. Moroberekan, also a local variety, is low tillering and its grain does not shatter. The crosses were made to get favorable recombinations of characteristics. Some early-maturing families have so far been detected in the progeny.

A series of diallel crosses was made at Bouaké in 1967 between Taichung Native 1 (high-yielding, short-statured) and Iguape Cateto (from Brazil-1, drought- and disease-resistant), OS 6 and RT 1031-69 (tall varieties, from Yangambi), and between 63-105 (natural hybrid of 560 from Madagascar) and Moroberekan (from Ivory Coast).

Crosses have been made between Taichung Native 1, Ebandioulaye, and Bignou, two local mangrove swamp rice varieties, with fairly good yield and disease resistance. Selection in the progenies is made in upland and in mangrove conditions, according to the bulk method at Sefa (Senegal).

In 1968, at Sefa, crosses between IR8 and 1031-69, Iguape Cateto, and 63-83, and between Tunsart and Taichung Native 1 were made, also by the bulk method. The variety 63-83 is similar to 63-105 and has the same origin. It does well in Casamance and seems absolutely resistant to diseases. Tunsart is an upland rice from Vietnam with limited yield ability but very good resistance to adverse conditions.

In 1969 at Bouaké, 63-104 was crossed with MMR 67-8a, Taichung Native 1, and OS 42. MMR 67-8a is a short duration line from the cross R 67 x Miro-Miro. The variety 63-104 has the same origin as 63-105 and 63-83, but it has a longer duration and erect leaves. OS 42, from Yangambi, is shorter than 63-105 and is susceptible to diseases.

A crossing program involving *O. sativa* and *O. glaberrima* has also been started to test and take advantage of the hardiness of *O. glaberrima*.

In 1969, Institut National de la Recherche Agronomique in France irradiated five varieties, TS 123, Tainan 2, I-Kung-Pao, Taichung Native 1, and IR8, to induce resistance to blast. Their progeny are being examined at Sefa (Senegal).

In nitrogen response trials in Sierra Leone of local varieties and lines from IRRI, and of Taiwanese and other introduced upland varieties, IRRI lines did not compete successfully with the locally established varieties under the prevailing upland conditions (H. Will, G. S. Banya, C. D. Williams, and S. M. Funnay, *unpublished*). On the other hand, although these IRRI lines were selected for flooded cultivation, an upland observational nursery at IITA indicated that many have high potential for upland cultivation. For instance IR503-1-91, IR269-26-3, and 81B-25 from Surinam were superior yielders.

A nursery of 578 upland varieties from the IRRI world collection and advanced breeding lines, planted in 30-cm rows, was subject to severe moisture stress in a 1970 trial. About 70 days after planting an unusually early dry period occurred (less than 5 mm/day precipitation) and lasted for 60 days. A few of the early maturing varieties (M1-48, M8-19, and IR126) produced modest yields but most of them failed completely. Many lines that had not yet initiated panicles remained alive, but they were greatly delayed in maturity. About 6 weeks after resumption of rainfall, many varieties produced normal yields. An IR503 line which had 130 days duration in the flooded paddy, required 195 days to mature in this test. Some rows of OS 6 were harvested in the early group, normally 115 to 120 days, but later heading rows yielded poorly and had over 185 days duration.

In northern Nigeria, nine sites were chosen to test for more suitable upland varieties in derived savanna areas (Federal Republic of Nigeria, *unpublished*). The two top-yielding varieties were F. 425 and OS 6. F. 425 produced the highest yields at five stations (0.9, 1.0, 1.7, 2.2, and 2.5 t/ha) out of nine. OS 6 ranked first at only two stations (2.1 and 2.7 t/ha). Thus F. 425 has higher yield potential and adaptability in parts of the savanna zone.

An important characteristic of an upland variety is early maturity since its dependence on rainfall requires that the life cycle be completed soon after the rainy season ends. In Ghana, E. J. A. Khan (*unpublished*) reported that IR8 and IR5 matured much later in upland yield trials than under lowland conditions. In a trial by A. N. Aryeetey (*unpublished*) with 12 varieties, the time to blooming ranged from 80 to 113 days (Table 1). Rainfall, with unsatisfactory distribution, was just over 500 mm (20 inches) from March to August.

VARIETIES AND YIELD IMPROVEMENT

In Nigeria, until 1966, Agbede 16/56 was recommended for upland culture (Nigeria, 1968). It is long-grained, but it is not highly resistant to blast and it does not respond well to fertilizer. OS 6 was found to be higher yielding than Agbede 16/56 in a series of experiments from 1964 to 1966 and was recommended. More recent tests in the northern states show F. 425 to be superior to other varieties. In Ghana, Palawan has been recommended on the basis of yields of 2.2 t/ha with only 635 mm of rain during the growing period (E. J. A. Khan, *unpublished*). Anethoda, a recommended variety in Sierra Leone, produced over 70 percent more than the local variety. Anethoda 24, a reselection from the West African Rice Research Station, gave a still higher yield.

In francophone West Africa, with low levels of farm management and unsophisticated extension organizations, IRAT has been restrained in recommending highly improved varieties such as Taichung Native 1, IR8, I-Kung-Pao, and others. Instead, well known hardy varieties, with lower yield potential, but less risk have been recommended (Chabrolin, 1970). Depending on the

Table 1. Grain yield and number of days from planting to flowering of 12 varieties, Kpong, Ghana, 1969.

Variety	Days to flowering (no.)	Yield (t/ha)
C4-63	105	1.77
Palawan	110	1.31
C 21	98	2.08
617A	100	1.97
Milpal 17	105	.89
M2-2	113	.98
HBDa 2	101	1.65
Soavina	80	
C 18	106	1.27
C 2	110	1.05
Inacaba	104	2.13
Azucena	101	1.75

duration of the moist period the choices have been Moroberekan (about 150 days duration) and OS 6, Iguape Cateto, 63-83, or Tunsart, with durations of about 120 days. Taiwan Sen 123 has the shortest duration (about 110 days) among the varieties released. Yield differences vary greatly for some varieties such as Taichung Native 1 or I-Kung-Pao (from 0.1 t/ha to 4.0 t/ha), while those traditional varieties, such as Moroberekan or Iguape Cateto, vary less (from 4 t/ha) without this improvement being detrimental to the consistency of yield.

MANAGEMENT PRACTICES

Traditional management throughout West Africa is unusually low in technical standards. It consists of clearing the land, scraping it slightly by hand, hoeing, and broadcasting the seed. Spacing is usually very wide; other crops are often interplanted with rice. No fertilizers are supplied, and weeding, if practiced, is always late and inefficient. The land is abandoned when three successive crops have been harvested.

Whatever the choice of varieties, these methods must be improved in many ways if yields higher than about 0.5 t/ha are to be achieved. A deep (15 to 20 cm) and thorough plowing is a basic requirement for upland rice. The best way to achieve it is to plow the soil just after harvesting the previous crop (peanuts and maize are good before upland rice). This practice however is not practical in the zones that have two rainy seasons (at Bouaké, for instance). Soil moisture at plowing should be adequate to permit establishment of good porosity that can be retained for some time under the heavy rains that frequently occur at the beginning of the rainy season. The seedbed should be softened by light tillage (covercrop, offset, Canadian hoe). Proper tillage not only improves yields (Table 2), it also reduces the growth of weeds.

Sowing must be done as early as possible in accordance with the rainfall pattern. Rice is fairly tolerant of drought at the seedling stage if seeds are

Table 2. Effect of land preparation (plowing 20 cm deep, and scraping 6 cm deep) on grain yields of four varieties at Sefa Nicou (Senegal), 1970.

Variety	Yield (t/ha)	
	Plowing	Scraping
Taichung Native I	4.4	1.2
63-83	3.4	0.9
Iguape Cateto	2.7	1.0
IR8	2.6	0.5

sown about 2 cm deep. Rows can be spaced as much as 40 cm apart, allowing easier hand weeding, without reducing the yield greatly. Rates of 50 to 70 kg of good seed per hectare are satisfactory and recommended in Ivory Coast for spacing between 30 and 40 cm.

Known soil deficiencies in major or minor elements must be corrected. When deficiencies are corrected, nitrogen sometimes depresses yields because of the poor plant type of the cultivated varieties and the severe lodging that results. Water metabolism and fertilization deserve more study.

Without a water layer on the soil, weeds grow vigorously and continuously in upland rice fields. Weeds are a management problem that limits upland rice yields and frequently negates the effects of good varieties. It is almost impossible to control weeds satisfactorily without herbicides if rice seeds have been broadcast. The currently available chemicals lack the residual activity and selectivity needed for complete control. Drilling seeds in lines facilitates weeding, mechanically or by hand. Weeding can be by hoe or with drawn implements but care must be taken not to trample the soil excessively, thus destroying its porosity, and causing yield reduction.

Preliminary experiments aimed at developing maximum yields in plots with complete protection have so far failed to show economic benefits from insecticides. It would nevertheless be unfair to conclude that insect problems are not important in upland rice cultivation. Many insects occur; *Sesamia*, *Chilo*, and *Maliarpha* are among the major pests. Insect parasites and other insectivores keep pest populations in check.

MAJOR PROBLEMS FOR SOLUTION IN FUTURE PROGRAMS

In strict upland rice cultivation, the most important limitation apparently is irregular water supply. The plant's sensitivity to drought can be improved by breeding and by improving cropping practices (physical condition of the soil, seed quality, sowing methods, and weeding and fertilizer practices).

Most of the recommended varieties do not have improved plant type. They are too tall, weak-strawed, and non-responsive to nitrogen. More crosses between adapted upland types and the improved upland or lowland varieties that have desirable features must be made to break the 3 t/ha yield ceiling at experimental stations. Several locally adapted varieties also need much better resistance to blast.

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Discussion: Upland rice improvement in West Africa

Y. L. Wu: I understand that a good root system is associated with drought resistance and good seedling vigor is also associated with drought resistance. Do you think that seedling vigor possesses a high correlation with root system in upland rice varieties?

A. O. Abifarin: I do not have any data on this point, but depending on when you measure the seedling vigor and root system, it looks like there might be some correlation.

S. S. Virmani: Please name the cultivated varieties of *Oryza glaberrima* that you need to bag to ensure self-fertilization?

R. A. Marie: By the use of bags we ensure only the purity of the progeny and maintain *O. sativa* and *O. glaberrima* strains as pure lines.

S. S. Virmani: What is the extent of sterility that you have come across in *O. glaberrima* x *O. sativa* crosses?

R. A. Marie: In such crosses, the spikelet fertility ratio was about 1 in 10,000 under good climatic conditions.

A. C. McClung: How do the root systems of *O. glaberrima* compare with the root systems of *O. sativa* varieties?

M. Jacquot: In West Africa, only a few observations have been made on root system of *O. glaberrima* varieties and no differences are observed in morphological features of roots between varieties of *O. glaberrima* and the OS6 type of *O. sativa* varieties studied. But perhaps there are some differences in the rate of root growth in seedling stages.

Upland rice in the Peruvian jungle

K. Kawano, P. A. Sánchez, M. A. Nureña, J. R. Vélez

Upland rice in the Peruvian jungle is grown under shifting cultivation. Several IRRI selections are superior to all traditional varieties under a wide range of planting seasons. They consistently yield from 4 to 6 t/ha while local varieties yield from 1 to 3 t/ha. The concept of the IRRI plant type developed for lowland conditions seems applicable to the development of a variety for primitive upland conditions. Blast and Helminthosporium leaf spot are the most serious diseases of rice in the Peruvian jungle; Helminthosporium leaf spot can be as destructive as blast. A variety that is both high yielding and tolerant of these diseases has not yet been found. Eighteen date-of-planting experiments showed that yields are closely related to rainfall pattern. An average monthly precipitation of about 200 mm was needed for producing over 4 t/ha. Three consecutive rice crops produced up to 12 t/ha in 14 months. Yield responses to closer spacings were higher than to planting methods, planting densities, or fertilization.

INTRODUCTION

In Latin America, about 65 percent of all the rice produced is grown under upland conditions (Brown, 1969). In Peru, upland rice is grown under shifting cultivation in various parts of the Amazon jungle basin.

The climate of the Peruvian jungle is humid-tropical, characterized by mean annual temperatures higher than 24 C and by rainfall that varies from about 600 to 3,500 mm/year. Upland rice is grown only where the monthly rainfall is more than 150 mm for 4 consecutive months. In these areas, the soils are mostly acid Ultisols with low or high base status and young alluvial soils with high base status along the major rivers (Sánchez and Delgado V., 1969; P. A. Sánchez and S. W. Buol, *unpublished*).

Two kinds of cropping systems, known locally as *tacarpo* and *barriales*, are practiced but some mechanized direct seeding is done in the Tingo Maria area. In the *tacarpo* system, farmers cut and burn the jungle during the drier months and, without further land preparation, drop eight to 25 seeds into holes, 8 to 15 cm deep, spaced 50 cm apart, that have been punched into the soil in an irregular pattern with a stick called a *tacarpo*. Usually the crop gets little care between sowing and harvest. The major varieties planted are

K. Kawano, P. A. Sánchez. National Rice Program (NRP) and North Carolina State University Agricultural Mission to Peru, Lambayeque. *M. A. Nureña, J. R. Vélez.* NRP and Ministry of Agriculture, Lambayeque.

Table 1. Yields at various planting seasons in Yurimaguas and Tingo Maria.

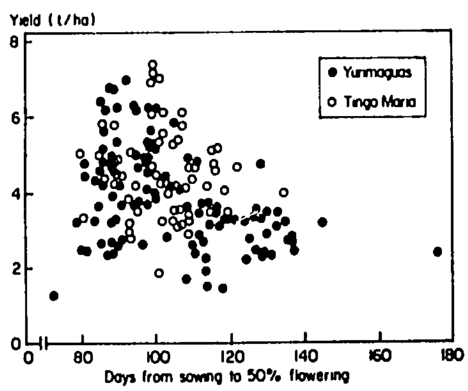
Line or variety	Grain yield (t/ha)										
	Yurimaguas								Tingo Maria		Mean
	Nov 1968	Jan 1969	May 1969	June 1969	Sept 1969	Nov 1969	Feb 1970	Sept 1970	Nov 1969	Dec 1970	
IR8	5.07	3.29	0.73	0.83	4.82	3.84	2.55	5.17	5.20	4.19	3.57
IR4-2	6.30	3.04	0.90	1.03	5.59	4.12	2.30	5.32	5.38	4.72	3.87
IR4-93-2	3.51	3.37	2.34	1.82	4.71	–	2.49	3.68	5.20	4.19	3.48
IR578-8	–	–	–	–	6.25	3.92	4.99	6.93	7.22	5.75	5.85
Carolino (local)	2.93	1.71	0.42	0.44	2.25	2.01	1.05	2.76	4.53	1.81	1.99

relatively low-tillering, early-maturing, tall indicas. Varietal mixtures or heavy segregation always occurs. Maturation is therefore irregular and harvest is done by hand, panicle by panicle. Yields are low, between 1 to 2 t/ha. The fields are normally abandoned after one crop because of the fast jungle regrowth. In *barriales*, the seeds are broadcast on the deposition shores of major rivers when the water level goes down. The crop is harvested before the water rises again (R. E. Zumaeta and S. Barba, *unpublished*).

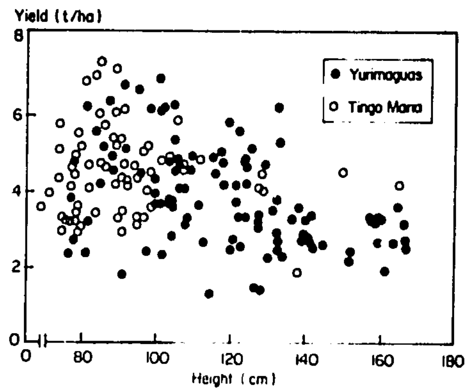
Experiments have been conducted in two representative areas, Yurimaguas and Tingo Maria, to determine the possibility of introducing newly developed genotypes and of improving cultural practices.

VARIETAL IMPROVEMENT

Yield comparisons during several seasons at Yurimaguas and Tingo Maria, in *tacarpo* and drilled plantings, demonstrated the superiority of several IRRI lines over the local variety (Table 1). In the September-to-December plantings, some IRRI lines yielded more than 6 t/ha. In the May and June plantings, when rainfall during the growing season was insufficient, yields were low but some IRRI lines consistently outyielded the local check varieties.



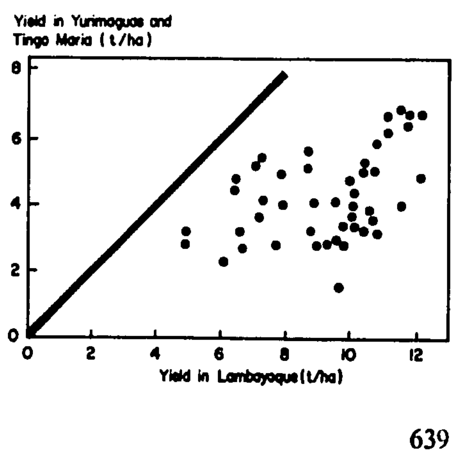
1. Relationship between growth duration and grain yield.



2. Relationship between plant height and grain yield.

In three advanced yield trials at Yurimaguas (Nov. 68, Sept. 69, and Sept. 70) and in two in Tingo Maria (Nov. 69 and Dec. 70) (M. Nureña, J. Vélez, and K. Kawano, *unpublished*), the effects of growth duration (number of days from sowing to flowering) and plant height on yields were analyzed (fig. 1 and 2). All the high-yielding lines flowered between 80 and 110 days after sowing, although many lines that flowered during the same period failed to produce high yields. Most high-yielding lines had short plants (80 to 100 cm). Thus, it is reasonable for breeders to select for relatively early maturity and shortness for these conditions

Rice cropping in the Northern Coast of Peru is considered highly productive. It is characterized by favorable climatic conditions, fertile soils, and more or less constant water supply (K. Kawano and S. Velásquez, *unpublished*). Varietal yield data obtained in Yurimaguas and Tingo Maria and in this highly productive environment (K. Kawano, P. Arriola, and S. Velásquez, *unpublished*) were compared (fig. 3). The genotypes that yield low under the highly productive environment also yield poorly under primitive upland conditions. The high yielding genotypes under primitive upland conditions also yielded well under the highly productive environment, but the high yielders in the highly productive environment did not always perform as well in primitive upland conditions. Thus, breeders have a better chance of obtain-



3. Varietal yield comparison between highly productive conditions (Lambayeque, Northern Coast) and upland jungle.

ing good selections for primitive upland culture from the materials that are high yielding in productive, transplanted, and well-irrigated environment. Rice breeders probably could extend the same concept of plant type developed for lowland rice varieties to the more primitive upland condition.

PLANT DISEASES

Rice blast and Helminthosporium leaf spot are the main diseases in this area. Blast attacks are sometimes so severe that farmers lose a major part of their harvests. Recent studies have shown that varieties can be grouped into three categories based on their reactions to blast. The first category consists of varieties that were attacked heavily by blast in almost any place and season; the second consists of varieties that were susceptible to changes in some places and seasons, but not in others; and the third consists of varieties that showed a constant resistance in any trial during 3 years (H. Huerta, M. Nureña, H. Olaya, L. Chang, and G. Ezcurra, *unpublished*; H. Huerta, *unpublished*).

Helminthosporium leaf spot can become a serious problem when it also attacks the panicles. Since soil improvement is unlikely in this area, new varieties must have resistance. Many genotypes are clearly susceptible. Some genotypes seem to have more tolerance than others, however no lines are completely free from this disease. So far, a combination of high yield and resistance to blast and Helminthosporium leaf spot has not been achieved.

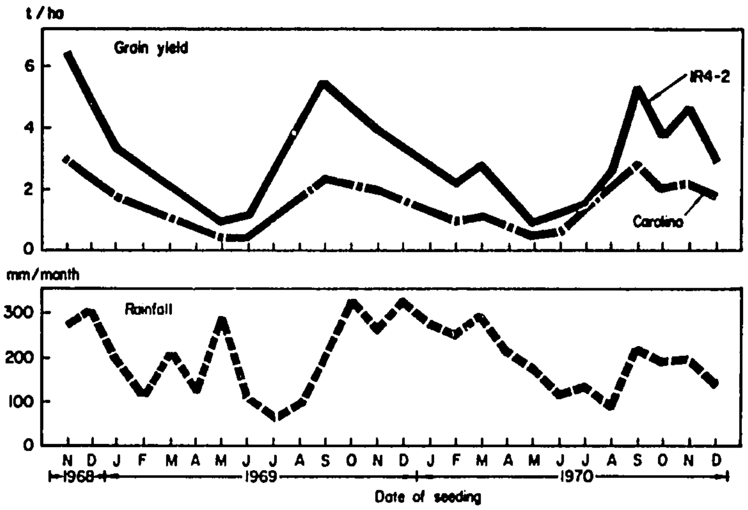
Insect problems are often serious, but no significant research on them has been conducted.

AGRONOMY

Studies were conducted in Yurimaguas to determine the yield response of the varieties with improved plant type to date of seeding and rainfall, to spacing, to fertilization, and to continuous cultivation under upland conditions.

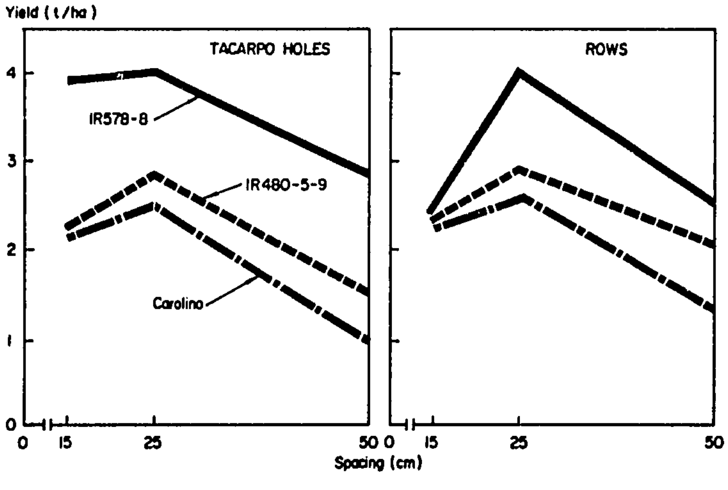
The most important weather variable affecting upland rice yields in the Peruvian Selva is total rainfall and rainfall distribution during the 120-day period of plant growth. Figure 4 shows that the grain yields obtained with an improved variety and a conventional variety in 18 plantings at Yurimaguas are closely related to the rainfall pattern in that region. The improved plant-type selection, IR4-2, outyielded the local variety, Carolino, even when droughts reduced yields. In the five plantings in which IR4-2 produced over 4 t/ha, the rainfall during the growing season averaged about 200 mm/month but high rainfall did not always result in high yields.

The conventional 50-cm spacing of *tacarpo* holes is the most limiting cultural practice. The responses to closer spacing, whether in tacarpo or in row seeding, of three varieties differing in plant type are illustrated in figure 5 (M. Nureña, *unpublished*). The spacing of 25 cm between holes or rows is optimum for all plant types tested. Combining a superior plant type, such as that of IR578-8, and close spacing can produce a yield three to four times that of a conventional

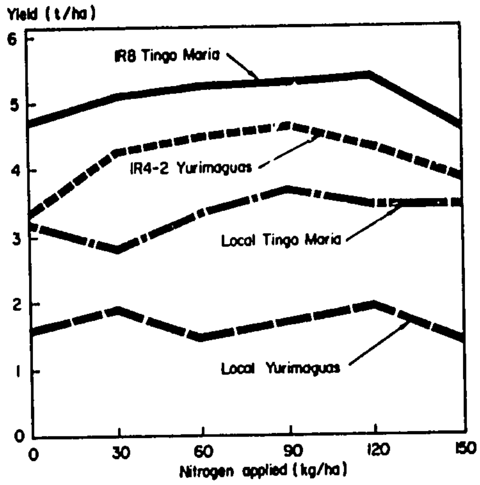


4. Performance of IR4-2 and Carolino, the local variety, as a function of date of planting under upland conditions and rainfall. Yurimaguas, 1968-71.

variety planted at the conventional 50-cm spacing. Studies have shown no great difference between seeding rates ranging from 25 to 100 kg/ha at the same spacing (Salhuana and Sánchez, 1969; P. A. Sánchez and M. Nureña, *unpublished*; J. R. Vélez, *unpublished*; M. Nureña, *unpublished*). Germination is superior in row seeding (M. Nureña, *unpublished*), but in general yields do not differ between the *tacarpo* and drilled systems at the proper spacing. The choice between the two seeding systems depends on how clean the fields are of tree trunks and other debris.



5. Effects of spacing and plant type on the performance of upland rice under the primitive planting system and row seeding. Yurimaguas, 1970.



6. Nitrogen response of contrasting plant types at two upland rice locations in the Peruvian Selva.

Closer spacing did not affect the intensity of blast attacks (P. A. Sánchez and M. A. Nureña, *unpublished*), but it reduced weed competition and thus permitted harvesting with a sickle, instead of by hand, with improved varieties.

Results from Yurimaguas (P. A. Sánchez and M. A. Nureña, *unpublished*) and Tingo Maria (Candela, 1968; J. R. Vélez, *unpublished*) show no response to NPK fertilization during the first planting after the forest was cut, and responses to N only afterwards. The varietal response of the short-plant types to N at two locations (fig. 6) was positive up to 60 to 90 kg/ha, while little or no response was obtained with the tall lodging local varieties. The graph resembles wet season data from the Philippines, the solar radiation levels being similar. The soils of both stations, however, are representative only of the most fertile areas where upland rice is grown and not of the more extensive low base status Ultisols of the Low Selva.

An attempt was made in Yurimaguas to keep the cleared land continuously cropped with rice beginning in September 1968 (P. A. Sánchez and M. A. Nureña, *unpublished*). Three consecutive crops were grown in approximately 14 months. Nitrogen rates were 20 kg/ha in the first crop, 0 kg/ha in the second crop, and 150 kg/ha in the third crop, except for a plot that received no nitrogen. Total yields ranged from 5 to 12 t/ha per year, compared with the conventional level of 1 to 2 t/ha. Weed control seems to be the most limiting factor but fertility depletion must also be considered. Further research must demonstrate the feasibility of abandoning the shifting cultivation system and developing a realistic continuous cropping scheme with modest amounts of inputs for small farmers.

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Discussion: Upland rice in the Peruvian jungle

N. E. BORLAUG: Where does the inoculum of the blast fungus and Helminthosporium come from in the *tacarpo* type of rice culture in the Peruvian jungle?

K. Kawano: We did not find any difference in blast and Helminthosporium attacks between *tacarpo* system and other systems. Disease outbreaks are all by natural infections.

A. O. ABIFARIN: It has been shown that incidence of Helminthosporium leaf spots is associated with low fertility level and *Piricularia* to high fertility level. It is uncommon to have an attack of both diseases. What are the conditions that brought the simultaneous incidence of these two diseases on your plot?

K. Kawano: Our NPK experiment in an upland jungle area did not give us any indication that Helminthosporium can be corrected by fertilization, although there certainly is a soil problem in this area, too. Varieties susceptible to blast are always attacked by blast in Yurimaguas regardless of nitrogen level.

Agronomic and growth characteristics of upland and lowland rice varieties

T. T. Chang, Genoveva C. Loresto, O. Tagumpay

Based on a study of 25 varieties, the plant characteristics and growth features of the so-called lowland and upland rice varieties vary continuously. One or more varieties in one group fall in the range of the other group for one or more major characteristics associated with their performance in upland culture. Low tillering potential and constant leaf area appear to be distinctive features of many upland varieties. Under severe water stress, most upland varieties are less damaged by drought and have lower panicle sterility than lowland types, but certain lowland types, such as Dular and IR5, tolerate drought as well as the upland varieties. Drought resistance is associated with a high proportion of thick roots, a dense root system, a high proportion of long roots, and a high root-to-shoot ratio. There is a genotype-environment interaction among upland and lowland varieties with respect to root development. Many upland varieties are more responsive to water stress. They produce more long and thick roots under dry growing conditions. Leaf characters such as moderate droopiness and the ability to fold when water stress occurs may also be associated with drought resistance under field conditions. It appears feasible to recombine by hybridization and selection the above root and leaf characters associated with drought resistance and other traits which contribute to high grain yield, such as plasticity in tillering ability, high panicle fertility, heavy grains, and resistance to blast and other pests.

INTRODUCTION

Upland rice culture encompasses a wide range of practices, from the strictly non-irrigated culture where seed is planted in granulated and aerated soil to the shifting type of cultivation on hilly slopes. In the humid tropics, upland rice sometimes includes rainfed fields where the rice plants grow in intermittently flooded or saturated soil for a substantial portion of its life cycle. In the tropical areas of Asia, an upland field refers to a field without levees, irrespective of whether it is low lying or located on a flat, well-drained site. In the Philippines, Taiwan, and Japan, the so-called "upland rice culture" may even include transplanting of direct-seeded plants when soil and water conditions are favorable for transplanting.

The characteristic features ascribed to upland rice varieties do not clearly differentiate them from the lowland varieties which are grown in submerged

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soil. The term "upland variety" has been loosely used to designate any strain suitable for upland culture. In Japan and the Philippines, recommended varieties are described as either lowland or upland. A few accessions in the IRRI collection were received with an upland designation, such as "NARB (upland)." A survey of rice literature several years ago showed that a number of the so-called upland varieties grown in the tropics have the following characteristics in common: rapid emergence from the soil following direct seeding, vigorous seedling growth to compete with weed growth, low to medium tillering ability, insensitivity or weak sensitivity to photoperiod, and maturity ranges of 100 to 180 days (Chang and Bardenas, 1965). Certain upland varieties had high levels of drought resistance. Among Japanese varieties, contrasts in morphological, physiological, and anatomical features between the upland (rikuto) and the lowland (suito) types were described by Nagai (1958) and Hasegawa (1963).

In a recent study, we took representative varieties from the upland and lowland groups and compared their agronomic features and growth characteristics under upland and flooded cultural practices. The study was aimed at determining if there are true differences between the two variety groups that ought to be considered in improving upland rices.

PROCEDURE AND MATERIALS

Twenty-five rice varieties were used in the 1970 wet season and 20 in field plantings at the IRRI in the 1971 dry season on slightly acid to neutral Maahas clay soil. Most of the varieties were included in both seasons.

The upland entries were Jappeni Tunkungo, Sintiane Diofor, Agbede, E425, RT 1095-S-26, OS 4, and OS 6 from Africa; M1-48, Miltex, Palawan, and Azmil from the Philippines; Hirayama and Rikuto Norin 21 from Japan; and NARB from China. Azmil, E425, and NARB were grown only in the wet season and OS 6 was grown only in the dry season.

The lowland entries were the semidwarfs Taichung Native 1, IR8, IR20, IR22, IR305-4-20, IR532-1-218, IR579-48-1, IR747B2-6-3, IR773A1-36, IR841-67-1, and IR937-55-3, and the nondwarfs IR5, Peta, and Dular (also used as an upland variety in East Pakistan). IR20, IR532-1-218 and IR579-48-1 were grown only in the wet season. IR841-67-1 and IR937-55-3 were grown only in the dry season.

Two types of cultural management were used in the wet season and three types in the dry season. For upland culture, seeds were planted at 100 kg/ha in rows spaced 25 cm apart. The plots were not irrigated in the wet season, but in the dry season water in furrows between plots provided the minimum amount of water needed to keep the plants growing without severe signs of water stress. Each plot contained four 5-meter rows. For transplant flood culture, 20-day-old seedlings raised in trays were transplanted at one seedling per hill on puddled soil at 25 × 25 cm spacing. The plots were continuously flooded. For drill flood culture, seeds were sown at 100 kg/ha in rows spaced 25 cm apart on shallow furrows in puddled soil. The seeds were later covered with fine soil. The plots were continuously flooded from the seventh day after seedling emergence. This practice was used only in the dry season.

In the 1970 wet season experiment, seeds were sown on June 11, on July 2, and on July 23. Precipitation during the growing period after three planting dates amounted to 670 mm, 970 mm, and 1,209 mm, respectively. The 1971 dry season experiment was sown on January 18.

To compare quantitative traits in different treatments, a plasticity index was computed from the ratio of the transplant flood upland measurements or from the ratio of drill-flood upland measurements.

VARIETAL DIFFERENCES IN AGRONOMIC AND GROWTH CHARACTERISTICS

Seedling emergence

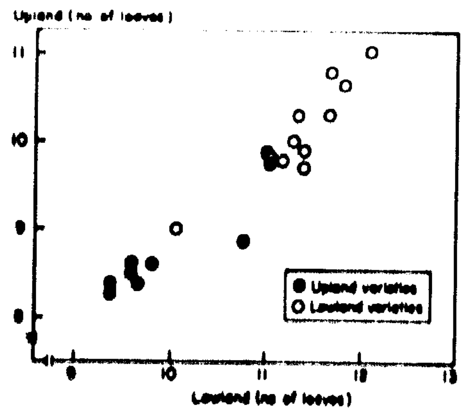
The maximum differences in emergence among 60 upland and lowland varieties ranged between 6 and 18 hours. IR 3472B2 6-3, Palawan, IR5, and Sintianne Diofor invariably emerged early. Obviously, in moist soil, rapid emergence is not a unique feature of the upland varieties.

Rate of leaf production on the main culm

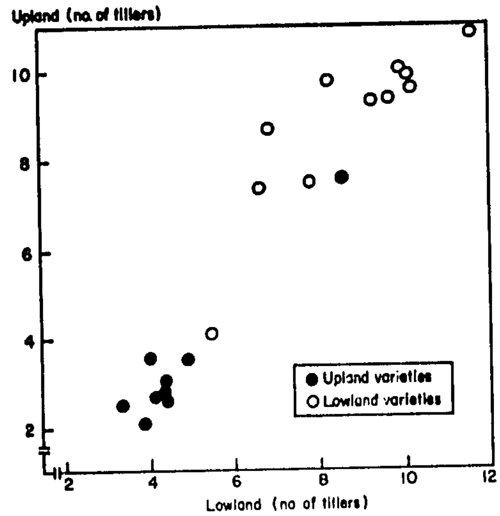
Nine upland and 11 lowland varieties were rated for leaf production on the main culm under upland and drill-flood conditions up to 60 days after seeding. At 60 days after seeding the difference in leaf number between the two plantings was small: 9.5 to 12.0 in the drill-flood plots and 8.5 to 11.0 in the upland planting.

More obvious differences were found among varieties. In the upland plots, all the lowland varieties produced more leaves than the upland group in the upland plots, from 20 until 60 days after seeding, except for Dular. In the drill-flood plots, all the lowland varieties had larger leaf counts from 20 days after seeding to 60 days after seeding (fig. 1).

Among the lowland varieties, IR305-4-20 had the largest leaf number; it was followed by IR5, IR773A1-36, IR8, and IR841-67-1 in both upland and



1. Leaf number of nine upland and 11 lowland varieties grown under both upland and lowland culture



2. Tiller number of nine upland and 11 lowland varieties grown under upland and lowland culture.

lowland plantings. Dular produced the fewest leaves, though the maximum difference in mean leaf numbers among lowland varieties at 60 days after seeding was two.

The upland varieties differed by 1.5 leaves or less at 60 days after seeding in both treatments. Hirayama and Rikuto Norin 21 produced the most leaves at 60 days after seeding at which time heading occurred, indicating that leaf number was associated with early maturity.

Rate of tiller production

The nine upland and 11 lowland strains differed more in tillering than in leaf development. As a group, the lowland varieties tillered earlier and had more tillers at 60 days after seeding.

In the upland planting, most upland varieties began to tiller after 22 days from seeding, while the lowland varieties began tillering at 19 days after seeding. At 25 days after seeding, the lowland group averaged two tillers while most of the upland types averaged 1.1 tillers. At 60 days after seeding, the lowland types produced between four to 11 tillers, and the upland varieties from two to 3.5, though there was no water stress (fig. 2).

In the drill-flood plots the lowland varieties began to tiller about 1 week earlier than did the upland varieties. At 20 days after seeding the varieties had on the average more than one tiller. The difference between the variety groups was more distinct but smaller proportionally in the drill-flood plots than in the upland plots. IR747B2-6-3 again led all varieties. It had a mean of 12 tillers per plant at 60 days after seeding. IR8 and IR773A1-36 were also among the early-tillering and high-tillering entries. The upland varieties had means ranging from 3.4 tillers (in Rikuto Norin 21) to 8.5 tillers (in Sintianne Diofor) while the means of the lowland types ranged from 5.4 to 12 tillers. Among the lowland varieties, Dular produced the fewest tillers in both plantings.

Tiller number at 60 days after seeding

In the wet season, upland varieties in upland plots averaged 46 tillers within a 50-cm section in the row, while the lowland types averaged 77 tillers. In the transplant-flood plots, the semidwarfs averaged 24 tillers per plant, twice as much as the upland types.

In the dry season planting, the upland varieties produced nearly the same number of tillers in the upland plots, while the lowland types showed slightly reduced tillering. In the transplant-flood plots, the lowland strains had 13.5 tillers per plant which again doubled that of the upland types. But in the drill-flood plots, the upland group averaged 56.6 tillers in a 50-cm section, while the lowland types averaged 63.1 tillers. Close spacing between plants in a flooded soil thus did not reduce the tillering in upland varieties as much as it did in lowland varieties.

Among the upland varieties, Rikuto Norin 21 consistently had the fewest tillers, while Sintianne Diofor tillered nearly as well as the lowland types (Table 1). Dular was consistently the lowest tillering entry in the lowland group.

When the transplant-flood and upland plantings were compared for tiller number per unit area, the lowland group generally produced higher plasticity indices (0.79 in wet season, 0.40 in dry season) than the upland group (0.37

Table 1. Range in tiller number of selected upland and lowland varieties and mean of selected varieties sampled at 40 and 60 days after seeding (DAS), IRRI, 1970 wet season and 1971 dry season.

Variety	Tillers (no.)							
	Wet season				Dry season			
	Upland[a]		Transplant-flood[b]		Upland[a]		Drill-flood[a]	
	40 DAS	60 DAS	40 DAS	60 DAS	40 DAS	60 DAS	40 DAS	60 DAS
Upland varieties								
M1-48	46	35	7	12	48	44	80	69
Palawan	38	28	9	10	37	38	81	64
OS 4	41	33	5	11	37	37	54	46
Sintianne Diofor	67	67	14	25	38	52	72	66
Rikuto Norin 21	40	38	6	9	44	45	38	31
Hirayama	38	38	6	8	43	39	47	52
Lowland varieties								
Dular	52	46	12	17	40	43	56	54
Taichung Native 1	75	82	12	26	54	64	80	62
IR8	75	87	15	19	52	64	62	61
IR747B2-6-3	94	104	14	26	53	61	87	80
IR5	75	130	15	22	49	65	71	70
Peta	68	79	15	26	43	55	62	58

[a]Per 50 cm section in the row. [b]Per hill.

in wet season, 0.21 in dry season), but the indices varied widely within a group and overlapped between groups. Rikuto Norin 21 and Hirayama had consistently low indices, while Sintianne Diofor repeatedly produced high indices. Among the lowland varieties, IR8 showed fairly low indices, Peta showed high indices, and IR5 showed intermediate indices. Dular produced the lowest indices in the lowland group.

All varieties except Rikuto Norin 21, IR8, and Taichung Native 1 produced more tillers in the drill-flood culture than in the upland planting. The plasticity indices were generally higher in the upland types (0.69 to 1.77) than in the lowland group (0.95 to 1.26).

Plant height at 60 days after seeding

Among the upland varieties, the African and Philippine entries were tall types, reaching 150 cm at 60 days in the wet-season, transplant-flood plots. The two Japanese varieties averaged only 120 cm. The plants grown in upland plots were generally shorter by more than 50 percent than those grown in transplant-flood plots. In the dry season, plant height was further reduced in the upland plots and the plasticity indices between transplant-flood and upland treatments increased to an average of 180 percent.

The lowland types, except Dular, were much reduced in plant height when grown in the upland plots. Most of the plasticity indices between transplant-flood and upland plantings were more than 200 percent, except for IR5.

Plant height at flowering

Most of the African and Philippine upland varieties grew taller than 150 cm in the upland plots, compared with the 120-cm Japanese varieties. The plasticity indices between transplant-flood and upland treatments in the wet season averaged 130 percent. Plant height generally decreased in the dry season. The upland and drill-flood plots had similar values for plant height.

The lowland varieties showed a more marked reduction in height when grown in the upland plots. The semidwarfs seldom grew taller than 68 cm during either season. The plasticity indices between the transplant-flood and upland treatments ranged between 160 and 215 percent in the wet season. In the dry season, the reduction in height of semidwarfs in the drill-flood plots was about 20 percent of that in the upland plots. IR5 plants were much taller in the upland plots of the dry season than in the two flooded plantings, mainly because maturity was delayed in the upland planting.

Leaf characters

The leaves of upland varieties from Africa and the Philippines generally are light green and longer and wider than those of the semidwarfs in the lowland group. They are similar to Peta, except that Peta has the longest leaves. The two Japanese upland varieties have slightly shorter but rather broad leaves.

Leaf dimensions and area (measured by automatic leaf area meter) can indicate a variety's response to different levels of water and nutrients. Among the three measurements, length, width, and area, taken at 60 days after seeding,

Table 2. Differences in leaf dimensions between upland and transplant-flood plots given as plasticity indexes (transplant-flood compared with upland), IRRI, 1971 dry season.

Variety	60 days after seeding			At heading		
	Length	Width	Area	Length	Width	Area
			Upland varieties			
M1-48	129	100	116	146	127	183
Palawan	160	100	189	135	113	146
OS 4	147	117	140	93	106	93
Rikuto Norin 21	111	93	114	—	—	—
			Lowland varieties			
IR5	178	171	268	133	107	149
IR8	209	138	283	121	116	137
IR747B2-6	167	113	181	158	128	221
Taichung Native 1	252	143	385	125	120	201

the largest changes were noted in leaf area. These changes were largely due to similar variations in leaf length. In the three planting methods the upland varieties generally had smaller plasticity indices for all three measurements. Rikuto Norin 21 produced the lowest plasticity indices—none were above 115 percent. M1-48 and OS 4 showed a small increase (10 to 30%) in all three measurements in transplant-flood and upland plots, while Palawan increased mainly in leaf length and area and attained indices of about 190 percent (Table 2).

Among the five lowland types, IR747B2-6-3 reacted to flooding like Palawan and Miltex. Taichung Native 1 showed the largest increases in the indices: 225 to 252 percent in leaf length, 140 percent in leaf width, and 304 to 385 percent in leaf area. IR5 and IR8 produced plasticity indices of 270 to 280 percent for leaf area in the transplant-flood treatment, mainly because of a twofold increase in leaf length. IR5 showed a relatively small increase (205 percent) in leaf area in the drilled-flood treatment compared with that in the upland plots.

The African and Philippine upland varieties had rather droopy leaves at 60 days after seeding. Their leaf angles (of openness) usually were double those of the semidwarfs in different plantings. The two Japanese upland varieties had leaf angles intermediate between the two groups. The differences in leaf angle decreased as plants approached flowering.

More erect leaves generally occurred in the drill-flood treatment. The upland varieties had similar leaf angle values in the upland and transplant-flood treatments, but the lowland varieties produced more droopy leaves in the transplant-flood treatment than in the upland planting.

Although the upland varieties have more droopy leaves, the light intensity measured at ground level between rows early in the morning under a cloudy sky at 60 days after seeding in the upland plantings was only slightly lower than the light intensity between rows of semidwarfs. The differences between groups increased at flowering. It appears that the semidwarfs produced fairly good ground cover with the higher number of tillers and the larger number of lower leaves which remained photosynthetic.

Growth duration

The ranges of the seeding-to-harvesting period of the test varieties were rather similar because the varieties were chosen to facilitate comparison.

In the 1970 wet season, the period from seeding to full heading in the three dates of planting in upland plots ranged from 59 days (for Rikuto Norin 21) to 105 days (for Sintianne Diofor) for the upland group, and from 60 days (for Dular) to 117 days (for IR5 and Peta) for the lowland group. The three Philippine upland varieties averaged 94 days and the African varieties, 91 days. Taichung Native 1 averaged 88 days and IR8, 104 days.

All the varieties sown on June 11 produced panicles earlier in the transplant-flood plots than in the upland plantings. The difference in number of days to heading between the upland and the transplant-flood treatments varied from 1 day in Hirayama to 44 days in Palawan. Miltex, Palawan, OS 4, RT 1095-S26, and Sintianne Diofor differed by more than 15 days between the two treatments. In the lowland group IR8, IR5, and Peta showed differences ranging from 17 to 23 days between the two planting methods.

In the 1971 dry season, the period from seeding to heading of the upland varieties was longer by a few days in the upland plots than in the 1970 wet season upland plot because the temperatures were lower in the early part of the dry season. The lowland varieties, except Dular and IR22, took longer to head than did the upland varieties. The heading of IR5 and Peta was much delayed in the upland planting in the dry season.

All varieties showed a more marked reduction in the vegetative growth period in the drill-flood planting than in the upland planting. The reduction ranged from 6 to 17 days in the upland group. It was much greater in the lowland group—from 8 days in Dular to 37 days in IR5. The semidwarfs showed reductions that varied from 15 days in IR8 to 31 days in IR305-4-20.

Weights of shoot and root of juvenile plants

At 40 days after seeding, the two variety groups had similar root weights (dried) in both the upland and drill-flood plots. But the lowland group produced heavier shoots. The root-to-shoot ratios were about 10 percent higher in the upland group under both cultures and the difference between groups was significant. Among the 20 varieties, Rikuto Norin 21, IR305-4-20, and IR841-67-1 produced the highest root weights in the upland planting. Rikuto Norin 21, M1-48, and IR305-4-20 also gave the highest root-to-shoot ratios, which approached 50 percent.

At 60 days after seeding, the upland group generally had smaller shoot and root weights in both types of culture. In the upland planting, the upland group had a slightly higher root-to-shoot ratio, but the difference between groups was not significant. Among the 20 varieties, Rikuto Norin 21 maintained one of the highest root weights and the highest root-to-shoot ratio (60%) in the upland planting. Dular produced the highest root weight, but the root-to-shoot ratio was not outstanding. IR305-4-20 produced a root-to-shoot ratio of 57 percent. IR22, IR937-55-3, M1-48, OS 6, Miltex, IR5, IR841-67-1, and IR773A1-36 also produced ratios of more than 50 percent in the upland plots.

In the drill-flood plots, however, the lowland group showed a higher ratio than the upland group. M1-48 and IR305-4-20, IR841-67-1, and IR937-55-3 gave the highest ratios, ranging between 26 and 28 percent. The ratios of most of the upland varieties ranged from 8 to 21 percent.

Grain yield

Although yield data for upland plantings in the 1970 wet season were incomplete for each of the three dates because of the damage by two typhoons, yield estimates for those varieties which appear indicative of the varietal performance are given as references. Rikuto Norin 21 consistently produced yields of about 2 t/ha in the three plantings. Palawan, Dular, and IR5 produced 1.7-ton mean yields in spite of the typhoons. IR8 gave a similar grain yield level when it escaped typhoon injury. Miltex gave the highest yield, 2.4 t/ha, in one date. IR5 produced 2.2 t/ha in the third date of planting.

In the 1971 dry season, yields from the upland planting were generally slightly higher, but a serious infection of sheath blight in June reduced yields of late-maturing entries. The upland types, such as M1-48, RT 1095, and Rikuto Norin 21, produced between 2.6 and 2.8 t/ha. Among the lowland varieties, Dular produced the top yield of 2.2 t/ha. Because of either sheath blight or water stress, the mean yields of five semidwarfs ranged from 1.0 to 1.4 t/ha.

In transplant-flood plots in the 1971 dry season, the upland varieties yielded between 2.6 and 4.6 t/ha while the semidwarfs yielded from 4.2 to 6.8 t/ha. IR5 and Peta gave 6-ton yields in the transplant-flood plots, but their yields in upland plots were reduced to less than 1 t/ha by sheath blight.

In the drill-flood plots, the upland varieties yielded between 2.7 and 3.8 t/ha, while the semidwarfs yielded between 3.0 and 4.6 t/ha. Peta produced the highest yield, 5.0 t/ha. IR5 and IR8 produced 4.6 t/ha.

Grain weight

The 20 test varieties differed appreciably in the 100-grain weight. OS 4 and Sintianne Diofor had the heaviest grains, while IR22, M1-48, Taichung Native 1, and Peta had lighter grains. Dates of planting and planting method had little influence on grain weight.

Harvest ratio

Transplant-flood plots in the 1971 dry season generally produced the highest harvest ratios. Upland plots produced the lowest harvest ratios, but the upland varieties in these plots generally had higher ratios than lowland varieties. In the drill-flood plots, IR841-67-1 produced the highest harvest ratio, 70 percent. Most other varieties had around 40 percent. In the transplant-flood plots, the semidwarfs produced ratios of 50 percent or more, while the African and Philippine upland varieties were in the 40-percent category. The two Japanese upland varieties had ratios of about 56 percent.

DROUGHT RESISTANCE AND ROOT DEVELOPMENT

Field resistance to drought

Dry spells occurred during the growing period of the first two plantings in the 1970 wet season. Visible symptoms of drought stress made possible the classification of varieties for drought resistance.

Drought-susceptible varieties, such as Taichung Native 1, NARB, IR579-48-1, and IR747B2-6-3, showed yellowing and extreme rolling of leaves during the tillering stage. Plants became noticeably stunted later. More severe drought symptoms appeared in susceptible varieties during booting and heading. Drought-susceptible varieties, which headed during or shortly after this period, such as Taichung Native 1, IR579-48-1, IR20, Jappeni Tunkunoyo, and NARB showed 5 to 30 percent whitish, sterile panicles. These varieties subsequently yielded from 0.2 to 1.4 t/ha of grain. The extremely low yields of Taichung Native 1 (0.21 t/ha) and IR579-48-1 (0.45 t/ha) were partly caused by typhoon damage and by leaf blast. On the other hand, the drought-resistant, upland varieties, such as Miltex, M1-48, Rikuto Norin 21, and Hirayama, which escaped typhoon damage, yielded from 1.9 to 2.8 t/ha.

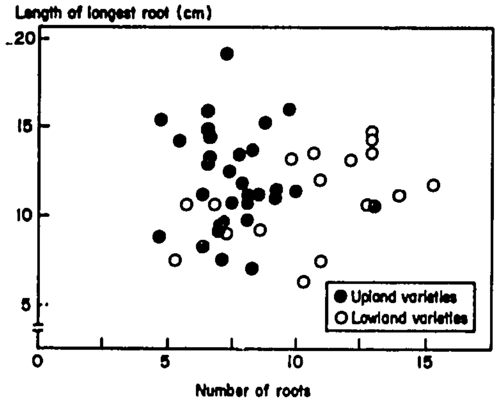
Mild drought symptoms again appeared on Taichung Native 1 and IR747B2-6 during the 1971 dry season.

Using leaf yellowing and folding, stunted vegetative growth, sterile panicles, and low grain yield as signs of drought stress, the 26 entries tested may be classified into four groups: 1) resistant—IR5, Peta, Rikuto Norin 21, Hirayama, Dular, E425, RT 1095, and Palawan; 2) moderately resistant—Agbede, Miltex, M1-48, OS 4, OS 6, IR8, IR305-4-20, IR773A1-36, and Azmil; 3) moderately susceptible—IR22, IR20; and 4) susceptible—IR579-48-1, NARB, IR532-1-218, Jappeni Tunkunoyo, Sintianne Diofor, IR747B2-6-3, and Taichung Native 1.

The leaves of drought-resistant varieties tended to roll from 8 AM to 4 PM on hot, sunny days when soil moisture began to diminish. Leaf rolling in Peta began as early as 7:30 AM and continued until 5 PM. Leaf rolling was observed on the rather short leaves of the semidwarfs only when water stress became severe. Plasticity in leaf rolling may be associated with resistance to water stress.

Root development during vegetative growth period

Root samples of 49 upland and lowland varieties were collected at 14 days after seeding, from 12 entries at 30 days after seeding, from 20 entries at 40 days after seeding and at 60 days after seeding. Varieties and plants of the same variety grown on puddled soil or on granulated upland soil were compared. For young plants, the "upland" treatment consisted of planting on fine,



3. Number of seedling roots and length of the longest root of 32 upland and 17 lowland varieties grown in granulated soil inside mylar tubes measured at 14 days after seeding. IRRI, 1971 dry season.

granulated soil inside a mylar tube (10 cm in diameter, 30 cm in height) and watering from the bottom of the tube. Figure 3 shows root number and maximum root length of 14-day-old seedlings. Table 3 summarizes the measurements on root characteristics at 30 days after seeding. The upland varieties had lower root number, nearly constant root length, and higher proportion of thick roots under both cultures. On the other hand, the lowland varieties responded to flooding mainly with an increase in root number. Their root length decreased slightly or remained the same. Root samples taken from 60-day-old plants showed features similar to those taken from 30-day-old plants.

Root growth traced by radioactive phosphorus

The growth of roots of rice seedlings planted on granular soil inside mylar tubes was traced by ^{32}P placed at three depths (7.5, 15.0, and 22.5 cm from

Table 3. Root features of five upland and seven lowland varieties at 30 days after seeding in two types of culture, IRRI, 1971 dry season.

Variety group	Root features					
	Number		Length (cm)			
	Range	Mean	Range	Mean	Diameter	Rootlets
			Upland culture			
Upland	6 to 12	9	8 to 21	10	Many thick, others thin	Uniformly branched along entire root
Lowland	12 to 19	14	6 to 22	9	Several thick, mostly thin	Uniformly branched along entire root
			Drill-flood culture			
Upland	21 to 32	27	8 to 20	10	Several thick, mostly thin	Mostly from root tip
Lowland	30 to 55	40	6 to 19	8	Predominantly thin	From midportion of root and downward

Table 4. Root development of selected upland and lowland varieties in the June 11 upland planting, IRRI, 1970 wet season.

Variety	Predominant type[a]	Density[b]	Rootlets[c]	Root length (cm)		Root diameter (mm)	
				Mode	Max	Avg	Thickest
			Upland varieties				
Jappeni Tunkunoyo	2	2	4	15	24	0.88	1.0
M1-48	6	5	2	18	25	1.22	1.4
NARB	1	2	2	16	19	0.88	1.0
Palawan	6	4	1	18	34	1.38	1.6
OS 4	6	4	3	17	36	1.16	1.3
Rikuto Norin 21	6	2	2	19	22	1.04	1.2
			Lowland varieties				
Dular	5	2	2	16	22	1.14	1.4
IR5	4	3	4	13	24	1.18	1.4
IR8	3	1	2	12	24	0.94	1.3
IR20	1	1	1	10	15	0.66	0.8
IR747B2-6-3	1	2	2	12	19	0.48	0.6
Peta	5	4	4	17	26	1.14	1.3
Taichung Native 1	2	1	2	14	21	0.88	1.0

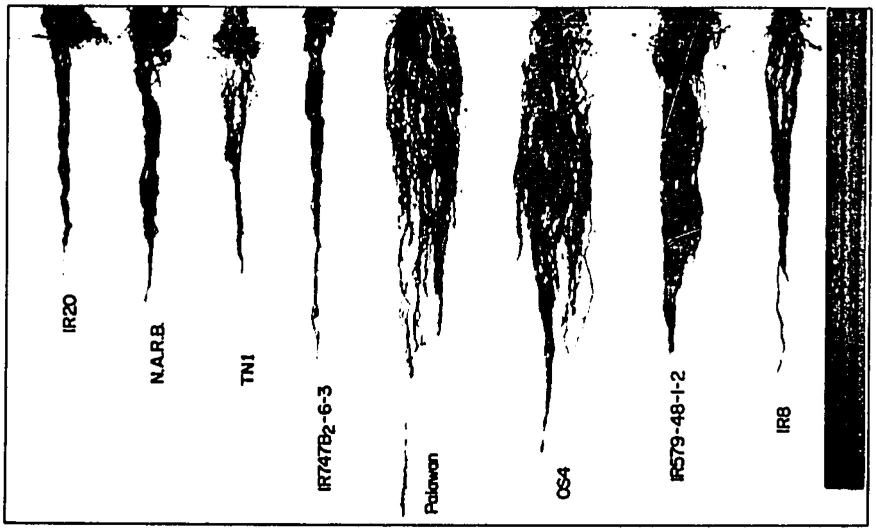
[a]1-very fine, to 6-very thick. [b]1-very few, to 5-very dense. [c]1-very few; 2-from lower portion of root only; 3-midportion to root tip; 4-uniformly branched from base to tip.

soil surface). The plants were watered from the top. Root growth was tracked by assaying ^{32}P activity in the leaf tissues sampled at weekly intervals. For IR841-67-1, IR305-4-20, IR5, Hirayama, Rikuto Norin 21, and OS 4 the highest radioactive counts occurred at 8 to 15 cm deep at 28 days after seeding. At 15 to 23 cm deep 30 days after seeding, Hirayama, Sintianne Diofor, IR305-4-20, OS 6, and Peta showed marked activity. Sintianne Diofor, Dular, OS 6, IR305-4-20, and RT 1095 produced their highest counts at 23 to 30 cm deep 60 days after seeding.

Root system of mature plants

Some measurements and counts of root samples taken from the first date of planting in the upland plots of 1970 wet season, which suffered the most severe drought, are in Table 4. When root features were compared with field reaction to drought, the resistant varieties generally had predominantly thick roots, densely formed at the crown, and many deep roots (fig. 4). Between the first date and the third date or between the first date and transplant-flood treatment, the drought-resistant upland varieties, such as Palawan and OS 4, responded to soil water stress by producing proportionally more thick and long roots, while the drought-susceptible lowland or upland varieties produced thin roots that were similar in diameter or length to those produced under flooded soil conditions but were fewer.

Among the upland varieties, OS 4 had the longest roots. Rikuto Norin 21, M1-48, and RT 1095 produced the thickest roots. Among the lowland varieties,



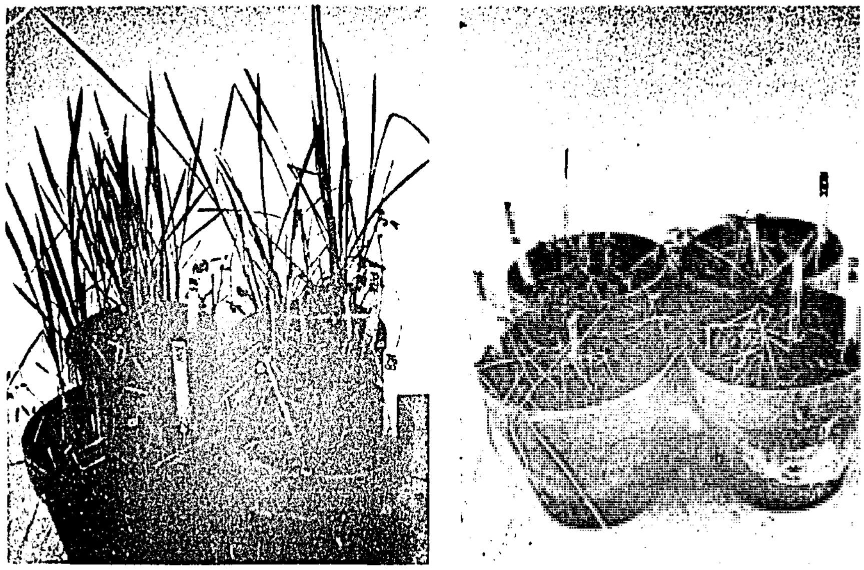
4. Root systems of three upland varieties (N.A.R.B., OS 4, and Palawan), and of four semidwarf lowland varieties in the June 20 upland planting. OS 4 and Palawan have especially dense and thick roots. IRRI, 1970 wet season.

Dular and IR841-67-1 produced the thickest roots. IR8 produced the largest number of rootlets though its roots were short and thin. Taichung Native 1 produced rather few roots but some were thick.

Root data collected from the upland planting and the drill-flood plots in the 1971 dry season verified that field resistance to drought is associated with the plants' ability to produce more long and thick roots during dry spells (Table 5). Among the resistant varieties maximum root length and maximum

Table 5. Root development of selected upland and lowland varieties in 1971 dry season upland planting, IRRI.

Variety	Predominant type	Density	Rootlets	Root length (cm)		Root diameter (mm)	
				Mode	Max	Avg	Thickest
Upland varieties							
M1-48	4 to 5	3 to 4	3 to 4	16	24	1.25	1.55
OS 4	5 to 6	2 to 3	2 to 3	17	26	1.45	1.75
OS 6	5 to 6	3 to 5	3 to 4	15	24	1.65	2.00
Rikuto Norin 21	4 to 5	4	3 to 4	22	34	1.30	1.50
Lowland varieties							
IR5	4	4	4	11	18	1.30	1.60
IR8	4 to 5	5	4	15	22	1.45	1.65
IR305-4-20	3 to 4	4	4	16	20	1.00	1.20
IR747B2-6-3	3	1 to 2	4	12	14	1.05	1.30
IR841-67-1	5	4	4	14	22	1.50	1.80



5. Potted plants of four varieties, left, showed slight damage and quick recovery from desiccati
Only the lower leaves of Peta and IR5 (back row) and older leaves and some young leaves of I
and Taichung Native 1 (front row) died. Plants of Dinalaga, M1-48, Rikuto Norin 21, and Milt
right, all died after the desiccation treatment, while the mimosa plants fully recovered. IRI
1970 dry season.

diameter of thick roots were negatively associated. Rikuto Norin 21 produc long roots whose maximum diameter, however, was smaller than that of t roots of OS 6 which produced a large number of thicker but slightly short roots. Dry weight of roots per unit length of row did not appear to be associat with drought resistance.

Recovery from desiccation

Twenty upland and 12 lowland varieties were tested for recovery from desicc tion by the Mimosa method (IRRI, 1971, p. 212-213). Damage to the plan at 45 and 65 days after seeding were recorded on the basis of leaf color chang death of leaf tissues, and subsequent plant growth. The varieties were group as follows (fig. 5): 1) light damage and quick full recovery—IR8, IR5, Taichu Native 1, Peta, IR20, IR22, Palawan, Jappeni Tunkunoyo, IR579-48-2-1- 2) appreciable damage, full but slow recovery—Azmil, Magsanaya, Agbed OS 4, OS 6, RT 1095, Hirayama, Td3, Td6, Tsai-yuan-chon, NARB, Bir-m fen; 3) significant damage and partial recovery—Azucena, 81B-25, IR747B 6-3, E425, Urasan and a strain of *O. glaberrima* (Acc. 101438); and 4) dea of plants—Miltex, M1-48, Rikuto Norin 21, Dinalaga, Custugucule, PI 21593 CI 5094-1.

Obviously drought resistance and recovery from desiccation were n necessarily correlated. The results agreed with our previous findings th many upland varieties are not superior to some lowland types, such as Pet in the ability to recover from extreme drought (IRRI, [1964], p. 17-18).

Starch and sugar

Plant samples from 90-day-old plants from upland and transplant-flood plots were analyzed for starch and sugar content. The sampling was done when the plants in upland plots began to show water stress symptoms. Six upland varieties contained lower levels of starch than four lowland varieties in both plantings and the differences were highly significant between groups. The transplant-flood plots generally had higher starch content than the upland plots. In the upland planting, IR8 had the highest starch content, 40 percent. Taichung Native 1 and IR5 contained about 30 percent starch. Starch content and recovery from desiccation appear associated in some of the test varieties.

The differences in sugar content were highly significant among 10 varieties, but they showed no consistent trends.

IMPLICATIONS

Data obtained at Los Baños indicate that most of the upland varieties from Africa and the Philippines have 1) inherently low tillering ability and slow vegetative growth in the juvenile stage; 2) moderately long, light-green, and moderately droopy leaves, which often roll when water stress begins, but retain nearly constant leaf areas under different water regimes; 3) moderately good to good drought resistance, characterized by the production of deep and thick roots and a high root-to-shoot ratio when soil moisture becomes deficient; 4) growth duration of 110 to 135 days; and 5) inherent low yielding capacity due to limited panicle number per unit area.

The two Japanese upland varieties have most of these features but they differ from the tropical group in that they have a shorter and less variable growth duration (90 to 103 days), a relatively higher rate of grain production per day, a stable yielding ability, and a higher harvest index. They are particularly suitable as short-duration crops. Dular, a lowland variety, belongs to a similar category.

On the other hand, some of the lowland varieties, such as IR5 and Peta have levels of drought resistance comparable to those of the upland types and show a greater capacity for recovering from desiccation. Because of its weak photoperiod sensitivity, IR5 fits well into the monsoon rainfall pattern of the tropical areas and has often produced good yields in upland plantings during the wet season in the Philippines (IRRI, 1967, p. 171-172; 1970, p. 121-122; 1971, p. 144-150). IR5, however, did not perform well in our 1971 dry season planting. Its leafy growth during the vegetative-lag phase led to serious sheath blight infections and a low harvest index.

Our observations suggest that several features would raise the yield potential of varieties grown under upland culture: 1) Early vegetative vigor and moderately long and slightly droopy leaves to provide ground cover and to facilitate leaf rolling when soil moisture becomes deficient; 2) a vigorous root system capable of developing deep and thick roots when moisture supply diminishes near the soil surface; 3) a greater ability to tiller so that the plant can use the additional water and nutrient supply if the climatic conditions become more favorable later in the vegetative phase; 4) a high tiller-to-panicle ratio and a high harvest index; 5) satisfactory levels of resistance to the major diseases, such as blast and *Helminthosporium* leaf spots, to insect pests, and to to soil problems, such as deficiency or excess of certain elements.

Some of these features are present in various combinations in both variety groups and their expression appears heritable. Therefore, it should be feasible to recombine the desired traits by conventional hybridization, testing, and selecting methods.

We crossed IR8 and IR22 with each of the African upland varieties and made F_2 plant selections in the 1971 dry season. We have also crossed Rikuto Norin 21 with IR5 and with IR841-67-1. More crosses in multiple combinations will be needed to recombine divergent sources of resistance to water stress and resistance to diseases and insects.

Because plantings must be made in alternate seasons involving disruptive selection processes in the wet and the dry seasons, or alternately under upland and lowland cultures, we need to know the reliability and efficiency of selecting progenies intended for upland culture under such a breeding procedure. We made individual F_2 plant selections in the 1971 dry season. Besides the criteria of maturity and grain features, we relied mainly on growth vigor, plant height, leaf color, and tiller number which partly indicate drought resistance during periods of mild water stress. Comparisons between succeeding plantings or generations should furnish guidelines in developing an efficient breeding procedure which could involve different seasons or cultural systems.

The maximum root length of 30 cm and the low yield levels obtained from the upland plantings on Maahas clay suggest that our experimental site on heavy soil may not be representative of many upland soils in Asia. To confirm our findings, we need further testing on a wide range of soil types involving several dates of seeding at each site. Methods of testing for drought resistance have been discussed by Sullivan (1971) and Hurd (1971), but reliable and simple field techniques must be developed. It appears that growing large bulk populations in early generations and selecting for the desired plants under dry growing conditions is the most expedient method of field testing for drought resistance. Replicated dates or sites of planting, or both, will increase the chances of having typical dry environments for these tests.

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Discussion: Agronomic and growth characteristics of upland and lowland varieties

G. SATARI: In Indonesia, we call rice upland if soil preparation and soil management are done dry, that is when soil moisture is below field capacity, and direct seeding is used. Can you clarify your statement about upland rice in the Philippines, Taiwan, and Japan being transplanted?

T. T. Chang: My understanding of upland rice includes the two points that you have mentioned plus one more — no levees. On the other hand, I am quoting from books and journals to indicate that an extremely wide range of cultural practices are lumped under "upland rice."

S. B. CHATTOPADHYAY: Dular is widely grown in West Bengal, India, as an upland variety. This variety has been found there to react adversely to standing water so it cannot be grown successfully in puddled soil. Dular is included as a lowland variety in your paper. Please comment.

T. T. Chang: From the rice literature, I learned that Dular is a drought-resistant lowland variety. It is listed in the genetic stocks book of East Pakistan as a recommended paddy variety.

R. K. WALKER: In East Pakistan, Dular is grown as an aus paddy.

K. KAWANO: What is the definition of an upland variety?

T. T. Chang: I don't have one yet. We are looking for the real differences between the so-called lowland and upland groups.

J. K. ROY: Besides longer and thicker roots, we found that varieties adapted to upland conditions also develop sclerotic pith in the adventitious roots.

S. D. SHARMA: At Hyderabad (India), the erect-leaved types often perform better.

Some water stress effects on rice

H. K. Krupp, W. P. Abilay, E. I. Alvarez

Moisture stress is one factor that often limits economical and stable yields of upland rice. Experiments at the International Rice Research Institute show that varieties differ in response to moisture stress. Differences were observed in the relative response of root and shoot growth of different varieties to stress. In lowland rice, as moisture stress increases, the yield difference between traditional and improved varieties become smaller. One reason is that lodging decreases with poor water management. Stomatal density and desiccation rate of detached leaves were interrelated. The protein content and yield of lowland rice were reduced by increasing the duration of moisture stress. Much more research is necessary, but, as understanding of drought tolerance and avoidance mechanisms increases, it should be possible for the plant breeder to incorporate some advantageous characteristics of moisture stress resistance into rice varieties for upland conditions.

INTRODUCTION

Recent experiments conducted at IRRI with the purpose of improving cultivation methods and varieties for upland rice allow some observations on vegetative growth and grain yield to be made. Many of the conclusions are still speculative. Much work in both agronomy and plant physiology remains to be done to define clearly the plant properties desirable for increased yields of upland rice.

Upland rice is unirrigated. It is dry seeded on nonpuddled, nonbunded fields on generally sloping land of medium to moderately coarse soil texture. A major constraint on grain yield is moisture availability. Large areas are devoted to upland rice in Asia, Africa, and South America.

Much of the rice grown in Asia is transplanted on bunded, puddled soil, but is unirrigated and is dependent on rainfall. It is likely that information obtained from studies designed to increase the resistance of upland rice to moisture stress or drought can also be applied to rainfed paddy rice.

Studies on upland rice may be oriented in either of two ways. They may be directed towards obtaining yields approaching those of irrigated (lowland) rice with the use of the currently available improved varieties, good management, high rates of fertilizer application, and most important, soil nearly saturated with moisture throughout the growing season. Or they may be directed towards obtaining some yield when adverse soil moisture conditions

H. K. Krupp, W. P. Abilay, E. I. Alvarez. The International Rice Research Institute.

Table 1. Tiller count at harvest, leaf area index (LAI) at the heading stage and grain yield of M1-48 and IR22 grown under upland conditions at four seeding rates. IRRI, 1971 wet season.

Seeding rate (kg/ha)	Tillers (no./sq m)		LAI		Yield[a] (t/ha)	
	IR22	M1-48	IR22	M1-48	IR22	M1-48
25	426	197	5.6	6.7	2.10	1.69
50	519	234	5.1	4.8	2.66	1.78
100	500	243	4.2	6.3	2.59	1.84
150	208	330	4.2	5.8	2.56	1.53

[a]Yields reduced by a typhoon.

prevail. The latter approach, puts emphasis on the drought resistance of varieties. Many plant factors contribute to drought resistance. Some of them are discussed in this paper.

PLANT TYPE AND WATER STRESS RESPONSE

Upland varieties are generally tall and low tillering. Such characteristics are undesirable for irrigated cultivation where lodging resistance is necessary and where high tillering to compensate for wide plant spacing and missing hills is essential for high yields. Under upland conditions, where the crop is sown in rows, high tillering may not be as essential a varietal characteristic. High seeding rates can partially compensate for a low tillering capacity of a variety. Table 1 shows that M1-48, a Philippine upland rice variety, produced more tillers as the seeding rate was increased. The increased tiller number did not result in a higher leaf area index or grain yield. Also, lodging in upland fields is not as severe as it is in irrigated fields where grain may rot. Gentle lodging of the plants near harvest time under upland conditions probably results in higher grain recovery and yield than an upright stand during periods of high winds when grain shattering occurs.

Competition from weeds is an important limitation in upland rice production. Tall plants with a less erect leaf habit than that of the improved varieties should be better able to compete with weeds.

In the 1971 dry season, we studied the relative performance of improved and traditional varieties under different levels of water management or of irrigation efficiency. We used three improved varieties, IR20, IR22, and C4-63, and two tradional varieties, Peta and Sigadis. The five varieties were grown in puddled soil in the same plot for each water and nitrogen treatment, thus they were subjected as nearly as possible to the same soil moisture and nitrogen conditions. The irrigation treatments were continual flooding 5 cm deep (good water management), alternate wetting and drying to allow some soil cracking with moderate moisture stress between irrigations (average water management), and alternate wetting and drying with severe soil drying and moisture stress between irrigations (poor water management). Ammonium sulfate was applied 1 day before transplanting at 0, 50, and 100 kg/ha nitrogen.

Table 2. The effects of different levels of water management and nitrogen on the grain yield of improved and traditional rice varieties. IRRI, 1970 dry season (M. L. Bhendia and H. K. Krupp, *unpublished*).

Nitrogen applied (kg/ha)	Yield (t/ha)				
	IR20	IR22	C4-63	Peta	Sigadis
	Good water management				
0	6.04	5.76	4.98	2.98	4.72
50	6.72	5.13	6.18	2.08	4.25
100	6.52	5.96	5.93	2.04	2.84
	Average water management				
0	4.85	3.47	4.31	3.95	5.28
50	4.58	2.82	4.57	4.10	4.62
100	3.32	4.27	5.34	4.00	4.75
	Poor water management				
0	4.27	3.81	4.19	4.64	5.65
50	5.22	4.56	5.20	4.51	5.84
100	5.46	5.37	6.38	5.10	5.87

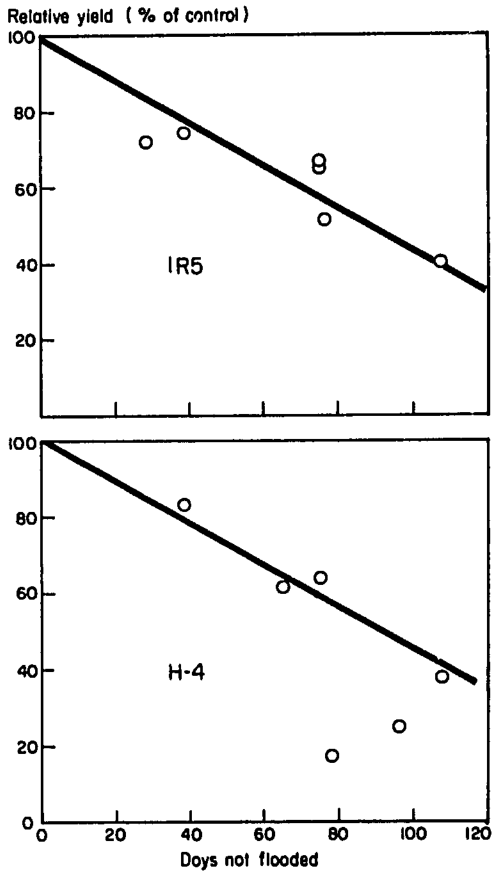
Some results of the study are presented in Table 2. The grain yields are means of two replications. IR20 and IR22 required good water management for maximum yields. As the level of water management declined, yields were reduced by a tone or more. The more vegetative and slightly taller improved variety, C4-63, was less affected by water management than IR20 and IR22. The traditional varieties, Peta and Sigadis, however, showed yield increases as the level of water management became poorer. Sigadis, under poor water management, produced yields almost equivalent to those of the improved varieties grown under good water management. The main reason for this response appeared to be the increased lodging resistance under water stress. Also, the natural nitrogen fertility level of the field was high. IR20 yielded over 6 t/ha without nitrogen under good water management. No nitrogen response was obtained with the improved varieties under good water management. But as the level of water management decreased a nitrogen response was observed with the improved varieties and the level of available soil nitrogen was decreased as shown by the low yield of the zero nitrogen treatment. The combined effects of reduced availability of soil nitrogen and soil moisture stress reduced lodging in the traditional varieties. As a result the yields of the tall varieties and the improved varieties under moisture stress, were similar, suggesting that breeding for short plants may not be necessary or desirable in an upland variety

The sensitivity of different varieties to moisture stress at different growth stages must also be considered in relation to tillering. Tanaka et al. (1964) described varieties as either panicle-number or panicle-weight types. Yield response to applied nitrogen results from an increase in panicle number per unit area (panicle-number type) or from an increase in grain number per panicle (panicle-weight type). In recent experiments at IRRI, a low-tillering, panicle-weight type, H 4, and two high-tillering, panicle-number types, IR8 and IR5, were compared to determine their relative sensitivity to moisture stress at different stages of growth (H. K. Krupp, S. K. De Datta, and S. N. Balaoing, *unpublished*). The improved varieties were equally sensitive to moisture stress at any growth stage and grain yield was reduced in proportion to the duration of the moisture stress. But grain yield appeared independent of the stage of growth at which the moisture stress was imposed on the plants (Table 3 and fig. 1). Stress early in the development of the plant reduced tillering and, hence, panicle number. Stress later in the growth of the plant resulted in both lower grain weight and fewer grains per panicle. The panicle-weight type, H 4, behaved somewhat differently. Stress early in the growth of the plant reduced yields in proportion to the duration of the stress as it did with the improved varieties. But moisture stress after panicle initiation caused severe reductions in yield. Thus, panicle-weight varieties, unlike panicle-

Table 3. Yield components of three rice varieties subjected to moisture stress at different growth stages in a greenhouse experiment. IRRI, 1971.

Stress period[a]	Tillers (no./hill)	Panicles (no./hill)	Filled grains (no./panicle)	100-grain wt (g)	Unfilled grains (%)
			IR8		
None	7.2	7.2	89	2.55	22
T - MT	4.8	4.4	114	2.57	24
T - PI	4.0	3.9	116	2.52	17
T - H	4.1	3.5	91	2.77	17
MT - H	8.2	7.7	76	2.50	18
PI - M	7.3	6.5	67	2.50	20
H - M	7.7	7.4	79	2.40	34
T - M	7.0	5.3	12	1.58	63
			IR5		
None	8.6	8.5	112	2.67	10
T - MT	5.5	5.4	128	2.63	10
T - PI	4.7	4.7	101	2.63	16
T - H	5.4	5.4	89	2.61	15
MT - H	9.2	9.2	84	2.53	8
PI - M	9.3	9.0	92	2.55	14
H - M	9.5	8.7	109	2.43	16
T - M	4.7	4.2	21	1.76	74
			H 4		
None	8.2	7.6	150	2.57	21
T - MT	4.2	4.1	170	2.73	25
T - PI	4.0	4.0	148	2.60	15
T - H	3.5	3.2	118	2.52	27
MT - H	6.8	6.5	95	2.75	28
PI - M	8.0	7.3	75	2.53	46
H - M	10.9	9.8	69	2.32	53
T - M	3.5	1.4	3	1.50	89

[a]T = transplanting; MT = maximum tillering; PI = panicle initiation; H = heading; M = maturity.



1. Effect of the duration of moisture stress at different physiological growth stages on IR5 and H 4 grown in pots in a greenhouse.

number varieties, seem to be particularly sensitive to stress in the reproductive and maturation stages.

The differences between panicle-weight and panicle-number types should be examined further when the characteristics of an "ideal upland variety" are being discussed. If, by an increase in panicle weight, panicle-weight types can recover from early stress and partially compensate for the reduced yields caused by inhibited tillering, these varieties might be most susceptible to moisture stress only during the later half of their growing period. Despite low rainfall during the vegetative phase, restoration of good soil moisture conditions just before and after the panicle initiation stage might allow some compensation for the early stress through a panicle-weight increase that does not occur with the panicle-number type varieties.

A simple analysis of precipitation data shows that the probability of encountering moisture stress increases greatly as the period of study lengthens. Thus, the probability of encountering moisture stress from seeding to maturity in a panicle-number variety is much greater than that in a panicle-weight variety.

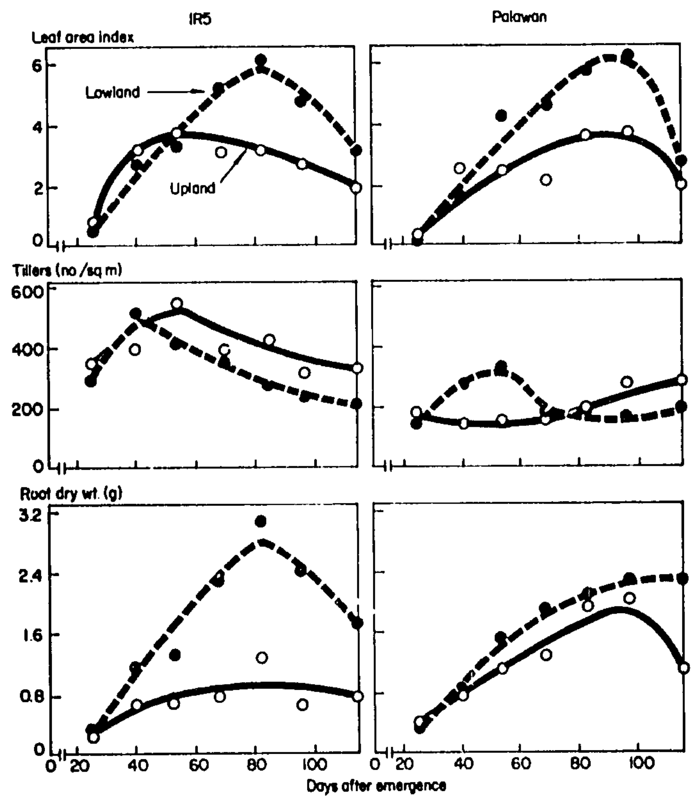
Obviously, more experimental work is needed to clarify these points but at this early stage in the development of breeding objectives for upland rice such speculation is not out of place.

GROWTH DURATION

Like the panicle-weight types, short-season varieties are less likely to encounter periods of severe moisture stress. Alles (1969) working in Ceylon on models of soil moisture balance has shown that the probability of encountering a 5-day drought period in Ceylon decreases from 90 to 65 percent when the growth duration is decreased from 4 months to $3\frac{1}{2}$ months.

GROWTH RESPONSE TO MOISTURE STRESS

Different varieties exhibit different growth responses when subjected to moisture stress (Hurd, 1971). Careful study of these response differences should provide a clearer insight into desirable breeding objectives for upland rice varieties.



2. Root weight, tiller number, and leaf area index of an upland variety (Palawan) and a lowland variety (IR5) grown under flooded and upland conditions. IRRI, 1970 wet season.

In the 1970 wet season, the unimproved upland variety, Palawan, was compared with IR5. The varieties were grown under irrigated conditions and under upland conditions. Leaf area index, tiller number, and root dry weight were measured every 2 weeks. Tensiometers installed in the upland plots were used to monitor the soil moisture tension and thus indicate the amount of plant moisture stress. In this experiment, severe moisture stress occurred only in the period from 45 to 60 days after seeding.

The growth responses of IR5 and Palawan to moisture stress were quite different (fig. 2). The root development of IR5 was retarded by moisture stress in the upland plot; that of Palawan was much less affected. On the other hand, the leaf area index and the tiller number of IR5 were very similar under both systems of management. In Palawan, however, moisture stress reduced tillering and leaf area index in the upland planting. The root and shoot response of these two varieties indicate that Palawan adapted to the imposed stress in a manner better suited to ensure survival than did IR5.

RECOVERY FROM MOISTURE STRESS

Another aspect of the problem of resistance to moisture stress is the ability of a variety to recover from severe stress. Laude (1971) has emphasized this characteristic and he suggests it is worthy of much greater attention than it is currently given. IR5 seems to possess greater ability to recover from severe moisture stress than many other varieties. For example, during a severe drought in the rainfed area of Central Luzon (Philippines) in 1969, many varieties were killed. When the rain resumed, however, IR5 began to grow again and produced up to 4 t/ha in some of the drought-affected areas (T. Wickham, *personal communication*).

Other data indicating large differences among rice varieties in their ability to recover from drought were obtained by J. C. Moomaw (*unpublished*) in an upland trial in Nigeria. In this experiment, a period of low rainfall (averaging less than 0.25 cm/day) occurred between 80 and 140 days after seeding. The shorter season varieties were harvested during the drought period and the yields of most of them were greatly reduced by the moisture stress. The highest yield in this harvest was obtained from a Philippine upland variety, M1-48. The maturity of many of the longer season varieties was delayed by the moisture stress, and when favorable soil moisture conditions were reestablished they began to grow again. The delay between the two harvest periods was 47 days. In the second harvest period, yields up to four times as great as the earlier harvest were obtained. The highest yields at the later harvest were obtained with selections from the IR503 and IR269 lines and from a Surinam variety, 81-B25. But many other entries in Moomaw's trial did not recover from the moisture stress, and even after 220 days produced negligible yields.

Similar results were recently obtained at IRRI. Large differences were observed in the ability of varieties to recover from severe moisture stress (IRRI, 1971, p. 214-216).

GRAIN QUALITY

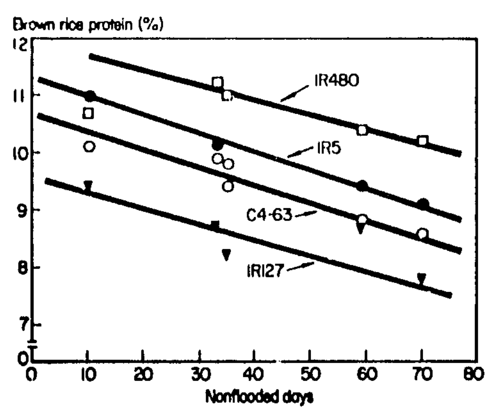
To the nutritionist, perhaps the most important grain characteristic is the protein content of the grain. In the 1971 dry season, an experiment was conducted at IRRI using irrigation intervals of 4, 6, 8, and 10 days. Each variety was thus subjected to differing amounts of moisture stress. Grain yields decreased as the interval between irrigations was increased. The most significant yield decrease occurred between the 8-day and the 10-day intervals.

The effect of the duration of moisture stress on protein content (in brown rice) is illustrated in figure 3. With increasing amounts of stress the protein content decreases. The possible cause of this behavior is reduced nitrogen uptake because plant water stress or aeration of the soil, or both, affect nitrogen availability (B. O. Juliano, *personal communication*). It is not apparent if varietal differences in the response of protein content to water stress occur but other more detailed experiments may reveal that they do. If so, it would be worthwhile to attempt to breed insensitivity of protein content to moisture stress into an upland rice variety.

ROOT FACTORS

Probably the most important varietal characteristics in terms of water uptake efficiency and drought resistance are root morphology and rate of root development. An experiment was conducted at IRRI in the 1970 wet season to examine the root development of IR5 and M1-48 under upland and flooded conditions. The plots were fertilized with 40 kg/ha N at planting and with 20 kg/ha N at flowering. The upland rice was dibble-seeded at the same 20 x 20 cm plant spacing used in the transplanted, flooded plots. Soil and root samples were taken at 2-week intervals throughout the growing period and root weight at different soil depths was recorded.

Under flooded conditions the rate and amount of root development of the two varieties were similar (Table 4). In the upland field, however, M1-48 showed greater root development at both the 0- to 15-cm and the 15- to 30-cm depths than did IR5. Both varieties produced more roots under flooded conditions, but in the upland field, root development of M1-48 was less



3. Protein content of IR5, IR127-80-1, IR480-5-9, and C4-63 as influenced by the duration of moisture stress. IRRI, 1971 dry season.

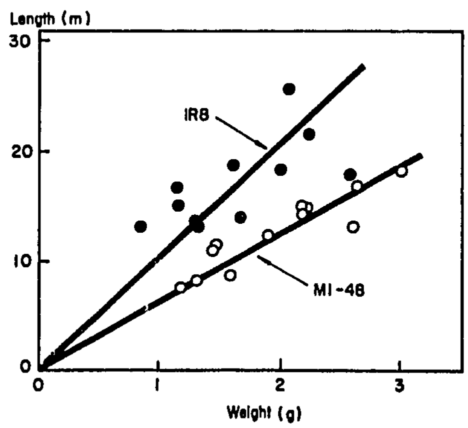
Table 4. Root weights of IR5 and M1-48 at two soil depths grown under flooded and upland conditions at 60 kg/ha nitrogen. IRRI, 1970 wet season.

Days after emergence[a]	Variety	Root wt (g) 0 to 15 cm Flooded	Root wt (g) 0 to 15 cm Upland	Root wt (g) 15 to 30 cm Flooded	Root wt (g) 15 to 30 cm Upland
25	IR5	0.4	0.3	0.01	0.02
	M1-48	0.2	0.4	0.01	0.05
40	IR5	1.2	0.7	0.10	0.06
	M1-48	1.1	0.4	0.11	0.08
53	IR5	1.3	0.7	0.23	0.08
	M1-48	1.3	1.1	0.32	0.26
68	IR5	2.3	0.8	0.35	0.04
	M1-48	2.1	1.1	0.44	0.06
82	IR5	3.1	1.3	0.32	0.06
	M1-48	2.4	1.7	0.26	0.16
96	IR5	2.4	0.7	0.23	0.08
	M1-48	2.5	1.5	0.25	0.15

[a]For upland rice, subtract 11 days to convert to days after transplanting for the flooded plots.

restricted than that of the IR5. This characteristic of M1-48 should enable it to exploit a larger volume of soil more efficiently for both mineral nutrients and water.

G. N. Kalwar (*unpublished*) in an experiment at IRRI observed another difference in the roots of the varieties IR8 and M1-48. He subjected these two varieties to various combinations of rainfed and continually flooded conditions and found that the ratio between root length and root weight was constant for each variety, but it differed by 50 percent between the varieties (fig. 4). The roots of the upland variety were thicker. This difference might be important to water uptake and translocation. Many research workers believe that a significant resistance to water flow exists in the conducting vessels of the roots



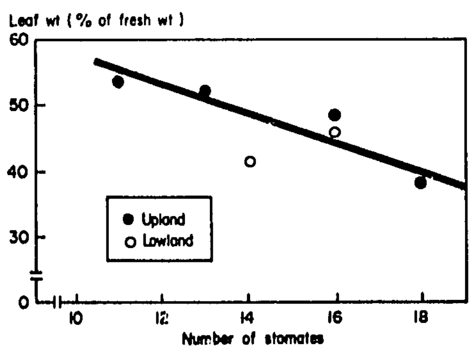
4. The relationship between root length and root weight for IR8 and M1-48 grown in puddled soil under both flooded and rainfed conditions. IRRI, 1970 wet season.

(Wind, 1955; Rawlins, 1971). If this is true, the resistance may be less in thicker roots, and, as a result, the aerial portions of the plant would be less likely to suffer from soil moisture stress. Furthermore, the larger surface area per unit length available for water absorption may be an advantage of a thicker root. Mathematical analysis of moisture flow to cylindrical roots in unsaturated soil shows that the moisture potential at the root surface, which in part determines the amount of water stress in the plant, is highly sensitive to root diameter. As the roots become thinner, the amount of moisture stress at the root surface increases greatly for the same rates of water flow through the plant. Although these factors must be studied further, it nevertheless appears that they help upland varieties withstand water stress.

LEAF FACTORS

Plant physiologists at IRRI have suggested that rice varieties differ in photosynthetic efficiency (IRRI, 1963). A "loose" positive correlation between leaf thickness and photosynthetic rate was observed. Because transpiration of the plant depends more on leaf area than on leaf thickness, thick leaves may be an important character for which to breed to increase water-use efficiency. Obviously, this increased efficiency would be most important at the early stages of plant growth before a high leaf area index develops. At the late growth stages both photosynthesis and transpiration depend more on environmental conditions and on the morphology of the whole plant canopy than on individual leaf characteristics. Some improvement in water-use efficiency should still be evident at the later growth stages, however.

The above discussion applies to adequately watered rice. When water stress develops, an important question, yet unanswered for rice, is the relationship between photosynthesis, respiration, and transpiration. Carbon dioxide exchange and water vapor exchange are both governed by the stomatal aperture or stomatal resistance. In addition, mesophyll resistance to carbon dioxide exists but this is not important for water vapor exchange. The relative magnitudes of stomatal and mesophyll resistance affect the transpiration-photosynthesis ratio. The effects of stomatal resistance and mesophyll resistance on the relative photosynthetic and transpiration rates as a function of variety must be studied more closely. Such experiments might permit the identification of



5. The relationship between stomatal density and water content of excised rice leaves of six varieties after drying for 3 hours.

Table 5. Dry matter production, height, leaf area index, and grain yield of IR20 variety in a rotational irrigation experiment. IRRI, 1971 dry season.

Irrigation treatment	Dry matter production (g/hill)	Plant ht[a] (cm)	Leaf area index[b]	Yield[c] (t/ha)
Continuous flooding	37	90	4.7	6.98
2 cm every 4 days	35	84	3.9	5.44
3 cm every 6 days	34	79	3.6	5.42
4 cm every 8 days	30	71	2.5	5.36
5 cm every 10 days	31	79	2.5	4.05

[a]At harvest. [b]At heading. [c]Mean of two replications.

leaf characteristics that could be bred into upland rice varieties to enhance their water-use efficiency.

Zemánek (1965) described a technique in which detached leaves from two varieties of barley of differing resistance to drought were weighed periodically while they were drying. The more drought-tolerant variety dried at a slower rate than did the drought-susceptible variety. We used a similar technique in our laboratory on six rice varieties grown under upland conditions. The samples were taken during the early vegetative stage. Stomata on the lower surface of the leaves were counted. The inverse relationship between the number of stomata and the water content of the leaves suggests that stomatal control of water loss is important and that the effect persists when water content is relatively low (fig. 5). In general, the upland varieties had higher water contents after 3 hours of drying than the other varieties. Thus, the rate of leaf drying may prove a simple and useful technique for screening varieties for leaves better adapted to resist desiccation during periods of moisture stress.

WATER DISTRIBUTION AND INTENSITY FACTORS

A rotational irrigation experiment with IR20 conducted at IRRI in the 1971 dry season involved applying an average of 0.5 cm/day of water to different plots at 4-, 6-, 8-, and 10-day intervals. Plant height, dry matter production, leaf area index, and grain yield decreased as the interval between water applications increased (Table 5). The highest yield, obtained in the continuously flooded plots, was 1.5 t/ha greater than the yields obtained in the rotationally irrigated plots. These data show that water distribution is a critical factor in determining grain yield and it must be considered together with the total amount of rainfall received during the growing period when discussing the effect of precipitation or irrigation practice on grain yield.

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Discussion: Some water stress effects on rice

S. K. SINHA: Does moisture stress cause non-synchronous flowering and maturity of tillers in high-tillering varieties?

H. K. Krupp: Yes, we frequently observe non-synchronous flowering and maturing of tillers in water-stressed plots of high-tillering varieties, such as IR20.

S. K. SINHA: Do varieties suitable for upland conditions show rapid and vigorous growth of roots even in the seedling and early stages?

H. K. Krupp: Our early data suggest this.

H. L. CARNAHAN: Are the yield differences in your Table 5 due to the water differences or could they be due to nitrogen losses associated with irrigation treatments?

H. K. Krupp: Both nitrogen losses and water stress probably cause the yield reduction shown in Table 5. It is difficult to determine the relative importance of these two factors at this time but we do have experiments in the field now in which both nitrogen and water level are varied systematically. These experiments may provide more information on this question. We applied ammonium sulfate at a rate of 125 kg/ha N in a split dose (75 kg at planting, 25 kg at maximum tillering, and 25 kg at panicle initiation) to remove some of the problems of nitrogen availability as affected by the water management.

A. O. ABIFARIN: I should like to comment on your statement on plant type, especially in reference to lodging. There is very little difference between shattering loss in upland and lowland. A variety that would shatter due to wind will also shatter in the process of lodging. Lodged panicles are more exposed to rat and ant attack than when upright. Sprouting and rotting also occur on lodged panicles in tall upland types. Lodged plants are more difficult to harvest thus the grain recovery is less.

H. K. Krupp: If all other factors are equal, a taller variety that lodges easily will be less subject to grain shattering than will a short, stiff-strawed variety. Moreover, our experience with rats shows that the standing crop is in no way protected from attack. Finally, sprouting and rotting no doubt occur in an upland field but probably to a much lesser extent than would occur in a flooded, lowland field.

S. TSUNODA: Thicker leaves generally exhibit a high photosynthetic rate as well as a ;h photosynthesis-transpiration ratio, and leaf thickness seems to be closely related to ɔught resistance, as you stated. I would like to point out that thicker leaves tend to be ;ociated with a lower tillering ability. Also in Japan, traditional upland varieties are ıerally tall as compared with lowland varieties. I suppose that the wide row spacing d difficulty in weed control under upland conditions have been the factors responsible · this difference. If we can change the row distance and if we can control the weeds by ıer means, it may be possible to use a modern short-statured plant type for upland tivation. In addition, thicker leaves can rather easily be combined with shorter stature, he tillering ability is low or moderate.

Varietal differences in resistance to adverse soil conditions

F. N. Ponnamperuma, Ruby Uy Castro

Nearly 150 varieties or selections were tested for resistance to four adverse soil conditions in pots and in outdoor tanks. IR20 and H 4 were the most widely adapted of the high yielding varieties. Of 52 varieties tested for adaptability to three aerobic soils, on the average, M1-48, E425, and IR661-1-170 performed best. Peta, a typical lowland indica, was the worst. M1-48 and the IR661 line did uniformly well, and Peta, uniformly badly on the acid, neutral, and alkaline soils; E425 fared relatively poorly on the acid soil. Among 80 varieties screened for resistance to iron toxicity, IR20, IR22, IR665-8-3, and H 4 were among the least susceptible; IR5, IR8, IR424-21-PK2, and IR878B4-220-3 were among the most susceptible. Of 52 varieties, IR20, IR22, IR1168-21-3, and H 4 were most resistant to phosphorus deficiency; IR498-12-1, IR626-1-112, IR878B4-220-3, and Dawn were the least resistant. Twenty-nine of 32 varieties grown on a zinc-deficient soil perished within 5 weeks of transplanting but IR5, IR20, and H 4 survived. IR20 and H 4 were the best of 92 varieties in resistance to reduction products; the upland varieties, along with IR5 and IR8, performed the worst.

INTRODUCTION

Rice is grown from the equator to 45°N, from sea level to 2,500 m. It thrives in the hot, wet valleys of Assam and the irrigated deserts in Pakistan. The soils on which rice is grown are as varied as the climatic conditions to which rice is exposed: texture ranges from sand to clay; pH, from 3 to 10; organic matter content, from 1 to 50 percent; salt content, from almost 0 to 1 percent; and nutrient availability, from acute deficiencies to surpluses. Besides, rice is grown on flooded and non-flooded soils, and even in 6 meters of flood water. Combinations of these varying soil and climatic factors produce innumerable environments. The 14,000 varieties of cultivated rice in the IRRI collection reflect natural or artificial selection of types suited to these diverse environments.

Rice breeders have used genetic variability to produce varieties that have the right plant type, and that can tolerate cold, disease, insects, drought, and even floods. But apart from testing and breeding rice varieties for resistance to the straighthead disease of rice (Atkins, Beachell, and Crane, 1957) and some selecting for resistance to salinity (Chalam, 1954; Rao and Reddy, 1966; Sakai and Rodrigo, 1960), little has been done to identify and breed varieties adapted to adverse soil conditions that cannot be easily corrected by manage-

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ment. Among such unfavorable soil conditions are strong acidity, alkalinity, salinity, iron deficiency, iron toxicity, phosphorus deficiency (in soils that fix P strongly), and certain effects of oxidation or reduction. If the natural genetic resistance that some varieties may have to these conditions can be combined with the right plant type and resistance to pests, it may be possible to produce improved varieties suited to these soil conditions. Our preliminary tests indicate that varietal differences exist in resistance to growth-limiting factors in aerobic soils, to iron toxicity, to phosphorus and zinc deficiency, and to reduction products.

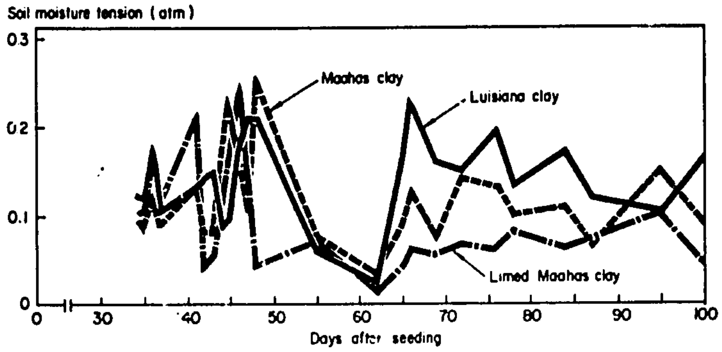
AEROBIC SOILS

The poor yield of rice on non-flooded fields is usually attributed to water stress and weed competition. But we found that even in the absence of water stress and weeds, rice yields less in aerobic than in anaerobic soils. We identified the main retarding factors in aerobic soils at field capacity as iron deficiency on neutral and alkaline soils and manganese and aluminum toxicity on acid soils fertilized with ammonium sulfate (IRRI, [1964], [1965], 1966, 1967*a*, 1967*b*, 1971). Since the severity of iron deficiency decreases while that of manganese toxicity increases as pH decreases, a calcareous soil, a neutral soil, and an acid soil, all at field capacity, were used to screen varieties for resistance to yield-limiting factors in aerobic soils.

Two common drawbacks of field experiments with upland rice are the absence of quantitative data on two important parameters—redox potential and soil moisture tension (redox potential reveals whether a soil is aerobic or anaerobic; soil moisture tension indicates the degree of moisture stress). In the absence of the control and the measurement of these two factors, yield differences among varieties depend on the rainfall pattern and cannot be related to resistance to the growth-limiting factors in aerobic soils. For this reason, we controlled and measured both factors.

We conducted a screening test in three concrete tanks, each 10.8 x 8.3 x 0.3 m, which were filled with air-dry Luisiana clay (pH 4.6, organic matter, 3.2%); Maahas clay (pH 6.9, organic matter, 2.4%); and Maahas clay limed to pH 7.6. To maintain the soils at field capacity, sprinklers were installed above the tanks and drainage pipes were fitted at the bottom. The seedbed was prepared and 100 kg/ha N, 50 kg/ha P, [illegible] kg/ha K were broadcast. Then pre-soaked seeds of 45 varieties were sown in furrows 20 cm apart. The tall varieties were grouped together and at later growth stages they were supported to prevent lodging. Eight tensiometers and eight platinum electrodes were set at a depth of 10 cm in each tank. The tensiometer readings were taken daily at 2 PM and redox potentials weekly. The soils were sprinkler-irrigated and the soil moisture tension was kept at 0.1 to 0.2 atm. The low soil moisture tension and the strongly positive redox potentials observed (fig. 1 and 2) showed that the soils were moist but aerobic.

The two top yielders were the upland varieties M1-48 and E425; the lowest was Peta, a typical lowland variety (Table 1). The variety IR5, which has been



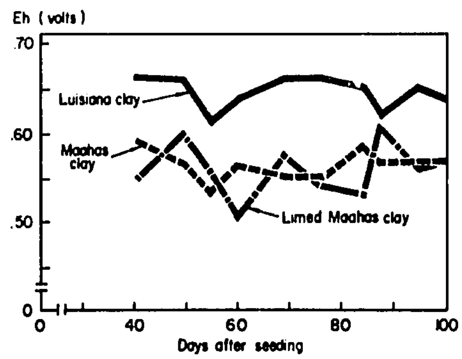
1. Changes in soil moisture tension of three soils at field capacity.

reported to yield well as an upland rice, was 34th in rank among the 45 varieties tested because it suffered severely from iron deficiency on limed Maahas clay and from manganese toxicity on Luisiana clay. On Maahas clay, however, it ranked as the fifth highest yielder. In spite of good vegetative growth, Peta, Dima, Texas Patna, M1-329, and IR332-2-10, on the average, produced little grain. The Philippine upland varieties, Azmil 26, Azucena, Palawan, and Dinalaga, produced moderate amounts of straw but little grain.

Most varieties roughly maintained their relative ranks on all three soils, but there were some variety-soil interactions (Table 2). On all three soils, M1-48 was the top yielder, IR22 was a moderate yielder, and Peta was the lowest yielder. But Taichung Native 1, E425, and IR661-1-140 fared badly on Luisiana clay compared with their performance on Maahas clay and limed Maahas clay. IR5 did much better on Maahas clay than on the other two soils.

The upland variety M1-48, in spite of its moderate height and poor tillering, produced the highest yield of grain on the acid, neutral, and calcareous soils. The Nigerian upland variety E425 yielded almost as much as M1-48 on the neutral soil, but had low yield on the acid soil. Of the IRRI lines, only IR661-1-170 approached M1-48 in yielding ability.

M1-48, E425, IR661-1-170, and IR424-21-PK2 were greener than the others and showed no signs of iron deficiency or manganese toxicity. A healthy green color may be a manifestation of adaptability to aerobic soils that are not under water stress.



2. Changes in redox potential of three soils at field capacity.

Table 1. Mean yields (per linear meter) on three aerobic soils.

Variety or selection	Yield (g/meter)	
	Grain	Straw
M1-48	151	247
E425	120	228
IR661-1-170	119	133
PI 215936	105	163
IR577-11-2	102	123
IR127-80-1	102	147
Taichung Native 1	101	156
CI 5094-1	99	257
IR12-178-2	99	143
IR24	94	126
IR305-3-17	92	122
IR140-136	90	133
IR159B3-1-1	89	195
IR424-21-PK2	89	161
IR305	88	109
IR759-53-5	88	137
IR773-112-2	88	113
CP231 x SLO-17	85	133
IR20	81	130
IR262-43-8	81	113
IR789-8-3	81	146
IR22	72	106
Azmil 26	70	170
IR790-5-1	70	135

Table 1 (Continued)

Variety or selection	Yield (g/meter)	
	Grain	Straw
IR648-2-8	69	124
Nira	69	171
Dickwee 328	68	243
IR8	68	151
Azucena	65	163
C4-63G	61	174
Palawan	60	165
Texas Patna	56	263
Milfor	55	182
IR5	53	284
Agbede	51	132
Dima	50	293
Pinulot 330	50	155
IR159B2-3-1	49	111
IR878B4-220-3	48	168
Dinalaga	47	165
M1-139	36	232
Original Century Patna	32	97
Century Patna 231	32	96
IR332-2-10	32	210
Peta	14	462

IRON TOXICITY

Iron toxicity is a widespread physiological disorder of paddy rice. It occurs on strongly acid ferrallitic (lateritic) soils in India, Ceylon, Thailand, Malaysia, and the Philippines (Tanaka and Yoshida, 1970). Iron toxicity is also one of the main impediments to the growth of rice on acid sulfate soils (Mai-thi-My-Nhung and Ponnamperuma, 1966; Tanaka and Navasero, 1966), of which there are more than 15 million hectares in Asia alone. Since liming, perhaps the best remedy, may not always be economic, the possibility of selecting and breeding resistant varieties was investigated.

In the dry season, we grew 54 varieties outdoors in pots containing a lateritic soil that built up water-soluble iron concentrations exceeding 400 ppm and induced iron toxicity even in the presence of adequate amounts of phosphorus and potassium (IRRI, 1971).

All plants showed signs of iron toxicity, but the degree and expression of the symptoms differed among varieties. The discoloration of the leaves ranged from light orange, through orange and brown to purple. Some varieties showed marked leaf rolling, others showed little. The symptoms varied even within lines from the same cross. For example, IR759-79-2 had light-orange leaves while

Table 2. Comparison of grain yields of 15 varieties on three aerobic soils at field capacity.

Variety	Luisiana clay		Maahas clay		Limed Maahas clay	
	(g/m)	Rank	(g/m)	Rank	(g/m)	Rank
M1-48	138	1	154	1	161	1
IR661-1-170	129	2	116	4	115	5
IR577-11-2	104	4	111	7	91	11
IR127-80-1	109	3	104	11	92	9
CP231 x SLO-17	82	15	91	20	83	17
IR22	69	25	77	28	71	26
C4-63G	52	33	74	30	58	30
M1-329	21	45	50	42	36	42
Original Century Patna	18	46	45	44	34	43
Peta	6	48	28	46	9	46
Taichung Native 1	82	16	118	3	104	6
E425	83	15	150	2	124	2
IR24	76	21	112	5	94	8
IR20	87	12	108	8	48	34
IR5	42	35	113	5	3	47

IR759-54-2 had purple leaves; IR790-28-5 showed severe leaf scorch while IR790-54-1 exhibited severe bronzing. Based on grain yield, the varieties least susceptible to iron toxicity were IR22, H 4, IR506-1-89, H 105, and RD 17-1-3. Among the susceptible varieties where RD 3, IR20, and IR24. Among the very susceptible varieties were IR661-1-170, Palawan, and RD 1. Among the highly susceptible varieties were IR8, E425, and IR5.

A better measure of resistance to iron toxicity would be the yield on the ferrallitic soil relative to the yield on a good soil like Maahas clay. So 56 varieties were grown side by side on the two soils in pots in the greenhouse. The yield of grain, both absolute and relative to Maahas clay, paralleled the visual symptoms of iron toxicity.

The eight least susceptible varieties were Dima, IR665-8-3, BG79, RD 1, IR506-1-89, IR22, Sigadis, and RD 17-1. On the ferrallitic soil these varieties gave 30 to 45 percent of their yield on Maahas clay. Five of the varieties were bred in countries where strongly acid ferrallitic soils are widespread.

The susceptible varieties included H 8, Tadukan, PI 215936, IR20, IR24, LD27, IR661-1-170, IR262-43-8, H 4, RD 3, IR790-5-1, IR400-5-12, and Taichung Native 1. On the ferrallitic soil, their yields were 15 to 30 percent of their yields on Maahas clay.

The following yielded less than 7 g of grain per pot or less than 8 percent of their yield on Maahas clay: CP231, Wagwag, IR790-28-2, IR8, IR589-66-2, IR759-53-5, PD46, IR790-28-5, IR878B4-220-3, and IR424-21-PK2. The IR424 line died on the ferrallitic soil 6 weeks after planting, but gave 99 g of grain per pot on Maahas clay. This group of varieties is highly susceptible to excess iron.

The fairly consistent behavior of the varieties that have been grown in several experiments makes possible their classification into two extreme groups according to susceptibility to iron toxicity—*least susceptible:* IR20, IR22, IR262-43-8, IR506-1-89, IR665-8-3, H 4; *most susceptible:* IR5, IR8, IR424-21-PK2, IR759-79-2, IR790-28-1, IR878B4-220-3.

PHOSPHORUS DEFICIENCY

Phosphorus deficiency limits the growth of rice on vast areas of lateritic and acid sulfate soils, which not only are low in available P but also fix fertilizer phosphate as highly insoluble minerals. In these soils, the increase in availability of phosphorus brought about by soil submergence is slight (IRRI, 1967*b*; Kawaguchi and Kyuma, 1969). The phosphate fertilizer needs of such soils can be reduced if varieties that can extract phosphorus more efficiently can be developed. Since phosphorus deficiency and iron toxicity often go together but can occur independently, the soil used for screening should be deficient in phosphorus but should not induce iron toxicity. Fifty-two varieties of rice were grown outdoors on such a soil (Luisiana clay: pH 4.6; organic matter 3.2 %) in pots fertilized with 100 ppm N and 50 ppm K.

The following varieties yielded at least 50 percent more grain than IR8: IR20, IR22, IR665-58-2, IR790-28-2, IR790-28-1, IR790-28-6, IR879-183-2, IR1168-21-3, H 105, and H 4. The selection IR878B4-220-3 gave only 50 percent of the yield of IR8. E425 gave practically no grain.

In a parallel experiment, 52 varieties were planted in rows on flooded Luisiana clay in outdoor concrete tanks in the dry season. Unseasonally heavy rains and several typhoons damaged some rows and depressed the yield of grain, in all varieties. Of the 37 varieties harvested, nine yielded more than IR8. One, IR1006-28-6, yielded nearly three times as much as IR8. Seven of the IRRI lines that outyielded IR8 had BPI-76 as one of the parents. None of the varieties that were inferior to IR8 had BPI-76 as a parent.

The results of the wet season experiments are reported elsewhere (IRRI, 1972).

REDUCTION PRODUCTS

When a soil is submerged and the oxygen supply is cut off, soil microorganisms use oxidized soil components such as nitrate, manganese dioxide, ferric oxide, sulfate, and even organic metabolites as electron acceptors in their respiration. As a result, nitrate is reduced to nitrogen gas, and manganic and ferric oxides are reduced to manganous and ferrous compounds which are highly soluble. Also, organic reduction products may accumulate and poison the rice plant or cause nutritional disorders. Since the obvious remedy of draining and reoxidizing the soil is not always feasible, selecting and breeding varieties that are resistant to these reduction products merits study.

We have in our collection of problem soils a soil (Tungshan silt loam) from Taiwan, on which a nutritional disorder known as "suffocation" disease occurs. The symptoms of the disease are stunting and a brownish discoloration of the leaves. The disease occurs only when the soil is submerged. It is corrected by the application of such retardants of soil reduction as nitrate and manganese dioxide (Yuan and Ponnamperuma, 1966). It is not caused by excess iron:

the symptoms differ from those of iron toxicity and the soil solution does not contain harmful levels of iron. Thus the disease appears to be due to unknown organic reduction products. Tungshan silt loam was therefore used for testing varieties for resistance to harmful reduction products.

The upland variety Palawan showed the most acute symptoms and yielded no grain at all. H 4 showed mild symptoms and produced the third highest yield of grain. The 10 most resistant varieties were IR20, IR22, IR95-43-13, IR400-5-12, IR661-1-140, IR937-76-2, IR874B2-121-3, IR790-28-1, H 4, and H 105. The least resistant varieties included IR5, IR8, IR879-183-2, IR878B4-220-3, E425, Azucena, and Palawan. In an earlier experiment (IRRI, 1970) the upland varieties Dinalaga, Azucena, and Palawan performed disastrously on the same soil although they gave high yields in aerobic, oxidized soils. Apparently, these upland varieties cannot tolerate the toxins that accumulate in reduced soils.

ZINC DEFICIENCY

Although zinc deficiency can be corrected by applying zinc to soil or to plant, resistance to zinc deficiency in improved varieties might help the small farmer. So the performance of 32 varieties was tested on a zinc-deficient soil (pH 6.2; organic matter 5.0%; total Zn, 73 ppm; available Zn, 0.8 ppm; and available P [Olsen], 78 ppm).

Two to three weeks after planting, all varieties showed zinc deficiency symptoms but IR5, IR20, and H 4 had the least. Five weeks after transplanting these three were the only varieties surviving in all plots; the lines, IR1561-189-3 and IR1561-284-3 survived in some replicates. The following were dead: IR8, IR22, IR24, one IR5 line, one IR262 line, three IR506 lines, two IR665 lines, one IR759 line, three IR790 lines, three IR878 lines, one IR1170 line, and one IR1561 line.

At 5 weeks after transplanting, the zinc content of all plants, including those that survived, was less than 13 ppm. But the surviving varieties had lower concentrations of manganese and magnesium.

IR20 and H 4 appear to combine resistance to four soil problems: iron toxicity, phosphorus deficiency, zinc deficiency and injury due to reduction products. These varieties should do well on strongly acid soils and continuously wet soils. IR20, in addition, should yield well on neutral and acid upland soils.

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Discussion: Varietal differences in resistance to adverse soil conditions

J. H. COCK: Peta gave a large straw weight but very low grain yield in Table 1. Why?

F. N. Ponnamperuma: Peta suffered a setback at the later growth stages. Peta showed high spikelet sterility.

A. C. MCCLUNG: How do you explain the low yield of IR5 in Table 1 which seems to differ from other IRRI experiments?

F. N. Ponnamperuma: IR5 yielded moderately well on Maahas clay (Table 2). But its poor performance on limed Maahas clay and on Luisiana clay depressed the average yield for the three soils.

Y. L. WU: How do you differentiate iron deficiency and zinc deficiency in rice plants?

F. N. Ponnamperuma: The main symptom of iron deficiency is interveinal chlorosis of the younger leaves; that of zinc deficiency is slight interveinal chlorosis of the youngest leaf followed by brown spots in the older leaves.

Y. L. WU: Do you think it is possible to raise rice yield by planting upland varieties or using direct seeding method in soils high in reduction products?

F. N. Ponnamperuma: The best way to prevent injury by reduction products is to direct seed, grow the crop in dry soil, and flood about a week before panicle primordia initiation.

P. R. JENNINGS: Which soil problem do you consider the most important?

F. N. Ponnamperuma: Iron deficiency.

Varietal response to some factors affecting production of upland rice

S. K. De Datta, H. M. Beachell

For obtaining high yields of upland rice, rainfall distribution is more important than variation in intensity of solar energy. The maximum nitrogen response and grain yield for upland rice are the same as those for wet-season, rainfed, lowland rice. Breeding for upland rice varieties should be directed towards the desirable morphological characteristics of high yielding, lowland varieties. These characteristics include high tillering, erect leaves, and relatively short stature. In addition, the high levels of resistance to diseases and insects of seedling vigor, and of drought resistance, if it exists, are basic requirements of upland varieties. For the immediate future, varieties and lines for upland culture should be screened for resistance to short-term drought conditions rather than for resistance to prolonged drought since none of the upland and lowland varieties grown in upland rice experiments produced grain yields of 5 to 6 t/ha under prolonged drought conditions. At low moisture levels the differences in grain yields may be determined by the relative tolerance of the varieties to such adverse soil conditions as iron and phosphorus deficiencies or manganese toxicity. When moisture is not limiting or is between maximum water-holding capacity and field capacity, and management practices are optimum, varieties such as IR5 or IR8 yield more than the upland varieties, Palawan and M1-48. Under upland farm conditions in which soil fertility is low, slightly taller varieties, such as IR5 and IR442-2-58, may be superior to semidwarf indica varieties like IR8.

INTRODUCTION

Upland rice is grown on both flat and sloping unbunded fields that have to be prepared dry. These areas are unsuitable for lowland rice because of topography, soil texture, or water supply. Upland rice depends entirely on rainfall for moisture. It is grown under a wide range of conditions from shifting cultivation (Lee, 1965; P. A. Sánchez and M. A. Nureña, *unpublished*) to highly mechanized systems of some areas of Latin America.

The total area planted to upland rice is so large that a small increase in yield would have a substantial impact on total rice production. In Asia, India, Indonesia, Pakistan, mainland China, and the Philippines have the largest areas of upland rice. In East Pakistan, where vast areas are inundated during most of the monsoon season, 2.4 million hectares are grown to upland rice (A. M. Akhanda, *unpublished*). The Philippines had 412,000 hectares in 1970

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(Department of Agriculture and Natural Resources, Philippines, *unpublished*). Indonesia has 323,800 hectares (Grist, 1965). Sarawak has more upland rice than flooded rice—70,000 hectares compared with 40,000 (Lee, 1965). In South America, Brazil has the largest area of upland rice, 3.5 million hectares (A. Conagin, *personal communication*). In Peru, 20 percent of the nation's rice crop comes from upland rice grown in the Amazon basin (P. A. Sánchez and M. A. Nureña, *unpublished*).

The yield of upland rice is generally lower than that of flooded rice (Senewiratne and Mikkelsen, 1961; IRRI, [1965], 1966). In Asia, the national average grain yield of upland rice is 0.5 to 1.5 t/ha (A. M. Akhanda, *unpublished*).

REASONS FOR LOW YIELDS OF UPLAND RICE

Obviously, any shortcomings of management or varieties that limit the yield potential of flooded rice also limit the potential of upland rice. Some factors, however, have a more pronounced limiting effect on upland rice.

Inadequate moisture supply

Few studies have been made of the processes that limit the growth of upland rice under various degrees of moisture stress. There is abundant evidence that rice benefits from a good water supply but its water requirement is little greater than that of other common field crops. A recent study indicated that in 1 year 21 t/ha of rough rice can be harvested with three crops of transplanted rice grown on a saturated, puddled, montmorillonite clay without standing water (S. K. De Datta and R. K. Jana, *unpublished*). If flooding is not essential for high yields, then lack of standing water in upland rice fields is not directly responsible for the low yield of upland rice. Since upland rice usually depends on rain for its entire water supply the lower the rainfall during the growing season, the lower the yield. When rainfall is adequate, rainfall distribution becomes more important. At IRRI, for example, an area that receives 2,000 mm of annual rainfall, the distribution of the rain has a major influence on yield (IRRI, 1967*a*, *b*). At the IRRI farm, yields from upland rice from season to season have varied from 0.6 t/ha to over 5 t/ha, depending on the moisture supply (IRRI, 1967*a*, *b*; Jana and De Datta, 1971). Similar differences in grain yield were obtained in Peru by P. A. Sánchez and M. A. Nureña (*unpublished*) and by M. Nureña, J. Vélez, and K. Kawano (*unpublished*).

The differences in rice plant characteristics between upland culture and flooded culture at various growth stages were evaluated in California by Senewiratne and Mikkelsen (1961). They found that the initial growth of Caloro plants was better under upland culture than under flooded culture. Under field conditions in tropical Asia, any differences in the initial growth of upland rice and lowland rice seedlings probably have little significance. Even in California, the better initial growth under upland culture was not sustained long. Upland plants soon showed poor tillering, depressed leaf growth, delayed flowering, low moisture content, and foliar chlorosis. They yielded half as much as flooded rice (Senewiratne and Mikkelsen, 1961).

Some data are available on the influence of soil dryness at different stages of growth. The concept of "critical stages" has been much emphasized. In other words, injury from a given stress is greater at one growth stage than at others. After a mild stress, the plant development under favorable conditions may compensate for injury, but the injury from a severe stress is more persistent. Laude (1971) pointed out that greater attention should be directed to the plant's response after the plant has undergone stress, for there is less information on this than on behavior during stress.

Matsushima (1962), who studied flooded rice, reported that rice is most sensitive to moisture stress from panicle initiation to 10 days after heading. In studies at IRRI the grain yield of transplanted IR8 was reduced in every case by moisture stress. In flooded rice experiments, the reduction in grain yield of IR8 grown on Maahas clay was more related to the duration of moisture stress than to the stage of plant growth at which the stress occurred (H. K. Krupp, S. K. De Datta, and S. N. Balaoing, *unpublished*).

Variation in forms and availability of nutrients

In general, alternate wetting and drying of soils leads to losses of both native and applied nitrogen (Patrick et al., 1967; De Datta and Magnaye, 1969). Shapiro (1958) reported that rice takes up less nitrogen under upland conditions than under flooded conditions. The flood water may enhance nitrogen fixation by blue-green algae and other organisms. According to Senewiratne and Mikkelsen (1961), these increases in nitrogen fixation may be important in areas where low soil fertility limits grain yield.

Phosphorus deficiency in soil limits grain yield to a greater extent under upland culture than under lowland or flooded rice culture. Under upland conditions, the soil's capacity to supply phosphorus is considerably decreased (F. N. Ponnamperuma, *unpublished*). Chang and Chu (1959) for example, showed that the increase in available phosphorus content after flooding was equivalent to 132 kg/ha P. The applied phosphorus is also used more efficiently under flooded conditions (De Datta et al., 1966). Since soils tend to be less fertile under upland than under flooded conditions, suitable fertilizer management practices should be developed to overcome the natural disadvantage of rice grown under upland conditions.

Some upland soils are deficient in iron and others have excess manganese. Experiments by the soil chemistry department at IRRI suggest that iron deficiency is prevented in neutral and alkaline soils and manganese toxicity is suppressed in acid soils by growing rice under flooded conditions (IRRI, [1964], [1965], 1966, 1967*a*). In California, Senewiratne and Mikkelsen (1961) reported that the iron content in the leaves of Caloro decreased gradually as the leaves matured but there were no significant differences between flooded and upland plants. Since they used only one variety, varietal response to low iron content was not determined.

Similarly, manganese concentration in the leaves increased more in upland than in flooded plants. The data of Senewiratne and Mikkelsen (1961) were similar to those obtained at IRRI (IRRI, [1964], [1965], 1966, 1967*a*).

Zinc deficiency is another important factor in many neutral and alkaline soils. Recently, F. N. Ponnamperuma (*unpublished*) suggested that growing rice under upland conditions should alleviate zinc deficiency. Field studies should be carried out in areas deficient in zinc to investigate this idea.

Weed competition

Another reason for low grain yield in upland rice is heavy weed infestation. For example, Arai, Miyahara, and Yokomori (1955), reported that 83 percent more weeds emerged under upland than under flooded conditions. Weed population in rice decreases with increased water depths (De Datta, Levine, and Williams, 1970). The traditional method of weed control in upland rice may involve several tillage and handweeding operations requiring much time and labor. A. M. Akhanda (*unpublished*) found that 321 to 780 man-hours are needed to weed 1 hectare by hand once. For flooded rice, 100 man-hours is generally adequate for one weeding by hand (De Datta, Park, and Hawes, 1968). Pande and Bhan (1964) reported that chemical weed control in upland rice is a remote possibility. Our current results (IRRI, 1971) indicate that chemical weed control is both effective and economical.

Blast and Helminthosporium diseases

The incidence of blast disease is generally higher under upland than under flooded conditions. For example, IR22 rice, which is susceptible to blast under Philippine conditions showed a higher incidence of blast under upland than under flooded rice culture. In Peru, blast is quite common in the Amazon basin area, where upland rice is grown. IR5, which has performed well under upland conditions in the Philippines, performed poorly in Peru because of its susceptibility to blast, but IR8 and the line IR4-93 yielded between 3 to 5.6 t/ha at different dates of seeding. These differences in grain yields were primarily due to differences in the incidence of blast disease (P. A. Sánchez and M. A. Nureña, *unpublished*). Among the varieties or lines tested, IR224-7 and IR480-5 were the only two lines resistant to blast in Peru (Table 1).

M. Nureña, J. Vélez, and K. Kawano (*unpublished*) reported a widespread occurrence of *Helminthosporium oryzae* in upland rice in Peru. On the IRRI farm, sheath blight, bacterial leaf blight, and virus diseases have caused losses in upland fields. The highest possible levels of resistance to all important diseases and insects should therefore be incorporated into upland rice varieties.

VARIETAL DIFFERENCE IN ROOTING

Recently, Barber (1971) reported that plant roots can greatly alter the physical, chemical, and biological nature of the soil adjacent to them. He also pointed out that species differ in root morphology and extent, in the amount of nutrients absorbed, and in the amount of H^+ or HCO_3^- released. It is, therefore, possible that gene sources could be identified which would alter the pH of the rhizocylinder (root plus strongly adsorbed soil) toward a more favorable nutrient status around the roots.

Similarly, R. L. Chaney, J. C. Brown, and L. O. Tiffin (*unpublished*) have shown that the plants subjected to iron stress release a reducing agent that

Table 1. Varietal performance in relation to month of planting under upland conditions in Yurimaguas in Peru (P. A. Sanchez and M. A. Nureña, *unpublished*).

Variety or line	Grain yield (t/ha) Nov 1968	Jan 1969	May 1969	June 1969	Sept 1969	Nov 1969	Mean	Blast-reaction[a]
IR4-2	6.3	3.0	0.9	1.0	5.6	4.1	3.5	S
IR4-93-2	3.5	3.4	2.3	1.8	4.7	—	3.2	S
IR8	5.1	3.3	0.7	0.8	4.8	3.8	3.1	S
IR5	3.2	3.8	1.5	1.9	2.7	—	2.6	S
IR11-222-4	3.1	3.6	0.7	0.7	4.0	2.1	2.4	S
SML457-Apura	2.9	2.9	1.4	1.3	—	—	2.1	M
IR224-7-1	—	—	—	—	6.3	3.2	4.7	R
IR578-8	—	—	—	—	6.2	3.9	5.1	S
IR578-43	—	—	—	—	6.2	3.0	4.6	S
IR480-5-9	—	—	—	—	5.9	3.3	4.6	R
Carolino (local)	2.9	1.7	0.4	0.4	2.2	2.0	1.6	S

[a]S = susceptible, M = moderately resistant, R = resistant.

reduces iron at the root surface so that iron can be absorbed by the plant. World rice collections should be screened for rice varieties that release higher amounts of the reducing agent and thus take up more iron from iron-deficient soil. Varieties tolerant to high levels of manganese are also needed for areas with high manganese content. Recent studies at IRRI (IRRI, 1971, p. 117) indicate that varieties differ in tolerance to iron deficiency and manganese toxicity. The Philippine upland varieties, Dinalaga, Azucena, Palawan, and Azmil 26, had the highest tolerance to iron deficiency and manganese toxicity (IRRI, 1970). This tolerance to iron deficiency and to manganese toxicity should be incorporated into upland varieties and even into lowland varieties. However, rice breeders must have rapid and reliable techniques to enable them to screen world collections or breeding lines for characteristics that can be transferred to an improved variety. Such techniques are not yet available. For this reason progress is slow.

Knowledge of the rooting characteristics of rice varieties under upland conditions may prove valuable if such characteristics are associated with some aspects of drought resistance or are related in any way to tolerance to adverse soil conditions.

Varieties differ as much in plant parts below the soil surface as in parts above the ground (Hurd, 1971). For example, varietal differences are known in the root elongation, degree of branching, overall length of roots for a given soil volume, and diameter of roots. These differences should be carefully measured and related to the capacity of rice varieties to resist short drought periods. Methods and criteria for characterizing rooting behavior and its effect on drought resistance should be developed. Desirable root characters can then be transferred to rice varieties with good plant type and high grain yield.

The rooting characteristics of the African variety 63-83, the Brazilian variety, Iguape Cateto, and the high-yielding semidwarfs, Taichung Native 1 and IR8, were studied in Africa under upland conditions (Nicou, Séguy, and Haddad, 1970). A schematic diagram of rooting characteristics seems to indicate that IR8 had more branched roots than other varieties studied. It is not clear from the study how rooting behavior is related to drought resistance or to other factors associated with stable high yield in upland rice.

VARIETAL RESPONSE TO SOIL MOISTURE, SOLAR ENERGY, AND NITROGEN LEVEL

Like that of rainfed flooded rice, the performance of rice varieties under upland conditions depends on the levels and interrelationships of soil moisture, solar energy, and nitrogen.

At the IRRI farm the effects of these three variables were examined in rice seeded in upland plots (Maahas clay soil: pH 6.0; organic matter, 2%; cation exchange capacity, 45 meq/100 g soil) at various dates during the wet seasons of 1967, 1969, and 1970. During the 1970 wet season, a similar trial was also conducted at the Philippine Bureau of Plant Industry's Maligaya Rice Research and Training Center (Maligaya clay soil: pH 6.9; organic matter, 1.5%; cation exchange capacity, 36 meq/100 g soil).

The varieties used in the 1967 experiment were IR8 and IR400-28-4 which are semidwarfs, Milfor-6(2), a medium-statured Philippine variety commonly grown under flooded and upland conditions, and Palawan, a typically tall Philippine upland variety. The yields of IR8 and IR400-28-4 responded positively to the increased solar radiation during the reproductive period, but those of Milfor-6(2) and Palawan did not (Tables 2 and 3). The June crop received the least rainfall, about 5.9 mm/day, during the vegetative period (Table 3). Inspite of the limited rainfall the grain yields of the improved varieties were high (Table 2). The extremely low yield of the September-seeded crop was primarily due to the soil moisture stress which occurred during the reproductive stage of growth (Table 3). The solar energy during the reproductive stage was close to that received by the June crop, but the total rainfall amounted to only 84 mm or an average of 1.8 mm/day.

Table 2. Effects of date of planting on the grain yield of upland rice. IRRI, 1967 wet season (Jana and De Datta, 1971).

Planting time	Yield (t/ha)			
	IR8	IR400-28-45	Milfor-6(2)	Palawan
June	4.7	4.9	3.1	2.5
July	5.0	5.3	2.8	2.2
August	1.7	2.0	1.5	0.6
September	0.7	0.8	0.5	0.4
Mean	3.0	3.3	2.0	1.4

Table 3. Solar radiation, rainfall, and grain yield of upland rice. IRRI, wet season (Jana and De Datta, 1971).

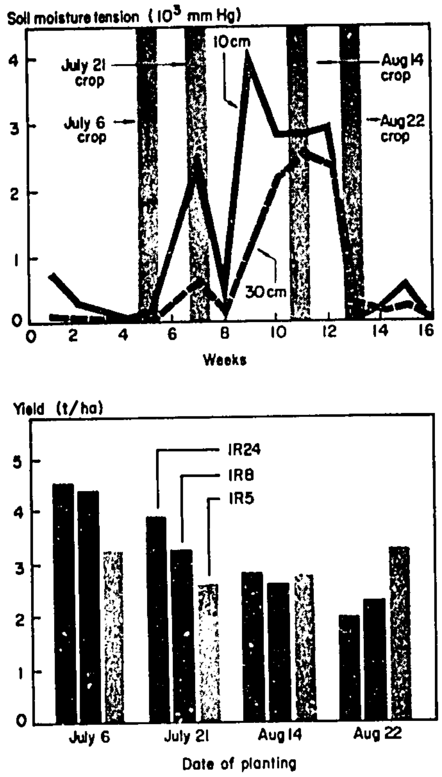
	Vegetative stage		Reproductive and ripening stage		
Planting time	Solar radiation (kcal/sq cm)	Rainfall (mm)	Solar radiation (kcal/sq cm)	Rainfall (mm)	Yield (t/ha)
		1967[a]			
June	29.3	401	19.0	466	3.80
July	24.7	435	20.2	341	3.82
August	24.6	650	16.7	510	1.47
September	24.5	783	16.8	84	0.61
		1969[b]			
July 6	30.1	562	18.8	175	3.75
July 21	33.2	355	19.0	113	2.93
August 14	32.1	374	18.0	134	2.13
August 22	33.8	383	14.1	345	1.87

[a]Average of four varieties or lines. [b]Average of six varieties and four nitrogen levels.

The results from the 1969 wet season showed that the grain yields of three varieties or lines gradually decreased as the planting date was delayed from July 6 to August 22 (fig. 1). Except for the IR5 crop, the crops planted on July 6 headed between September 22 and 28, when moisture tensions were low (fig. 1). The crops seeded on August 14, headed between November 3 and 9, when moisture tensions were very high. The seeding on August 22 produced low grain yields even though the soil moisture tension was low during the heading period (fig. 1). Senewiratne and Mikkelsen (1961) showed that soil moisture stress is less critical at the vegetative stage than at the reproductive stage. Severe moisture stress occurred during the entire vegetative period of the crop planted on August 22. This crop had the least plant height and lowest tiller number, indicating its failure to attain full vegetative development. That might account for the low grain yields. These data confirm our contention that the duration of the stress period is more important than the stage of the crop at which the stress occurs.

The results also indicate that nitrogen response of rice is influenced by soil moisture conditions. When the moisture tension remained above 250 mm Hg (field capacity) during the vegetative or the reproductive stages, grain yield response was positive only up to 60 kg/ha N. Leaves wilted temporarily at mid-day when soil moisture tension reached 250 mm Hg in plots that received 120 kg/ha N. In contrast, no symptoms of temporary wilting were observed when no fertilizer was applied or when it was applied at 60 kg/ha.

Since under a given moisture stress condition varieties responded somewhat differently to a given level of nitrogen, it may be possible to identify a variety that would respond to high rates of nitrogen with increased grain yield even under low moisture conditions (Jana and De Datta, 1971). The reasons for the differential responses to nitrogen under low moisture conditions are not



1. Top, soil moisture tension (weekly total) at 10- and 30-cm soil depths in relation to time of heading (shaded area) of upland rice planted on four dates. Bottom, grain yield of the crops at the four dates of planting (adapted from Jana and De Datta, 1971).

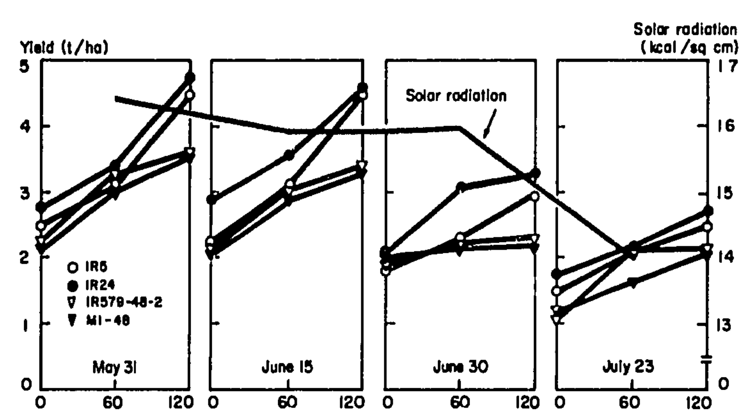
fully understood. In addition to the behavior of upper plant parts, the rooting behavior may also help explain the differential response of the varieties. At harvest the rice roots in this experiment grown on Maahas clay did not go deeper than 30 cm. Since soil moisture tension decreases with increasing depth down to 30 cm (fig. 1), rice varieties should have vigorous root systems to that depth. The importance of root length beyond 30 cm should be carefully evaluated in light- and heavy-textured soils.

To evaluate our earlier findings (Jana and De Datta, 1971), additional upland field experiments involving four dates of planting were conducted at IRRI and Maligaya during the 1970 wet season. Plots seeded on June 30 and July 23 at IRRI were severely damaged by two tropical storms during the reproductive and ripening periods of the crops. At the IRRI farm, the high yielding lowland varieties, consistently outyielded the upland variety M1-48 (fig. 2). At no time were soil moisture tensions higher than 250 mm Hg (field capacity). Therefore, none of the crops suffered from soil moisture stress.

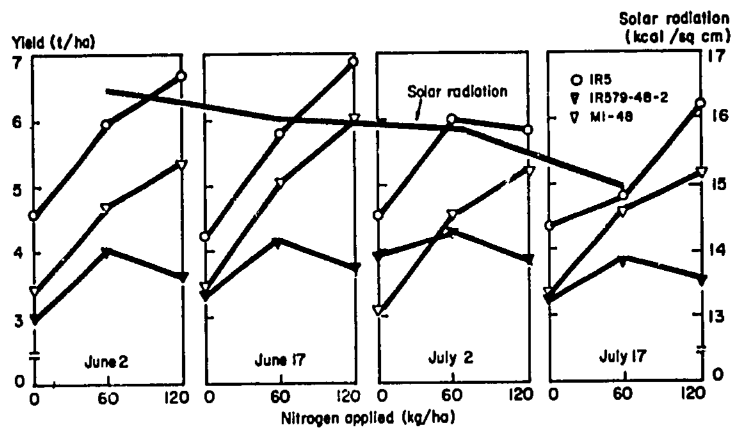
The crop seeded May 31 received the most solar energy during the ripening period while the crop seeded July 23 received the least (fig. 2). The low grain yield for the crop seeded July 23 may have been partly caused by the low solar energy during the ripening period. IR24 and IR5 were superior to IR579-48-2 and M1-48 in nitrogen response (fig. 2).

At Maligaya, IR5 produced consistently higher grain yields under upland conditions than the upland variety, M1-48, or the early maturing line, IR579-48-2 (fig. 3). Except for the crop seeded on July 2, the nitrogen response of IR5 was almost linear up to 120 kg/ha. On the other hand, M1-48 gave a positive grain yield response only up to 60 kg/ha N. The highest grain yield, 7 t/ha, was obtained with IR5 seeded on June 17. This is the highest grain yield obtained in any upland rice experiment conducted by IRRI. It was also higher than the highest yield obtained in any 1970 lowland experiment conducted at Maligaya (IRRI, 1971). The 7 t/ha yield is probably close to the upper limit for IR5 during the wet season when the total solar energy during the ripening period seldom exceeds 16.5 kcal/sq cm.

Judged by its performance at IRRI and at Maligaya (fig. 2 and 3) IR5 should be used in upland rice breeding programs. Increased resistance to lodging however should further help stabilize its grain yield and those of other varieties with similar plant type. IR5 has not performed as well as other high yielding lowland varieties in some upland experiments. In Peru, for example, IR4-2, an experimental line, and IR8 both outyielded IR5. Blast disease and possibly late maturity contributed to the low yield of IR5. IR4-2 had a low incidence of blast and produced the highest grain yield. The local varieties, Carolino and Lambayeque G-49, had a severe incidence of blast and they produced the lowest grain yields (P. A. Sánchez and M. A. Nureña, *unpublished*). In three other trials with upland rice in Peru, some newly introduced IRRI lines consistently outyielded the local varieties (M. Nureña, J. Vélez, and K. Kawano, *unpublished*). The highest yields, 7 t/ha, were obtained with IR578-43, IR578-8, and IR8. In the same trial the maximum grain yield of IR5 was 3.5 t/ha. The other lines yielded between 3 t/ha to 5 t/ha, depending on soil moisture conditions and on the incidence of blast and helminthosporium.



2. Nitrogen response of two varieties and two lines grown under upland conditions at four dates of seeding plotted with total solar radiation for the reproductive and ripening of each crop. IRRI, 1970 wet season.



3. Nitrogen response of IR5, IR579-48-2, and M1-48 under upland conditions at four dates of seeding plotted with solar radiation total for reproductive and ripening periods of the crop. Maligaya, Philippines, 1970 wet season.

The upland rice grain yields from the Amazon basin jungle were compared with the lowland rice yields from the northeastern coast of Peru. From these comparisons, M. Nureña, J. Vélez, and K. Kawano (*unpublished*) concluded that the highest yielding lines under upland conditions were those yielding highest under lowland conditions, but the reverse was not always true. Similarly in Colombia, two lines from the IR665 cross, which consistently yielded well under lowland conditions, performed poorly under upland conditions (P. R. Jennings, *personal communication*). It is not clear from the data of M. Nureña, J. Vélez, and K. Kawano (*unpublished*) if the poor performance of the high yielding lowland varieties under upland conditions in Peru was caused by blast, helminthosporium, unfavorable soil moisture conditions, or other factors. In Colombia, however, even under blast-free conditions, the high yielding IR665 lines performed poorly under upland conditions, contrary to our findings in the Philippines. We found that high yielding lowland varieties such as IR8, IR5, and IR24 consistently yielded between 4 and 5 t/ha under upland conditions if they received favorable moisture supply from rain, did not lodge, and were not attacked by blast. Under extremely unfavorable soil moisture conditions, no upland or lowland variety, irrespective of plant type, produces normal wet season yields (Jana and De Datta, 1971).

DESIRABLE PLANT CHARACTERS AND YIELD COMPONENTS FOR UPLAND RICE

Vigor during germination and seedling emergence is generally considered an asset for initial plant growth (Wright, 1971). High seedling vigor is essential for good stand establishment for unirrigated tropical rice. It is more important for upland rice than for flooded rice. Because of the prevailing suboptimal conditions in upland rice areas, high seedling vigor should be bred into upland rice varieties.

Hurd (1971) says that A. H. Bunting et al. refers to tillering in wheat as the "plasticity in the plant" which enables it to adapt to various conditions from year to year. According to Hurd (1971), high tillering in spring wheat is a luxury which cannot be afforded in dry areas. Many tillers use up moisture rapidly and cause the plant to suffer from moisture stress later in the season. For lowland rice however, a heavy-tillering, stiff-strawed rice variety will outyield a low-tillering variety under tropical conditions (Chandler, 1969; Fagade and De Datta, 1971). Our data clearly demonstrate that there are similar relationships in upland rice. IR5, which is heavy-tillering, outyielded the upland variety M1-48, which is low tillering at any level of nitrogen. The areas where upland rice is grown generally have poor soil fertility. Many Asian farmers do not apply fertilizer on upland rice. Under natural soil fertility, a heavy-tillering variety like IR5, may have an advantage over a low-tillering variety like M1-48. Furthermore, the increased tiller number brought about by nitrogen fertilizer helps increase grain yield if the crop does not lodge (Fagade and De Datta, 1971). This finding has been confirmed by upland rice experiments in the 1970 wet season. IR5 had higher dry matter production, primarily because it had higher tiller number, although it was shorter than the upland variety M1-48 (Table 4). High tiller number was a major factor in the superior performance of IR5 at IRRI and at Maligaya. Similar data were also reported from Peru by M. Nureña, J. Vélez, and K. Kawano (*unpublished*). The varieties that produced high grain yields under upland conditions in the Amazon basin in Peru had high tiller number and erect leaves. Late tillering should be avoided in upland rice however. Plants that have late tillers with small panicles or none at all waste soil moisture.

In our experiments, detailed measurements of yield components did not reveal any clear evidence of a single factor contributing to high or low grain

Table 4. Plant characters and yields (average of three nitrogen levels) of IR5 and M1-48 grown under upland conditions at IRRI farm and at the Maligaya Rice Research and Training Center in the 1970 wet season.

Planting date	Plant ht (cm)		Tillers (no./sq m)		Yield (t/ha)			
					Dry matter		Grain	
	IR5	M1-48	IR5	M1-48	IR5	M1-48	IR5	M1-48
			IRRI					
May 31	92	96	339	177	7.5	6.5	3.4	3.0
June 15	88	102	317	191	7.1	6.6	3.2	2.8
June 30	82	83	276	143	5.2	4.9	2.5	2.3
July 23	79	87	196	156	4.5	3.8	2.0	1.5
			Maligaya					
June 2	107	130	352	222	11.9	8.1	5.9	3.6
June 17	116	132	355	242	11.9	9.1	5.6	3.8
July 2	118	134	339	193	13.5	10.1	5.5	4.1
July 17	114	133	337	247	12.6	10.2	5.4	3.4

yield. For example, IR579-48-2 had the most panicles per square meter, but it had low weight per panicle and low 100-grain weight. On the other hand, M1-48 had few panicles but high weight per panicle and intermediate 100-grain weight.

The IR5 crops that produced 7 t/ha at Maligaya was 130 cm tall and averaged 380 tillers per square meter of which 352 had panicles. Each panicle had an an average of 88 grains and weighed 2.3 g. The weight of 100 grains was 2.92 g. The crop had about 20 percent unfilled grains. The dry matter produced at harvest was 15 t/ha.

In breeding upland varieties it may be desirable to aim for height, tiller number, and panicle number that is similar to that achieved by the crop that produced 7 t/ha, but with about 100 grains per panicle and a 100-grain weight of about 2.4 g. The slightly lower 100-grain weight might help improve the grain appearance. Generally, fine rices are more attractive to Asian consumers than coarse rice.

VARIETAL DIFFERENCES IN TOLERANCE TO SOIL MOISTURE STRESS

In experiments with upland rice we have had total crop failure in some years and high yields in others. The highest yields were usually obtained with IR5, but occasionally with IR8 and IR24 and lines such as IR400 and IR442. Before high yielding lowland varieties were introduced, the highest upland rice grain yield at the IRRI farm was 3.94 t/ha, obtained with Palawan in an experiment on weed control in upland rice in 1965 (A. M. Akhanda, *unpublished*).

In 1966, when IR8 was first introduced for lowland rice culture, several experiments were begun to evaluate the performance of high yielding lowland varieties under upland conditions. The entire upland rice crop suffered from a prolonged drought and the yields of all varieties were poor. During the 1967 wet season, when rainfall was favorable, the importance of good plant type and of heavy-tillering varieties for upland rice culture was fully recognized. Both IR5 and IR8, consistently outyielded the Philippine upland variety Palawan in all upland rice experiments (IRRI, 1967*b*).

In our tests at Maligaya no variety, including M1-48, IR5, and IR8, produced high grain yields if subjected to extremely high soil moisture stress. These data suggest that with the present upland or lowland varieties, it is almost impossible to obtain 5 to 6 t/ha grain yields if the crop suffers from prolonged, severe moisture stress. At all soil moisture conditions, however, IR5 outyielded local upland varieties grown under upland conditions. The Philippine upland varieties may be more tolerant of unfavorable moisture conditions than the higher yielding lowland varieties, but our data over the years demonstrate that these advantages are not reflected in grain yield at any moisture level.

Improving the plant type of upland varieties may increase their grain yield potential under upland conditions. A better approach might be to attempt to incorporate higher tolerance to drought and to adverse soil conditions with the plant type and other essential traits of the lowland varieties that have yielded well under upland conditions. But before undertaking such a program varietal tolerance to drought and to adverse soil conditions should be thoroughly evaluated. Reliable techniques for testing large numbers of early generation breeding lines will be essential.

SCREENING RICE VARIETIES FOR DROUGHT TOLERANCE

The ability to withstand severe moisture stress is a desirable trait in any crop grown under non-irrigated conditions. Most cereal crops are grown in semi-arid climates where the available moisture supply is often severely limiting (Hurd, 1971). Most flooded rice crops in Asia are dependent on rainfall. Drought tolerance in the seedling and early vegetative growth stages would also be desirable even for deep-water rice, since deep-water rice is seeded in dry soil and grown under upland conditions until sufficient rainwater has accumulated to flood the field. Perhaps deep-water varieties should be tested for drought resistance.

How should varieties be screened for resistance or tolerance to drought? Many techniques for measuring water stress in plants are available. The merits of some of these methods have been described by Sullivan (1971) and should be considered in developing a suitable technique for upland rice. If screening is done in the field in a wet season, when upland rice normally is grown, the rainfall distribution can not be predicted. On the other hand, moisture can be controlled in the dry season by applying a known increment of water. The results might not be directly applicable to a wet-season crop because the sunlight intensity in the dry season is about 50 percent greater than in the wet season.

Another approach is to plant rice at short intervals from the beginning of the wet season, assuming that the crop in each date of seeding would receive different amounts of rainfall and that the sunlight is relatively constant throughout the wet season. A similar approach for year-round monthly planting experiments has already been highly successful for flooded rice (De Datta and Zarate, 1970). Our 3-year data indicate that such an approach is also suitable for upland rice (Jana and De Datta, 1971).

During the 1969 wet season, the large-scale screening of varieties or lines under upland conditions was started at IRRI. Forty new lines, including a few high yielding lowland varieties, were planted. M1-48 was included for comparison. IR5 gave the highest yield, 3.2 t/ha, as against 2.2 t/ha for M1-48 (Table 5). Interestingly all the IRRI varieties included in these trials, IR8, IR5, IR22, and IR24, were among the best yielding varieties under upland conditions.

Similarly during the 1970 wet season, IR8 and IR5 consistently outperformed M1-48 at three dates of seeding (Table 6). The crops seeded on July 10 and August 11 were damaged by two tropical storms which occurred during the reproductive and ripening stages. Nevertheless, the high yielding lowland

Table 5. Grain yield of upland rice. IRRI, 1969 wet season.

Variety or line	Yield (t/ha)	Duration (days)
IR5	5.2	134
IR442-2-58	4.6	121
IR8	4.3	121
IR24	4.2	122
IR661-1-170	4.1	120
IR22	4.0	120
IR773A1-36-2	3.8	120
IR667-142-2	3.7	116
M1-48	2.2	112

varieties outyielded M1-48 in two later seedings. During the 1970 wet season, the worst outbreak of blast disease since the beginning of our research program occurred. As a result, the blast-susceptible variety IR22, did not yield as well as it did during the 1969 wet season. Even under blast-free conditions, IR22 yielded 1 t/ha less than IR5 primarily because it had less vegetative growth.

Other indirect approaches have been attempted to compare varieties for drought resistance. For example, to test drought resistance in all leading Taiwanese varieties, Tsai and Tang (1969) used the resistance to potassium chlorate toxicity, the water absorption power of germinating seeds in 0.6 M manitol solution, the water-retaining capacity of excised plants, and the changes in the sugar content of seedlings before and after the drought treatment. Their results suggested that japonica varieties resist potassium chlorate toxicity more than do indicas. Tsai and Tang (1969) did not indicate whether the varieties they used were improved indicas like IR8 or IR5 or traditional indicas. We have found that tall indicas, like H 4, do not have as good a drought resistance as semidwarf indicas, like IR8 or IR5 (H. K. Krupp, S. K. De Datta, and S. N. Balaoing, *unpublished*). Therefore the general conclusion of Tsai and Tang (1969) suggesting that indicas have poorer drought resistance than japonicas is misleading. They conceded, however, that using the water-absorbing power of germinating seed is a better method than using the toxicity of potassium chlorate. Their results indicate that the germinating seed of indicas have better water-absorbing power than those of japonicas. It would be better to compare

Table 6. Grain yield of upland rice seeded on three different dates. IRRI, 1970 wet season.

Variety or line	Yield (t/ha) June 9	July 10	August 11	Duration (days)
IR8	5.5	3.0	2.8	118 to 127
IR841-67-1	5.7	3.0	2.6	114 to 120
IR5	4.8	2.9	2.7	125 to 135
IR22	3.4	2.1	2.1	112 to 127
M1-48	3.5	2.0	1.4	105 to 112

drought resistance between varieties with good and poor plant types than between indicas and japonicas.

Garg and Singh (1971) related high levels of ascorbic acid, ascorbigen, and ascorbic acid use in fresh rice leaves to high drought resistance. When IR8 and Taichung Native 1 were exposed to wilting treatments, more Taichung Native 1 plants survived than IR8 plants. Leaves of Taichung Native 1 plants had higher levels of ascorbic acid and ascorbigen than IR8 leaves. Since ascorbic acid seems to be important in the osmotic status of the cells and therefore somewhat related to drought tolerance in plants, Garg and Singh (1971) associated higher ascorbic acid content in Taichung Native 1 with higher drought tolerance. But they had no data on grain yield with which to evaluate the importance of the alleged lower drought resistance of IR8. Data from IRRI (A. M. Akhanda, *unpublished*) and from Peru (M. Nureña, J. Vélez, and K. Kawano, *unpublished*) did not show high drought resistance in Taichung Native 1.

These indirect methods of screening for drought resistance, should be tested under field conditions to determine their importance.

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Discussion: Varietal response to some factors affecting production of upland rice

D. J. McDonald: The "upland" environment is more variable than "lowland." It therefore seems essential that even greater emphasis be placed on selection for dynamic plant characteristics such as wide adaptability. Varieties are needed that will not only perform well in harsh conditions but will also respond vigorously to increasingly favorable environments at the same or different location. Selection for such dynamic characteristics should perhaps be given as much weight as selection for specific morphological features.

Summary of general discussion on improving upland rice

Open discussion on improving upland rice was led by A. C. McClung. The conferees agreed that any significant technological improvement of the crop could benefit upland rice which is grown on nearly one-fourth of the world rice area by small farms in Asia, Africa, and South America. On the other hand, the rice researchers also recognized the great diversity in soil types, soil moisture supply and retention, cultural practices, genetic variability, diseases and insects, and cropping systems from one region to another. The critical needs of upland varieties are drought resistance, a higher yield potential, pest resistance, and tolerance to problem soils. These basic problems are not well understood at present. One major question is the kind of plant type that will perform well under upland conditions.

The conferees urged that a task force of competent researchers drawn from varietal improvement, agronomy, soils, plant physiology, and plant protection be organized to begin studies on the basic problems in upland rice production. IRRI was named as one of the research organizations that could provide such expertise. Initial research can be conducted in relatively favored upland rice areas where technological improvements could be more readily accepted.

On the other hand, the variability in national problems and needs requires the active participation of national agencies in the different research phases. Any leading role taken by an international institution such as IRRI may encourage more vigorous national efforts. International collaboration is essential to create a broad genetic base of breeding material and to facilitate widespread testing of germ plasm and management practices.

Training rice breeders

Training rice breeders for the tropics

N. Parthasarathy (India) reviewed the research areas in training that could assist young rice breeders in the tropics in their professional activities. Because of the diversity in regional research needs and the diverse technical background of trainees, three types of training programs are proposed. The first would be an elementary type of a 2-year duration covering agricultural botany, rice culture, elementary genetics, practical breeding techniques, and techniques for identifying diseases and insects and for scoring varietal reactions to pests. The second would be an advanced program of 6-months duration on breeding procedures as related to quantitative characters, pest resistance, physiological traits, quality features, and biometrical techniques. The third would be a refresher course once in 5 years on recent advances in breeding methods and allied fields, with emphasis on the organization of coordinated national testing programs. Training materials need to be developed for each of the programs. Communication between the trainer and the trainees should be sustained by correspondence, research reports, and newsletters.

B. R. Jackson (Thailand) discussed the continuous process of training young rice breeders by frequent and close association at the operational level. While it is essential to provide the young workers with scientific principles and technical know-how, much of the improvements in the productivity of rice breeding programs will come from the devotion of the trainer's personal attention to research training needs of individual workers, stimulation of enthusiasm, a development of mutual respect between the trainer and trainees, the strengthening of team work, and frequent evaluation by group discussion. This approach is aimed at initiating changes in young researchers that would have a lasting effect on their research attitude and competence.

H. M. Beachell reviewed the IRRI training program in varietal improvement which has involved 68 trainees in 8 years. The majority of the trainees received practical training in various phases of rice breeding: planting breeding nurseries and yield trials, recording heading dates, making crosses, scoring disease reactions, making plant selections, and evaluating grain quality. The duration of training varies from 6 months to 2 years. Thirteen of the trainees completed M.S. degrees at the College of Agriculture, University of the Philippines. Another group of 10 persons stayed for different durations as research fellows. Beachell urged the conferees to comment on the desirability of continuing the 6- to 12-month in-service training as compared to more intensive workshop sessions of a shorter duration. The desire of some trainees to develop special projects of national interest while residing at IRRI was mentioned as a subject worthy of appraisal.

T. T. Chang reported on the two IRRI workshops on field experiments held in 1968 and 1971. Each included 20 persons and lasted for 6 to 8 weeks. The participants were either general rice agronomists with dual responsibility in breeding and agronomy or researchers with graduate degrees who lacked experience with the rice crop. The training program was designed to provide skill in tropical rice production; basic knowledge about the rice plant, its physiology, the diseases and insect pests, and rice breeding; the design, execution, analysis, and interpretation of field experiments; and the use of experimental tools and scientific instruments. Lecture notes and training materials in 10 categories were prepared on the basis of a set of specific objectives developed for each lecture or exercise. This type of short-term group training can cover a fairly large number of general rice agronomists who will continue to operate many experiment stations in the tropics in the years to come.

Summary of general discussion on training rice breeders for the tropics

Much of the general discussion on training rice breeders led by D. S. Athwal revolved around the training programs of IRRI, CIMMYT, CIAT, and U.S. rice stations affiliated with state universities. The discussion focused on methods of training and assessment of their effectiveness. The consensus was that since universities in the advanced countries are now mainly concerned with research and instruction of a more theoretical nature, international centers such as CIMMYT and IRRI are gradually assuming greater responsibility for training plant breeders in practical aspects of plant breeding. The centers have various types of training programs such as 6-month to 12-month in-service training, thesis research and postdoctoral research fellowships.

Because of the great differences in the academic and professional background of trainees from different countries, the scientists in charge of training programs agreed that there is no easy way to formulate standard training programs that will meet all requirements. Some felt that additional staff should be provided to look after the special needs of the trainees. The conferees agreed that for generalized training in plant breeding, it is essential for trainees to receive broad training in related fields such as production skills, agronomy, plant pathology, and entomology. The trainees should participate in every operational phase of the breeding program including varietal or agronomic testing on farms and seed production. Instruction in basic aspects of genetics, crop physiology and statistics should be provided whenever the situation permits. Occasionally, intensive training in 2- to 3-month workshop sessions for a relatively large group might be advantageous.

The tendency of trainees to request and to develop research projects of their own was discussed. The conferees felt that while this idea may have merit, it is generally not feasible for short-term trainees or for the less qualified ones to carry out research projects without sacrificing the real objectives of practical training. On the other hand, the international centers should expand their collaboration with universities in providing Ph.D. candidates with opportunities to conduct thesis research at the centers.

The need to evaluate and select top quality candidates for advanced training was stressed by the participants. One approach of proven merit is to select among those workers who have had short-term training and have shown good performance at their home stations. The candidates should have demonstrated research leadership. It was also considered more desirable to place students at a university that has faculty members who can provide the trainee with adequate personal guidance rather than to select a university because of its name or size.

Discussions of international cooperation

Reports of three discussion groups

VARIETY RELEASE AND BREEDING METHODS

At the discussion on variety release, it was suggested that varieties to be named and released should be first tested and evaluated by workers in several related disciplines. The promising selections should be evaluated at many locations and in several countries and before release they should be widely tested in farmers' fields. At the time lines are entered in tests in farmers' fields, increase of breeders seed should begin. Cultural practices for farm production should be considered when making the recommendation. The new variety should be superior in at least one characteristic and equal to the variety it will replace in other characteristics. Varieties should be thoroughly evaluated for disease and insect reactions and cooking behavior before release.

In the Philippines, 2-year regional yield trials are required before a variety is released. The Philippine Seed Board is the release committee and consists of heads of cooperating agencies, technical personnel, and extension workers. IRRI names varieties from time to time, but only after they have proved to be superior at many sites in different countries. So far all varieties named by IRRI have been officially recommended by the Philippine Seed Board.

The discussion about breeding methods centered on the production of a composite consisting of modified bulk hybrid populations provided by participating countries. It was suggested that only the best one or two modified bulk populations from each country be considered and not merely any F_2 or F_3 bulk population.

The possibility of using a chemical gametocide to induce male sterility to increase recombination was suggested, but its usefulness requires investigation. Also, the possibilities of intercrossing various hybrid combinations for the international composite were discussed.

It was agreed that the objectives of each bulk population should be carefully investigated before it is entered in the international composite program. IRRI should serve as the coordinating agency in forming the bulk populations and in distributing the seeds.

Proposals concerning international yield trials were also explored. The experience of wheat breeders in conducting the International Wheat Yield Tests were particularly helpful:

1. Participating countries are free to reselect or directly use any material entered in the trials, but must give credit to the country of origin.
2. Initially, many of the yield tests failed but improvement in caring for the material was rapidly made.
3. Entries are increased at CIMMYT, packaged and shipped to participating countries. The material is also useful in the CIMMYT training program for practice in roguing off-types.

The censensus was that an international yield test for rice should begin with a small number of entries from each participating country. IRRI should coordinate and make the seed increase, and package and distribute the seed. Most breeders attending the meeting indicated a willingness to participate. They were requested to submit seed of the entries at least 5 to 6 months before the material is to be distributed.

H. M. BEACHELL, *chairman*
B. R. JACKSON, *secretary*

COOPERATIVE TESTING ON DISEASES AND INSECTS

The group favored beginning international cooperative testing of pest-resistant donors and breeding material from national and international rice improvement programs. The complexity of the variation in the pathogens and in the insects, the narrow germ plasm base of the new varieties, and the breeding system in rice—all make implementation of this program urgent.

Knowledge of three major diseases and three groups of insects is sufficient to provide a base for an accelerated and integrated program. The diseases are blast, bacterial leaf blight, and tungro; the insect groups are stemborers, leafhoppers and planthoppers, and gall midge. No existing program is strong in all these areas. The group agreed to start cooperative testing in 1972. The following guidelines were established:

—For each major objective in insect- or disease-resistance, local varieties and experimental lines with proven resistance should be assembled by the coordinator for cooperative testing.

—The coordinator designated for each screening test (see table) will contact various national programs and assemble materials worthy of testing, distribute

Proposed programs for coordinated international screening of pests and diseases.

Disease/insect	Composition of materials	Possible test locations	Approximate no. of entries	Coordinator
Blast	Donors and resistant selections	Philippines, Indonesia, India, Korea, Thailand, Colombia, Guyana, Nigeria	500	S. H. Ou
Bacterial leaf blight	Donors and resistant selections	Philippines, India, Thailand, Indonesia, Ceylon	500	H. E. Kauffman
Tungro virus	Donors and selections	IRRI, India, Indonesia, Thailand	100	K. C. Ling
Stemborers	Donors	Philippines, India, Indonesia, Pakistan, Ceylon, Thailand, Nigeria	50	M. D. Pathak
Gall midge	Donors and selections	India, Thailand, Ceylon, Indonesia	50	S. V. S. Shastry
Planthoppers and leafhoppers	Donors	Philippines, India, Ceylon, Korea, Thailand	50	M. D. Pathak

the material, formulate the screening procedures, process the data, and prepare reports to be made available to all cooperators.

—The cooperators, while permitted to further select and improve any materials in the test, are obligated to acknowledge the source of materials so used.

S. V. S. SHASTRY, *chairman*
G. S. KHUSH, *secretary*

GERM PLASM CONSERVATION AND UTILIZATION

Reports from representatives of several nations indicate that encouraging progress is being made in collecting, conserving, and using rice germ plasm especially in India, Nepal, and Pakistan. Nevertheless, much remains to be done to complete national and international germ plasm banks.

The discussion group felt that completion of national and international germ plasm banks is urgent. Therefore, they recommend the following resolution for the consideration and approval of the participants in the symposium.

INTERNATIONAL RICE COLLECTION AND EVALUATION

Recommendations

The nearly 100 rice researchers from more than 20 rice growing countries participating in the rice breeding symposium at IRRI, September 6-10, 1971, urge vastly accelerated efforts to collect seed of rice varieties and semi-wild forms from all rice-growing countries in the world.

The disappearance of the world's rice germ plasm has reached the crisis stage. All possible local sources of potentially valuable germ plasm must be systematically collected soon; otherwise they may be lost forever. In many areas, new improved varieties are rapidly replacing the native varieties. The adoption of one improved variety in a major growing area often results in the disappearance of dozens of varieties from farms in a short period. The need for field collection is especially urgent in areas where the indigenous genetic diversity is rich and where few or no surveys have been made to date.

Even the relatively limited number of varieties in existing collections has enabled scientists to identify examples of extremely valuable germ plasm by extensive screening. For example, the varieties Tetep and Tadukan which appear to be the most important sources of resistance to blast disease now available, and the wild species *Oryza nivara* which is the only known source of resistance to the grassy stunt virus. Such materials are available because of the foresight of workers who collected and maintained these and other varieties and types.

Although perhaps 20,000 varieties already are available in collections at IRRI and in India, U.S.A., Japan, Taiwan, and elsewhere, much work remains to be done. All present and future collections should be consolidated and stored at a minimum of one international center such as IRRI. This germ plasm should be described, evaluated, and maintained so that it is readily available to all rice scientists for the benefit of mankind.

Each country that has not already done so should send IRRI seed of all entries in currently existing national collections to insure against possible loss.

An expanded and systematically organized comprehensive international collection bank of germ plasm would be expected to provide sources of 1) better disease and insect resistance; 2) increased adaptation to varied environmental conditions such as low temperatures, deep water, drought, alkaline, acid or saline soils, as well as elementary toxicity or deficiency; 3) variations in inherent protein content of grain and nutritional quality; 4) desired differences in maturity; 5) differences in morpho-agronomic characters including those which may eventually become of economic significance; 6) other traits which may be identified as of significance in the future when such needs arise.

Natural or artificial mutations which appear to have significance also should be preserved.

Types of assistance that can be made available to help in organizing the work and making collections include funds for collecting, processing and shipping the samples to a central location for processing and permanent storage; consolidation and documentation of all information that is currently available; technical assistance to adequately train collection teams, probably at two or more locations; a brochure to provide guidelines in various aspects of collecting, classifying, evaluating, cataloging, packaging, and mailing to international centers for permanent storage.

We recommend that the primary responsibility for the coordination of these procedures be given to IRRI. We also recommend that funds from various supporting agencies be pooled insofar as possible and be made available to IRRI for providing the necessary services. These funds would be used as needed for local functions of the program at IRRI including screening, processing, and mailing samples, and other expenses, as well as for travel involved in training collection teams and in processing and mailing samples from national centers to the international collection centers.

Drafting Committee:
T. H. JOHNSTON
S. OKABE
S. D. SHARMA
R. I. JACKSON, *chairman*
Sept. 10, 1971

The discussion group urged that a brochure covering the technical aspects of collecting should be completed and made available as soon as possible. The brochure is being developed by the technical committee of the International Rice Collection and Evaluation Project (IRCEP) under the chairmanship of T. T. Chang.

To develop operational and financial aspects of the collection program in Asia, a meeting of IRCEP was held. The major areas of discussion were reported by R. B. Casady (chairman): 1) Collection and evaluation of schedules in various countries for implementation. 2) The role of special foreign currency programs of USDA in rice germ plasm conservation and use. 3) Other sources of funds that might be mobilized for the IRCEP activities. 4) Appraisal of future needs in training of personnel and seed storage facilities for national centers; establishment of working collections and improvement of seed exchange to meet regional requirements; improvement of long-term seed storage facilities at selected international centers for preservation of entire germ plasm; cataloging and documentation of collected samples; and standardization of operational procedures for evaluation and preservation.

The participants in the IRCEP meeting urged the IRRI to strengthen its role in coordinating the activities of the IRCEP.

T. T. CHANG, *chairman*
R. D. LANE, *secretary*

Summary of general discussion on international co-operation

On behalf of IRRI, A. C. McClung agreed to the proposal that IRRI coordinate the international variety yield trials at selected locations. The distribution of bulk populations would be started at a later date. Discussion brought out that international exchange of breeding lines and new varieties could be facilitated at the governmental level if the seed exchange becomes a routine part of an internationally recognized project.

The conferees recommended that the testing of promising selections in farmers' fields before release be encouraged, although the operational aspects in national programs may vary from one country to another. Providing the cooperating farmers with guidance on required cultural practices is an important phase of such a testing program.

On the proposed coordinated program for international pest and disease screening, the participating countries and agencies could be later expanded to meet the need. Each cooperator will submit an annual report to the appropriate coordinator who will summarize the data and make the information available to all interested parties. Report of visits by foreign cooperators should also be sent to the coordinator.

The conferees discussed and adopted the draft recommendations on international rice collection and evaluation in which IRRI is urged to assist national agencies in the collection, storage, systematic evaluation, and seed exchange of rice varieties. IRRI may also assist by pooling resources from various international agencies and by coordinating some of the operational functions. A position paper on rice germ plasm preservation will be prepared by T. T. Chang of IRRI to outline the present status and future needs at a crop germ plasm meeting sponsored by The Rockefeller Foundation. IRRI will need financial support to implement some of the added functions and sources. Discussion also brought out the point that IRRI needs to communicate with top national leaders in agriculture to draw their attention to the importance of genetic conservation. Assistance from FAO may be sought to encourage governmental support for such international activities.

To provide continuity in these international projects, program coordinators and national leaders in rice improvement should meet periodically to assess progress and to plan new activities. Besides the annual rice research conferences of IRRI, a small number of rice breeders may meet every few years at different locations to discuss and review such matters in depth.

Concluding survey

Prospects for the future

Lewis M. Roberts

This symposium on rice breeding has been an important and fruitful event. The papers match the standard of excellence established by the papers in the five previous symposia proceedings published by IRRI, which have stimulated international collaboration and are exceedingly valuable as current references in their respective fields. The ideas and views presented in this symposium will be equally valuable to all those interested in the improvement of rice, which vies with wheat as man's principal food crop. It is gratifying that this symposium includes several outstanding wheat breeders, because rice and wheat researchers have much information of mutual benefit to exchange.

The task I have been invited to undertake – to summarize the main points of this symposium – is a formidable one. Information and ideas of great interest and importance have been exchanged in both the formal papers and the thoughtful discussions that ensued.

I do not propose to make a systematic summary of the presentations. We have been given a good picture of the sequential steps that have been taken to improve the yields of the rice plant in the world's principal rice-producing countries and regions from the first scientific efforts at the turn of the century until the present time. Progress was steady but slow until about 10 years ago. During the past decade, this situation has changed rapidly and dramatically. Undoubtedly one of the major factors that helped bring about this change was the creation of IRRI in 1960.

IRRI provided something new that was greatly needed: a truly international institution to which rice workers in all disciplines, wherever they might be located, could relate and through which they could unite their efforts in a global network for the improvement of this crop. It was gratifying to me, as an outsider, to hear about the progress that is now being made in several of the national rice programs in different regions of the world. It is gratifying, too, to hear how these programs are drawing closer together in the international network of collaborative efforts. I am confident that this trend toward co-operation and exchange is destined to accelerate in the future.

One of the most important recent changes in rice improvement was the idea that instead of improving the varieties already in use, breeders would design a radically different plant. Building on progress achieved previously, such as the identification of a potent recessive gene from Taiwan that produces semi-dwarfness, rice researchers, especially those at IRRI, conceived of raising rice

Lewis M. Roberts. The Rockefeller Foundation, New York.

yields not by 10, 20, or even 30 percent, but by 100 or 200 percent. This entailed breeding new, short, stiff-strawed varieties adapted to tropical conditions, responsive to high rates of nitrogen fertilizer, and having a high degree of insensitivity to photoperiod. It also meant developing a complete new set of cultural practices that would enable the new varieties to come closer to attaining their genetic potential than was ever possible with the old traditional varieties. Fortunately a good stockpile of knowledge about physiology of the rice plant had been built up, especially by Japanese scientists, so that the rice breeders had a fairly good idea of the type of plant morphology and architecture that would be the most efficient under intensified cultural conditions.

The development of high yielding varieties and appropriate technology marked the beginning of a new era in rice improvement, and it set off a whole series of chain reactions, whose results we know from previous accounts and from accounts in this symposium. As exciting as all this has been, and as important as are the results achieved to date, this progress represents only a burst of acceleration along the road of rice improvement that began some distance back and has no visible end. The job of the plant breeder and his scientific colleagues never ends.

We have been given a clear and comprehensive picture of the current status of international cooperation in conserving and evaluating rice germ plasm resources. The germ plasm of the 20-odd species of *Oryza* has been fairly well collected and is maintained at IRRI, where it is available to all rice workers. The IRRI germ plasm bank now contains approximately 14,000 accessions of cultivated rice, a few hundred selected IRRI breeding lines that have special merits, and about 1,000 additional accessions that include cultivated rice of Africa (*O. glaberrima*), wild species of *Oryza* and related genera, and genetic stocks and mutants. Somewhat smaller collections are maintained in Japan and in the U.S. India has a larger total number of indigenous samples which are maintained at several centers. Most of the varieties in the IRRI collection have been described, and a varietal catalog of 8,000 accessions has been printed. Various research departments of IRRI have systematically screened thousands of varieties in the collection for desired traits, such as resistance to the major diseases and insects, as well as for protein and lysine contents and other characteristics.

With the rapid spread of the new improved varieties, the job of collecting the germ plasm in areas where there are still voids must be completed as soon as possible. It is equally important that steps be taken to ensure safe, long-term preservation of the world collection of rice germ plasm and at the same time to assure ready accessibility of this material to the growing body of rice scientists. The IRRI collection represents a gold mine of genetic resources for rice workers throughout the world; the contribution it has already made in furthering international collaboration to improve rice on a global scale has been great, and it will doubtless become even greater as time goes on.

I should like now to mention briefly a few points that to me seem important as I try to place myself in the position of a rice researcher dealing with the question, "Where should we go from here?"

PLANT TYPE

Present evidence indicates that the new semidwarf varieties approximate, if they do not fully achieve, the ideal plant type for both irrigated and rainfed conditions. We have heard that this type of plant crossed to deep-water varieties may also contribute to the improvement of rice grown under deep-water conditions—those varieties cultivated in 50 to 300 cm of flood water. Whether the new semidwarf varieties—with all of their other attributes such as short, erect, dark green leaves, insensitivity to length of day, moderate grain dormancy, and heavy tillering capacity—represent an optimum plant type for all or almost all ecological conditions, as some claim, is still to be definitely determined. It seems, however, that the cream has been skimmed from this avenue of research and that the future breakthroughs in the improvement of rice yields and in ensuring their protection will come from other directions.

IMPROVING PHYSIOLOGICAL EFFICIENCY

Breeding for increased physiological efficiency within the plant appears to offer one of the best prospects for raising yields further. To state this simply in the form of a question, we might ask, "Now that a new, efficiently designed factory has been built, what can scientists do to increase the efficiency of the production line within the factory?" Here the rice breeders must work hand-in-glove with not only the plant physiologists in particular but also with the soil chemists, biochemists, and others. This is a complex area for it involves interrelated physiological processes about which, in most instances, we still know relatively little—such things as efficiency of water and nutrient uptake from the soil, photosynthetic efficiency, reduced respiration rates, transportation and deposition of the photosynthates in the grain, etc. We do know that among varieties or genotypes there are differences in [illegible] physiological efficiency that appear to be genetically conditioned or controlled. This presents the breeder with opportunities for raising yields to even higher levels than those achieved through the creation of the more efficient plant type of the semidwarf varieties. Progress in breeding for physiological efficiency is likely to be slow. We should not expect dramatic breakthroughs from this line of research comparable to that which came from altering the plant type. The potential for substantial progress over a rather long period does seem to be great, however.

IMPROVING THE QUALITY AND QUANTITY OF RICE PROTEINS

Cereal grains account for about half of the total protein in the human diet and this is not likely to change appreciably during the next 25 years. Rice certainly provides a large portion of the protein supplied by all cereals yearly for human consumption. Virtually all of the 243 million tons of rice (the approximate current annual world production) is used directly for human food. Just think what it would mean to that half of the world's population that depends on rice as the basic food if the protein content in all this rice could be raised by even one or two percentage points — say, from the current estimated average of 8 percent to 9 or 10 percent. There are good indications that this can be done. In the screening of IRRI's world collection of rice varieties and promising lines, researchers have found a few that have up to 30 percent higher protein content than IR8. These high-protein varieties have been crossed with IR8, and promising lines crossed with a broad sample of breeding material. Preliminary results from these crosses indicate that it should be possible to develop new high-yielding varieties with 20 to 25 percent more protein than IR8.

Attention is also being focused on obtaining a better balance of the essential amino acids that constitute the protein fraction of rice, although this balance is already generally better in rice than in most cereal grains. If, paralleling the quantitative increase in rice protein, the quality of this protein could be maintained, some 1.5 billion people would benefit enormously from better nutrition. What a challenge this is for the rice researchers! The prospects for success are bright and the potential payoff on investments in this field of research are so enormous that an acceleration of the present efforts would seem highly justified.

To touch on a slightly different, but also very important, aspect of the improvement of rice quality, rice breeders in general accept as axiomatic that new varieties must be acceptable from the standpoints of consumer preference and cooking and eating characteristics.

PLANT PROTECTION: PROTECTING THE GAINS

Plant diseases and insect pests take a high toll of the production of all crops, including rice. Often diseases and insects are the limiting factors in the production equation. Potential gains from the use of new, high-yielding varieties plus improved cultural practices are impossible to realize in such cases unless adequate control of these enemies can be achieved through application of chemicals or use of resistant varieties.

Papers published here summarize present knowledge concerning the principal diseases and pests of rice. I shall not attempt to give a resume of all the information on these topics that was presented. I shall simply make a few general statements based on the impressions I have gained.

No other cereal crop is threatened by a greater array of major diseases and insects than rice. Among the major diseases are blast, bacterial leaf blight, tungro virus, and sheath blight. The more important insect pests include several stem borers, the green leafhopper, the brown planthopper, and gall midge. Several other diseases and insects which until now have been of less importance might become serious problems with more intensive cultivation of rice. The control of diseases and insects apparently presents rice researchers with the most important challenge now facing them, and this probably will continue to be so for years to come. There are several reasons for making this statement.

Shifting from the traditional rice production systems to new ones is conducive not only to much higher yields but also to a much greater increase in the incidence of pathogens and pests. The use of improved plant-type varieties with short stature, many leaves per unit of area, high tillering capacity, plus an increasing use of higher amounts of nitrogen, creates a micro-environment within the rice field that tends to favor the rapid multiplication of many important diseases and insects.

With the spread of the new photoperiod-insensitive varieties and increasing access to irrigation facilities, larger and larger areas are being devoted to continuous cropping with rice, producing two and sometimes more crops on the same plot of land in a year. Continuous cropping greatly increases the likelihood of large-scale build-up of insect populations and inoculum of disease organisms, especially the viruses and their vectors, but also other pathogens such as blast, bacterial leaf blight, and other pests The tropical climate where rice is mainly grown is, moreover, conducive to the year-round proliferation of diseases and pests.

The new semidwarf varieties are probably no more susceptible, on the whole, to the major pathogens and pests than the traditional varieties they are replacing. Nevertheless, the rapid adoption of a small number of varieties has resulted in large areas being planted to a few genotypes, thus increasing the vulnerability of this crop to its enemies. This potential weakness fortunately is being overcome with the release of several new improved varieties.

The recent serious outbreaks of the tungro virus in the Philippines were probably intensified by continuous cropping of rice throughout the year and by the widespread use of a few susceptible varieties. The apparent intensification of disease and insect problems is primarily due to micro-environments which are now more favorable to these enemies within the rice paddies.

Much emphasis is now being given by IRRI and by many of the national rice programs in the international collaborative network to breeding for disease and insect resistance. We have heard here of the results achieved thus far in the attempt to identify sources of resistance to many of the major diseases and pests and the incorporation of these genes for resistance into new varieties with improved plant type and other desirable characteristics. As an example, IRRI for several years has coordinated an international uniform blast nursery in many countries. Evaluation of uniform sets of samples in many areas and environments has identified certain varieties that have broad resistance, such as Tetep and Carreon. It would now be advantageous to expand this pattern of international blast nurseries to include advanced breeding lines and to undertake similar activities to test for resistance to other important diseases such as bacterial leaf blight and tungro virus, as well as to major insects.

We cannot overemphasize the need to strengthen constant cooperation of breeders, geneticists, pathologists, and entomologists in a tightly knit team approach in order to solve the disease and insect problems of rice. This cooperation, in which each team number has defined areas of responsibility and all have a common goal, is a prerequisite to successful realization of plant protection.

These diseases and insect pests are constantly developing new mutants or races, and the job of combating them is never finished. Combined use of genetic resistance and chemical means will be required to stay ahead of these shifty enemies. Fortunately a growing number of well-trained rice scientists are now collaborating internationally to deal with disease and insect problems. This group did not exist a few years ago. They should receive the support required to carry out their task. The risks are too high for us to neglect taking out the maximum insurance coverage possible in this way to protect the outstanding gains in increasing rice yields that are being achieved on other research fronts.

IMPROVING UPLAND RICE

Upland rice production has been largely neglected until now, and I can certainly understand why. Irrigated rice accounts for most of the world's rice production, but probably about half of the total rice area of 130 million hectares is produced as rainfed (rainwater impounded with bunds) or upland rice (no impoundment). In terms of world rice production, it is only logical that the initial emphasis be placed on increasing yields of irrigated rice because of its preponderance in total production. Admittedly, there is still a lot of unfinished business to take care of in the sector of irrigated rice.

The time seems propitious, however, to start giving attention to improving upland rice production, and it is good to see that the rice specialists are beginning to think and act. Progress in this sector will undoubtedly be harder and slower than in irrigated rice. Many difficulties are involved, but there is a need now to get on with this job and it is heartening to see that the international corps of rice scientists is starting to wrestle with these problems. I am confident that we can expect some very fruitful results from these efforts.

Two special problems in rice breeding—deep-water rice and rice that exhibits tolerance to cool temperatures—were discussed. The total area of deep-water rice is about 8 million hectares, which represents around 6 percent of the world's total area devoted to rice. We heard the results of the experiments being conducted by the rice improvement program in Thailand in collaboration with IRRI, in which the desirable traits of the new semidwarf varieties are being transferred into floating varieties of rice that survive in flood water as much as a meter or more deep. In the panel discussion on tolerance to cool temperatures, we heard about work under way to increase cold resistance of the rice plant at different stages of its growth in temperate or subtropical regions. Both of these developments forcefully call to our attention the extent of the genetic variability and biological plasticity that exists in the genus *Oryza*.

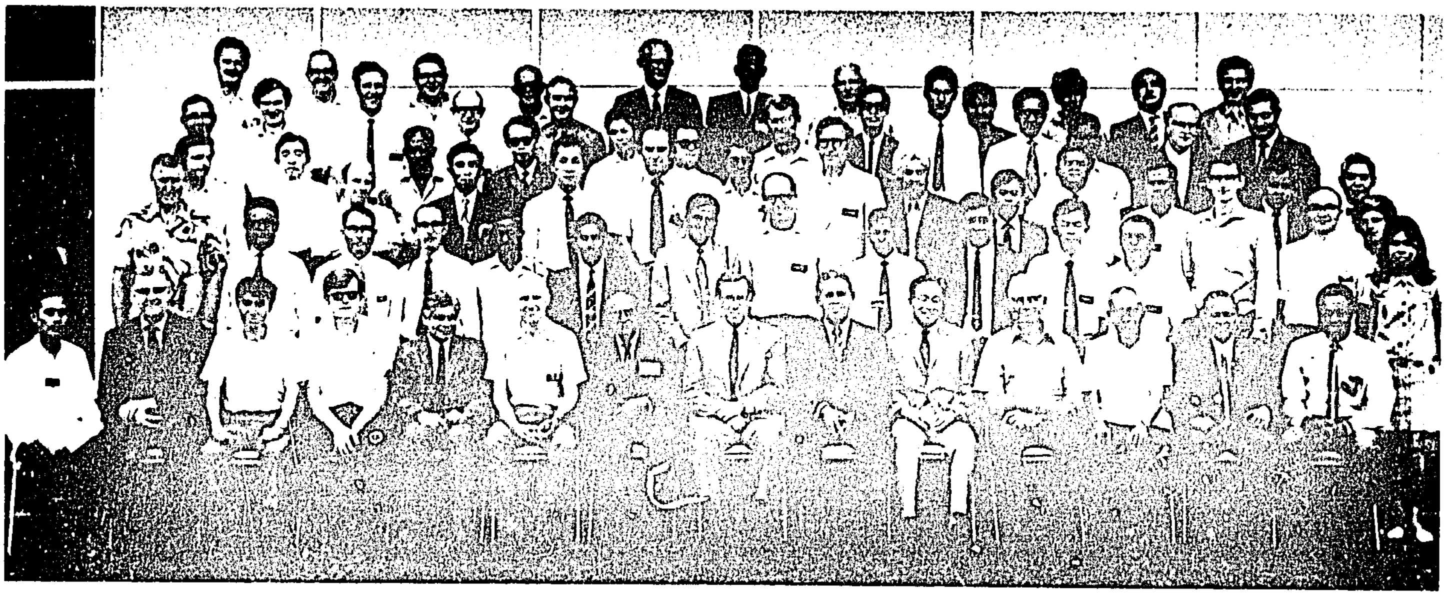
The potentialities of mutation genetics in breeding improved rices and the outlook for hybrid rice were special features of the discussion of breeding methods. It seemed to me that there was a fairly strong consensus that the prospects for achieving significant positive results from either of these two approaches in the short run appear to be somewhat unpromising and that, in terms of allocation of research efforts and resources, they should be given a rather low priority in relation to other breeding methods and problems.

The panel discussion on training rice breeders for the tropics underscored the importance of increasing the number of adequately trained young scientists.

PROSPECTS FOR THE FUTURE

The discussion brought out many cf the requirements that will prepare the young researchers for added responsibilities in the network of interdisciplinary and international collaboration.

This brief overview by no means pretends to be a comprehensive summary of all the important points that were taken up at this symposium. I have simply tried to outline a few striking trends in rice improvement in recent years and to spotlight some of the less dramatic but nonetheless vital fields of inquiry that may hold promise for the future.



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Index

*Chapter

CORRECTIONS

p. 5 last two lines. Should read:

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p. 11. line 3. Change Asahi x T812 to:

Norin 6 x T812

p. 21. line 1. Change H5 to:

H4

p. 22. line 20. Change pubescene to:

pubescence

p. 40. line 32. Should read:

about 20 to 22 cm long. The milled rice is medium in length and bold in shape.

p. 138. line 13. Change IR8 to:

IR8-246

p. 153. line 5. Change Z.M.H. Zaman to:

S.M.H. Zaman

p. 182. line 3. Change A few unimproved to:

A few thousand unimproved

p. 190. Table 2. last line. Change 6730 to:

6630

p. 190. line 8. Change 6,730 varieties to:

6,630 varieties

p. 203. Under INTRODUCTION. line 3. Delete:

or wild species

p. 204. Table 1B. Add line below line beginning *Av-z:*

Av-zt Av Av Av Av Av Av Av

p. 207. Caption fig. 1. line 5. Change *lm:* late maturity; to:

Lm: late maturity;

p. 216. Fifth line from bottom. Change *Pi-k* and *Pi-ta* or similar genes to:

Pi-k and *Pi-ta,* respectively, or similar genes.

p. 217. line 25. Change Norin 29 (*Pi-a*$^+$) x Kusabue to:

Norin 29 (*Pi-k*$^+$) x Kusabue

p. 358. Table 2. Under "Variety." Change RP 6-12, RP 6-13, RP 6-15 to:

RPW 6-12
RPW 6-13
RPW 6-15

p. 359. line 17. Change RP 6-13, to:

RPW 6-13

p. 359. lines 26 and 27. Change like W 12708 and RP-13, CR57-29 fine-grained, to:

like W 12708, RPW 6-13, and CR 57-29, and fine-grained,

p. 360. line 27. Change ***l-GM 1*** to:

I-GM 1

p. 360. Third line from bottom. Change C P. Yadara to:

C. P. Yadava

p. 361. line 4. Change C. P. Yadana to:

C. P. Yadava

p. 362. line 19. Change RP 6-13, RP 6-15, to:

RPW 6-13, RPW 6-15,

p. 440. line 30. Change Among adapted genotypes to:

Among widely adapted genotypes

p. 447. fig. 8. The broken lines should be labelled T36 and the solid lines should be labelled S18.

p. 473. line 13 from bottom. Change of rice leaves in equations (1) and (2) to:

of rice leaves as shown in equations (1) and (2)

p. 535. Second line from bottom. Change Davis to:

Biggs

p. 601. line 5. Change The use of additional lines to:

The use of addition lines

p. 646. line 23. Change clay soil to:

clay loam soil

p. 660. line 25. Change Maahas clay to:

Maahas clay loam