Rice Improvement

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Contents

Foreword

THE GREEN REVOLUTION IN THE TROPICS was sparked by the development in the 1960s of high-yielding, lodging-resistant, and fertilizer-responsive rice varieties. The new biological entities became the focal point of new production technologies that now provide farmers in the tropics with yield and production potentials equal to those of their counterparts in the temperate zones.

The earliest of the new varieties stimulated increased emphasis on plant breeding as a means of rice improvement — and even of overall agricultural development. Simultaneously, the early varieties called attention to the need for interdisciplinary research to develop improved rices. To be successful, the new cultivars needed resistance to insects and diseases, tolerance for adverse soil and weather conditions, and grain quality suitable for local tastes. In each case, plant breeders combined forces with scientists in other disciplines to genetically incorporate the desired traits into the new varieties.

In the early 1960s only a few well-trained scientists concentrated on tropical rice breeding. Their efforts were hampered by inadequacies both of financial support and of collaboration with scientists from other disciplines. The coming of the modern rices changed that situation. Today, an increasing number of young plant breeders are involved in rice improvement programs throughout the tropics. They want to collaborate with scientists in other disciplines, not only in their own countries but also internationally. They seek information that will help them achieve their goals. A primary objective of this book is to provide such information.

The authors of *Rice Improvement* have written an excellent practical manual for scientists to consult on each step in the development of improved rice varieties. The book is not an academic exercise with references and literature citations, but is based largely on the practical experience of the authors and their collaborators in many tropical countries.

As the title indicates, *Rice Improvement* is broader than plant breeding. Without the help of plant pathologists, entomologists, agronomists, and scientists from other disciplines, rice breeders cannot develop the wide range of improved varieties needed by hundreds of millions of small-scale cultivators in Asia, Africa, and Latin America. The authors have followed that interdisciplinary concept in writing the book.

The first chapters of *Rice Improvement* stress the basic philosophy of problem-oriented rice improvement, specific breeding methods, and field operational procedures such as land preparation, planting methods,

and the implementation of yield trials. But most of the book is oriented to breeding methodologies — step-by-step descriptions of how to select, cross, and screen for important agronomic and grain characters, and for resistance to specific insects and diseases, and tolerance for adverse environmental conditions such as drought, adverse soils, and extreme temperature.

The authors bring into this book their extensive experience both in rice improvement and in international agricultural development.

Dr. Peter Jennings, the senior author, has worked in rice improvement with The Rockefeller Foundation for more than 20 years. After working on the Mexican and Colombian agricultural programs, Dr. Jennings came to IRRI in 1961 where he headed the plant breeding department until 1967. In the 7 years that followed he was head of the rice breeding program at the International Center for Tropical Agriculture (CIAT) in Colombia. Dr. Jennings now lives in Costa Rica where he serves as CIAT's regional rice coordinator for Central America and the Caribbean.

Dr. W. R. Coffman, IRRI plant breeder, came to IRRI in 1971 after working with oats, wheat, and barley in the US, and with wheat at the International Center for Maize and Wheat Improvement (CIMMYT) in Mexico. He serves as chairman of the Operations Committee of IRRI's Genetic Evaluation and Utilization (GEU) program and is coordinator of the GEU Training Program.

Dr. Harold E. Kauffman, IRRI plant pathologist, is joint coordinator of the International Rice Testing Program (IRTP), a worldwide network through which interdisciplinary scientists systematically evaluate uniform nurseries of improved rices to select or develop varieties for diverse agroclimatic conditions. After working in agricultural development in Haiti, Dr. Kauffman joined the All India Coordinated Rice Improvement Project, Hyderabad, India in 1967. He came to IRRI in 1972. Dr. Kauffman has been instrumental in developing efficient screening techniques for resistance to bacterial diseases of rice. He has worked closely with plant breeders throughout his career.

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CHAPTER 1

Philosophy of breeding

SOCIETY SUPPORTS PLANT BREEDERS for only one purpose: to develop more productive varieties for farm use. Everything else is secondary to or supports that purpose. A scientist's success in developing improved rice varieties is directly proportional to his ability to accurately identify research priorities and to correctly orient his goals and activities.

Paradoxically, success is often hampered by the fact that the scientist in the tropics may be responsible to senior administrators who received postgraduate training in technologically advanced, temperate countries. Before the scientist can work unimpeded toward his objectives, he often must first convince his superiors to adapt their formal education to the realities and needs of tropical research programs.

University faculty members in the western nations advance in rank and prestige mainly by the number and quality of their publications and by the presentation of their research results to peer scientists in professional societies. Foreign students who study in the highly developed nations often adopt the same norms. When those students complete graduate study and return to work in tropical rice improvement programs, they must understand that the only realistic criterion of professional success is the degree to which they help increase national rice yields. Rice farmers and consumers around the world would benefit if all rice scientists insisted that they be judged by this criterion instead of by the number of publications written, conferences attended, or reports prepared.

Academic training in temperate areas may result in an inappropriate approach to rice breeding in the tropics. Because only one field crop per year is grown, the amount of instruction that neophyte plant breeders receive in graduate school in quantitative genetics, cytogenetics, and statistics is closely correlated with the severity and duration of the winter season when field work is impossible. Thus, graduate training is often an exercise in applied and theoretical genetics, leavened with exposure to plant pathology and a smattering of other courses. The thesis research of the foreign plant breeding student usually involves the inheritance of a character in a crop other than rice. The situation is similar for graduate students of pathology, entomology, and other disciplines essential to rice improvement.

Universities in highly developed nations generally organize their graduate instruction and research on a disciplinary basis. The departments representing each discipline have limited cross-contact. Rarely do researchers from various disciplines cooperate on teams organized to attack problems that limit food production. Although total funds for instruction and research in the universities are enormous, individual breeding programs are often small. The impressive productivity of temperate agricultural research usually results from many small, cumulative advances made by many university programs. In such a situation, the failure of an individual program is of little consequence.

But rice improvement in the tropics, where rice may be grown year-round and farm yields are low, does not fit the western-temperate pattern. Advanced branches of genetics and statistics are not the essential tools needed to attack the interdisciplinary breeding problems related to soil abnormalities, diseases, insects, agronomic conditions, irrigation deficiencies, farm size, and mechanization. Research funds are scarce and a few programs must cover huge areas. One program's failure or lack of progress means catastrophe to masses of local people for whom rice means food.

Inadequate facilities, professional salaries, and, in some regions, labor, have been major institutional deterrents to successful rice breeding in the tropics, except in the International Rice Research Institute (IRRI). Research is expensive and national programs in the tropics seldom receive sufficient funds, so scientists must concentrate their limited resources on the most essential activities and facilities. They must also seek supplementary support from farmers, regional or national rice growers' associations, foundations, and other granting agencies.

Although scientists may occasionally circumvent inadequate experimental land by routinely selecting early generation materials on private farms (land and water supplied by the owner), this practice is seldom successful. Incomplete control of the plot areas can result in more problems than benefits. Similarly, it is self-defeating to finance parts of the research program by selling commercial or pure seed grown on the experiment station if the breeder or his work crew must spend time on seed production instead of breeding activities.

Regrettably, administrators often spend scarce funds in two areas of limited benefit to breeding programs. First, the size of many experiment stations far exceeds the needs of their research programs, resulting in additional expenses for activities such as weed control or in the maintenance of roads, canals, and fences. Thus, less money is left for research. Second, administrators may spend building- and farm-development funds on elaborate offices and laboratories that are of little critical value to scientists. In temperate countries, where administrators may learn about such facilities, they may be needed for the 5 or 6 winter months

when field work is impossible. Unfortunately, they may unnecessarily duplicate such facilities in the tropics. To counter the diversion of funds into elegant but nonproductive facilities rice scientists are obligated to let administrators know their critical program needs. All production scientists must understand that the struggle to eliminate hunger will be won or lost on experimental fields and on farms — not within laboratories.

The few indispensable facilities that a rice improvement program must justify, insist on, and obtain for successful field work include:

- at least 10 ha of land of suitable topography and soil type;
- a dependable water supply;
- power to prepare fields and plots;
- sufficient labor; and
- a vehicle to transport labor and materials to and from the fields.

Enclosed facilities that are essential for all programs are:

- a small greenhouse or screenhouse for crossing and for evaluation of insect and disease resistance;
- a large seed-preparation and work room;
- a drying area;
- a modest grain-quality laboratory; and
- a small air-conditioned (cold) room for seed storage.

Anything less than these two lists is inadequate and a great deal more is probably superflous.

In some programs within or bordering the tropics, scientists may plant only once per year because of climatic or irrigation limitations. In such situations, scientists should acquire either irrigation for a second crop or the flexibility to move their material and support staff to a more favorable site every other season. No program can afford to advance fewer than two generations per year.

THE NEED FOR AN INTERDISCIPLINARY APPROACH

The great variability of problems that limits rice production in the tropics obliges scientists in successful rice improvement programs to adopt an interdisciplinary team approach to finding solutions. A scientist cannot effectively function alone; he must insist that his research organization ignore its heritage of discipline or departmental organization and form teams of scientists to attack basic rice problems. Ideally, the cooperating workers are, first, rice production scientists and, second, breeders, pathologists, or agronomists. Experience shows that team members will accept a lowered professional identity if the goal is clearly understood to be increased rice yields and if advancement and salary reflect achievement of this goal rather than the number of publications or other irrelevant criteria of success. To meet the challenge of rice improvement, team members must define areas of responsibility, constantly discuss problems and progress, and frequently hold informal reviews.

Breeders must understand the problems of other rice scientists well enough to communicate with or organize effective teams of plant protectionists, agronomists, crop physiologists, soil scientists, extension specialists, agricultural engineers, and economists. Thus, the breeder must supplement his specialized academic training in breeding and genetics with field experience and study to gain a broad understanding of a range of breeding-related disciplines.

Similarly, scientists in other fields who intend to apply their skills and knowledge to rice improvement must adequately understand plant breeding. Although one cannot reasonably expect an agronomist or pathologist, for example, to pay allegiance first to breeding instead of to his own discipline, he must view his field as a component of a much greater overall effort — the art and science of rice improvement. He must realize that even though the factors that affect the growth and productivity of rice are categorized into disciplines, the whole is greater than the sum of its parts. Maximum achievements will come only when scientists ignore the limitations of their respective disciplines and blend their efforts toward the common goal of improving the rice plant.

THE FARMER AS A TEAM MEMBER

The farmer should be a member of every research team, but he is often neglected. The farmer's years of field experience often make him a source of much practical information. He can help scientists focus their objectives on problems that are not normally found in experimental plots.

But farmers must be convinced that research will benefit them, and they must have confidence in agricultural scientists and their work. Thus, it is important for the rice breeder to understand farming systems and problems related to the commercial planting of distinct varieties. Because farmers often find it difficult to evaluate small plots on research stations, conducting regional trials of elite materials directly on farms is one of the best means of communicating with them. This not only gives the research team additional information on genotype-environment interactions under farm conditions, but also provides sites for a series of field days during which neighboring farmers can evaluate potential new varieties and cultural practices.

The extraordinary advances in rice breeding in the tropics during the 1960's were directed toward and accepted by farmers in the more favored rice-producing areas. The new technology has been almost completely adopted in the fully irrigated, more fertile areas of both Asia and tropical America. The relatively low risk involved has stimulated farmers in those areas to invest in fertilizer, protective chemicals, and water control so that they now realize much of the high yielding potential of the new dwarf[1] varieties.

The varieties and agronomic technology that caused the spectacular

productivity gains in the favored areas were developed under immaculate experimental conditions that favored heavy rates of nitrogen application, precise water control, early transplanting of seedlings, and chemical control of weeds and pests. This methodology was largely responsible for the impressive contributions of research.

But we now recognize that more than half of the world's rice farmers grow rainfed rice and lack precise water control. The bulk of these farmers have not adopted the new high yielding varieties and accompanying technology because rainfed farming is risky and the excellent technology that has been so beneficial to favored farmers is not satisfactory or practicable.

Rice productivity will not be increased in rainfed areas, or in areas of other environmental stress, by making the farmers into experiment station operators or by accepting their traditional varieties and cultural practices as ideal. Instead, the task is to adapt breeding technology to the realities of the areas. But few scientists are presently modifying their programs to correspond to major environmental stresses and cultural practices that constrain yields on typical rainfed farms. This transition will be difficult for programs accustomed to aiming for 8- to 10-t/ha yields under ideal conditions.

SELECTION CRITERIA

It is presently impossible to define all of the selection practices required to produce improved varieties for less favored areas. Nevertheless, it is essential that programs expose their materials to severe selection pressures. Too often we control insects, diseases, and water stresses simply to dress up our plots, which reduces our ability to recognize the most resistant or tolerant segregants. For stressed areas, we need to combine greater resistance to a wider range of problems such as diseases, insects, cold, heat, deep water, and injurious soils.

One procedure that merits consideration is to alternate practices on succeeding generations of segregating material. In such a system scientists could handle every other generation as precisely and as carefully as they handle the high yielding dwarf varieties for favored areas. But the alternate generations would be exposed to stresses that are common in less favored regions. Such stresses could include greatly reduced application of nitrogen, some weed competition, delayed transplanting, no chemical control of pests, modified plant spacing, and irregular water control. Thus, the selection criteria would be modified and resulting varieties would have higher yield potential under typical rainfed conditions.

[1]Some workers reserve the designation *dwarf* for extremely short mutants of little or no breeding value, and prefer the term semidwarf for Taiwanese varieties and their derivatives. The short rices are referred to as dwarfs in this book, however, for the sake of simplicity, because their short stature is simply inherited, and because they are usually about half as tall as normal rices.

For example, modern dwarfs do not compete with weeds or yield satisfactorily when they are subjected to periodic shortages or excesses of water, late transplanting, or moderate fertilizer rates. Rainfed farmers require varieties that will withstand such stresses and still be about 1 m or slightly taller at maturity. But breeders usually discard such lines during selection because of their excessive height and lodging, which give problems when heavily fertilized under the ideal conditions of favored farms and of most experiment stations. In any case, the development of useful technology for the less favored rainfed and other stress areas demands closer cooperation between rice scientists and the two groups of workers that they most often neglect — the rainfed rice farmer, who ultimately adopts or rejects varieties, and the social scientist, who often knows what limits farm yields but who seldom successfully communicates this knowledge to members of the breeding team.

After several years of experience with rice in Asia and Latin America, the authors believe in several generally unappreciated theories related to the improvement of crops, including rice, within their centers of origin. The following correlative statements seem to characterize all major food and industrial crops:

- Yields are lowest within the centers of crop origin.
- Yield-limiting factors are most numerous and complex in the centers of crop origin.
- Resistance to changes in crop production methods is greatest in the centers of origin.
- The impact of any technology is least within the centers of crop origin.

Several biological and social factors explain these characterizations. One factor of great significance is that within their centers of origin, crops are subjected to intense pressures from pathogens and insects that evolved concurrently with their hosts. The number of important pests within areas of origin always exceeds that found in distant production areas. Another factor is that crop varieties that have developed through natural selection in their centers of origin are vegetatively large and vigorous and have great intra- and inter-specific competitive ability. Human improvement of their yield potential inevitably reduces competitive ability. Thus, when man plants improved varieties he must artificially control those yield restraints that were partially curbed by the natural defense mechanisms of unimproved, competitive varieties.

From these observations, the authors conclude that it is extremely difficult to improve rice within its center of origin in Southeast Asia and that a complex technological package is essential for progress. But the export of a portion of that package to Oceania, Europe, the Americas, or Africa may dramatically increase yields there. Conversely, the importation of specific technology from these areas into Southeast Asia is futile.

AIDS TO RICE IMPROVEMENT

The greatest single factor facilitating rice improvement is the extraordinary varietal diversity found within *Oryza sativa* and its close relatives. Wide variability is the cornerstone of successful varietal improvement programs. Some 35,000 varietal accessions are maintained at IRRI and additional collecting continues in geographical areas of special interest. A catalog of field and laboratory descriptions of many of the accessions is available to all rice workers. Few programs, however, can or should maintain even a small percentage of the collected varieties because of the enormous difficulties involved. Fortunately, breeders throughout the world who need seeds with specific characters can refer to the catalog and request them from IRRI. Workers in national breeding programs, at IRRI, and at the International Center for Tropical Agriculture (CIAT) have transferred many desirable characters into improved varieties and breeding lines. Scientists may obtain those rices either directly from the national programs or through the international centers.

The rapidly developing international linkages among programs are another major aid to rice improvement. The resources and expertise of IRRI are available to all programs, although special attention is paid to tropical Asia. CIAT's rice program interlocks with that of IRRI. CIAT serves as a regional research, training, and information center for Latin America. The International Institute of Tropical Agriculture (IITA) serves Africa.

IRRI's greatest service to rice workers continues to be its ability and willingness to undertake international activities that are economically or politically impossible for national programs to undertake;

- IRRI's maintenance of the world germplasm bank for rice, coordination of the International Rice Testing Program (IRTP), provision of literature in translation, and periodic working conferences are of inestimable value to rice scientists.
- National programs are increasingly linking their programs to those of the international centers and there is good country-to-country cooperation on problems of mutual interest. Through the international linkages it is now possible to comprehensively evaluate parent material and elite advanced lines on a regional basis. Such international evaluation is necessary for breeding success.

THE CHALLENGE

Rice improvement requires years of constant, hard, dirty work, with many failures and rare successes. Perhaps one cross in 500 or more results in a new variety, and tens of thousands of lines are evaluated and discarded for every one that reaches farmers' fields. There is no easy way to improve rice production; it demands patience, dedication, continuity, and total physical and mental commitment to field work. Successful rice

scientists live with their plants. Unsuccessful ones delegate hard work to assistants and seek physical comfort while writing progress reports and attending conferences.

Paradoxically, as the scientist gains experience and is recognized for his contributions, the opportunities and temptations increase to spend time away from his fields. The scientist must resist this tendency if he wishes to remain productive.

But the number of young people who dedicate their lives to the improvement of rice is increasing, despite physical demands, frustrations, and inadequate financial support. Such rice workers are uniquely able to contribute to the well-being of mankind through the improvement of the world's premier food crop. For them, the satisfaction of having their new varieties accepted by farmers and consumers compensates for any hardships.

CHAPTER 2

Breeding systems

THE GENERAL PROCEDURES, advantages, and drawbacks of bulk, pedigree, and backcross breeding systems are thoroughly described in standard plant breeding texts. We discuss their relative merits specifically for rice improvement programs.

COMPETITION AND BREEDING SYSTEMS

The intense interplant competition in early segregating generations is one of the most critical factors that affect the choice of breeding systems. Strong competition is most pronounced in tall × dwarf crosses and occurs whenever the two parents of a cross are morphologically distinct.

Most competition in rice is for light. Competition begins early in the tillering stage and increases in intensity proportionate to the increase in plant size and the density of planting. Competition for nitrogen may occur at later growth stages but is readily overcome by adding fertilizer. But adding nitrogen aggravates the competition for light because it induces tall plants to grow taller. Competition for light is also increased by close spacing, the length and intensity of the rainy season, weeds, and other factors that reduce the penetration of light into populations.

Competition is caused by differential growth rates and sizes of neighboring plants. Large plants invade the space occupied by smaller ones, shade the other plants, and capture a disproportionate share of tile solar radiation. The smaller plants have reduced tillering, produce weak and spindly culms, accumulate less dry matter, exhibit premature leaf senescence, and have pronounced spikelet sterility. In short, the smaller plants, when intermixed with larger ones, appear agronomically undesirable.

Studies with mixtures of pure varieties of contrasting plant types clearly illustrate the effects of competition. Plants of the smaller varieties, originally mixed in equal proportion with the larger ones, are rapidly reduced in number. In extreme cases, all weakly competitive varieties are eliminated from mixtures after two or three cycles of competition.

Similar studies in segregating progeny populations of crosses of distinct plant types are more directly related to breeding methodology. The monogenic inheritance of dwarfism dictates that 25% of the F_2 popula-

tion of a tall × dwarf cross is dwarf. In the absence of competition and assuming equal fitness for tall and dwarf segregates, the theoretical percentage of dwarfs in subsequent generations is easily calculated. Thus, without competition, the dwarfs would increase from 25% of the population in the F_2 to 48.5% in the F_6. But in experiments on the competition of dwarfs and talls, with high nitrogen rates and close spacing, the dwarfs declined from 25% in the F_2 to about 6% in the F_6. This deviation from the number of expected dwarfs is theoretically a direct measure of competition. Such losses are similar but less drastic within populations that receive low nitrogen rates, that are spaced widely, or that are grown in a clear, dry season. These studies as well as field observations clearly confirm the intense loss of small plants in widely segregating populations.

Competition and yield

The critical issue for rice breeders is the association of competitive ability with agronomic worth. Competition would be no problem in breeding if highly competitive varieties or individual plants were the most agronomically desirable, or if competitive ability were not related to agronomic worth. Unfortunately, it has been demonstrated repeatedly that competitive ability in rice is negatively correlated with agronomic value for areas with reasonable water control. Thus, the more competitive plants are the least valuable and the desirable ones are lost in competition.

Yield experiments with rices of known competitive ability invariably demonstrate that weak competitors yield more when grown in pure stands. This yield advantage increases with applied nitrogen, close spacing, and improved water and weed control. Strong competitors might yield better under primitive and severely limiting agronomic practices, but no variety will yield satisfactorily under such conditions.

This strong negative correlation contradicts some data on segregating populations of other small grains, which show increased yielding ability during long-term bulking. Apart from questions about how the yield data in these studies are presented, it is important not to confuse or equate competitive ability with selection for adaptive characters, which occurs in all breeding populations grown under environmental stresses such as low temperature or adverse soils. The two phenomena are superficially similar, but unrelated, components of natural selection. Only competitive ability is dependent on plant density.

Competition in single crosses

Because of the extreme variability in most single-cross F_2 populations, the identification and selection of desirable plants is difficult even in the absence of competition. The difficulty is increased by the added complication of the competition effect on desirable phenotypes, especially in tall

× dwarf crosses. If competition is allowed to continue unabated until grain maturity, the selection process becomes almost impossible in the F_2. Most desirable plants are shaded so badly that they are partially sterile or otherwise are so abnormal that those that survive appear worthless and are erroneously rejected.

Competition in backcrosses

Single backcrosses, or three-way crosses, to dwarf parents are often practiced when only one or two traits are sought from tall, leafy rices. The F_1 backcross plants, which are 50% dwarf, may be grown in a screenhouse at three to five plants to a pot. Although competition of F_2 single-cross populations in pots is not as severe as in the field, it can occur, making the dwarfs appear undesirable. Individually selected F_1 plants produce in the field F_2 families that are either homozygous dwarf or that segregate for height. The homogenous-dwarf F_2 families are not affected much by competition. But competition affects the families that segregate into talls and dwarfs in a 3:1 ratio as much as it affects F_2 populations of single crosses.

A solution to competition

The effects of competition can be reduced by using a wide F_2 plant spacing or by not applying nitrogen. Neither practice, however, is satisfactory. Both practices reduce the size of genetically tall plants, making it more difficult to identify and evaluate the desirable, shorter ones. Furthermore, wide spacing increases land requirements and weed infestation.

A simple, practical procedure exists to reduce competition in F_2 populations of single crosses and backcrosses, but it requires much labor. First, inspect the F_2 plots plant by plant when flowering begins and cut the tall phenotypes at the soil surface. If the culms are not cut below the water level, the plants will ratoon. Drop the cut plants between the rows. Make a second pass after all of the plants have flowered to eliminate the tall ones missed in the first cutting.

To eliminate the labor-intensive roguing of tall segregates, some programs concentrate on multiple crosses involving both tall and dwarf parents and on producing a large number of F_1 plants of the final cross combination. The resulting F_1 will have both tall and short phenotypes; only the latter are advanced to the F_2 in the field.

When plants are desired that are intermediate in height between dwarf and tall, this procedure becomes less satisfactory and requires close supervision by the plant breeder. Although intermediate-statured plants are considered more desirable than dwarfs for the vast rainfed regions where water control is poor, a good procedure for selecting such types has not been clearly defined.

BULK BREEDING

Rice breeders have used conventional bulk breeding in both tropical and temperate areas for decades. Despite its inherent advantages of simplicity and convenience, years of bulk breeding in tropical Asia have been uniformly unsuccessful and have resulted in no significant gains in national yields. In fact, dependence on bulk breeding may be responsible for much of the stagnancy of national yields in the tropics. Some japonica breeding programs have had modest success, however, using closely related and morphologically similar varieties that, when hybridized, compete minimally, allowing slow but steady advances.

Bulk breeding has produced no major advances in tropical rice productivity because scientists have generally been unaware of two basic principles of rice improvement:

1. the influence of plant morphology on yielding ability and the need to replace the predominantly tall, leafy phenotypes with more productive types, and
2. the deleterious effects of competition on segregating populations and the consequent loss of valuable segregates.

Desirable plant types with high yield potential must have appeared repeatedly in F_2 populations in tropical breeding programs; a few segregates are sometimes found in crosses between tall, leafy parents. Such plants would resemble the variety IR5, with moderately short culms and leaves and early to midseason maturity. Dwarf mutants also may have appeared irregularly in segregating populations.

But breeders generally failed to recognize the value of these smaller segregates and either rejected them, or lost them because they were inferior in their ability to compete for light. Thus, bulk breeding brought no progressive gains in yield although it was effective in the selection of such density-independent characters as grain size, cooking quality, maturity, photoperiod insensitivity, resistance, and glabrousness.

More recently, awareness of the interactions of plant type, yielding ability, and competition has led most breeders to completely avoid or to modify conventional bulk breeding. Unrestricted bulk breeding is now widely recognized as futile when increased yield potential is sought in crosses that segregate widely for plant type.

But a modified system of bulk breeding is potentially useful in rice improvement. An F_3 generation of uniformly dwarf stature and free of excessive competition can be produced by thorough roguing of tall, competitive plants in the F_2 of single crosses between tall and dwarf parents, and strict selection of dwarf segregates. The F_3 and subsequent generations may then be bulked until the beginning of line evaluation in the F_6, when populations are relatively homozygous. Modified bulk breeding can also be used successfully for crosses between dwarf parents without losing valuable materials through competition.

One way to ensure an all-dwarf F_2 for bulking of tall × dwarf crosses is to use the heterozygous, tall, single-cross F_1 plants only for backcrossing, three-way crossing, or multiple crossing to dwarf parents. The better dwarf F_1 segregates can be bulked to establish a dwarf F_2 for continued bulking until the F_5 or F_6.

Modified bulking is successfully practiced in Japan. It is rapid and inexpensive once the populations are relatively free of competition for light. Modified bulk selection for a few cycles may be especially useful for upland rice breeding programs where drought resistance is to be combined with improved plant type, or where disease resistance is a primary objective and intense selection pressure can be applied to segregating bulked populations.

At IRRI, a modified bulk system similar to single-seed descent is used to rapidly advance generations in crosses where photoperiod sensitivity is involved. Early generations are planted at close spacings (1000 plants/sq m) in the greenhouse or phytotron and advanced through the F_5 under an artificial regime of short clays and high temperatures. This greatly shortens the time required to develop photoperiod-sensitive materials because a generation can be grown in less than 100 days. There is no danger of losing less competitive segregates because the seed of every plant is carried forward.

In most crosses, however, another factor must be considered that negates the advantages and simplicity of bulk breeding. Early generation testing of individual plants for characters such as disease and insect resistance, and size, shape, and quality of grain is critical to progressive breeding programs. This cannot be done using a conventional or modified bulk system. So why carry along volumes of undesirable plants when early testing, beginning with the multiple cross F_1, concentrates the superior segregates and progressively upgrades the material? The importance of early identification and elimination of undesirable material restricts the usefulness of either the conventional or modified bulk method of breeding.

BACKCROSS BREEDING

Rice breeders have not extensively used the backcross method, in which a character is transferred into an improved variety by its repeated use as the recurrent parent. The major disadvantage of backcrossing is that no single variety is so nearly ideal that it needs to be improved in only one character. Although active breeding programs are continuously developing newer and further improved varieties to replace older ones, no tropical rice program has reached a position where significant quantum improvement cannot be expected in grain quality, yields, or the stabilization of yield potential.

Conventional backcrossing might be considered for certain special problems. For example, the line Colombia 1 has useful monogenic, dominant resistance to blast disease. Thousands of early generation selections from crosses of Colombia 1 with improved dwarfs have shown that the resistant segregates occur in predicted frequencies, but that their plant types or grain are invariably poor. This suggests a strong linkage between resistance and the poor plant and grain characters of Colombia 1. In this case, repeated backcrossing to improved dwarf parents, coupled with strong selection in the F_1 following each backcross, might break the linkage.

Another example of the selective usefulness of conventional backcrossing was early in the IRRI breeding program when the variety Peta, which had grain of medium length with a chalky endosperm and low gelatinization temperature, was crossed with Belle Patna, which had long grain, clear endosperm, and intermediate gelatinization temperature. A series of backcrosses to Peta followed, using plants in each F_1 with grain characters similar to those of Belle Patna. The final product was a series of lines morphologically similar to Peta but with Belle Patna's grain traits. This case is of interest because the three characters are independently inherited and genetically complex. The simultaneous transfer of three complex characters from the donor parent illustrates the potential for conventional backcrossing, often considered useful only for the transfer of single, monogenic characters.

Backcrossing has been used in the IRRI program to transfer resistance to grassy stunt virus disease from wild rice to dwarf varieties of good plant type. The backcross method is now used in the program to breed for brown planthopper resistance. By 1977, several varieties had been released that carry either *Bph 1* , a single dominant gene for brown planthopper resistance, or *bph 2,* a single recessive gene. New biotypes of this serious pest are soon expected to arise and render those varieties susceptible. Two new resistant genes have recently been identified. The fastest and surest way to incorporate these genes into suitable varieties is through the conventional backcross method.

Single backcross method

A useful procedure in all crosses involving a dwarf and a tall, leafy parent is a single backcross to the dwarf parent. This is routinely and successfully done in the IRRI and CIAT programs. A modification of the single backcross is to topcross the F_1 to another parent with good plant type and grain quality to produce a three-way cross, which is then handled like a backcross. A single backcross to the parent with superior plant and grain types concentrates these characters while retaining adequate frequencies of the desired genes from the nonrecurrent tall parent. The single backcross gives the breeder two opportunities to look at the same parental combination. Planting the F_2 of both the single cross and the backcross

more than doubles the chances of finding good material because the backcross population is always an improvement over that of the single cross.

The appearance of the single-cross F_2 generally indicates the worth of the backcross reasonably well. But sometimes the F_2 of the single cross produces few desirable segregates while the backcross F_2 is excellent. The use of only one backcross results in sufficiently wide segregation and recombination to produce many segregates that are superior in plant and grain characters to those of the recurrent dwarf parents.

The success of the single backcross is directly related to the number of plants and the intensity of selection pressure applied to the F_1 population. Typically, from 50 to 100 or more backcrossed seeds are produced to give a large F_1. Scientists then evaluate each F_1 plant and discard those that are highly sterile, very late in maturity, or inferior in grain size and shape. The backcross of an F_1, heterozygous for the dwarf gene, to the dwarf parent produces 50% tall plants in the backcross F_1 population. The tall plants that are otherwise acceptable may be advanced to the F_2 along with the better dwarf plants in some programs. From 200 to 400 plants are grown of each F_2 family. The F_2 families that are derived from tall F_1 backcrossed plants segregate into tall and dwarf plants in a proportion of 3:1. The tall plants are rogued, as previously described, to reduce competition and to ensure the survival of the desired dwarfs.

The CIAT program practices a modification of the typical procedure for handling tall × dwarf crosses. The F_1 plants are backcrossed to the dwarf parent sufficiently to yield 200 or more backcrossed F_1 plants. All tall segregates are discarded, even though they may be heterozygous for dwarfism, to eliminate the need to rogue the tall segregates in the F_2 families. This leaves a minimum of 100 homozygous dwarfs that are further selected for fertility and grain characters. Only fertile dwarfs with good grain are harvested and advanced to the field to establish F_2 families. The F_2 seed of the original, single cross is harvested and stored without planting in the field.

Using this procedure, there is no need to rogue tall plants from F_2 populations because the single cross is not planted and only dwarf backcross plants are selected. Furthermore, one does not have to tediously sort through the single-cross F_2, which usually is preponderantly undesirable. The large number of backcross F_1 plants ensures that a large nursery of F_2 families, with a concentration of desired plant and grain characters, is available for continuing selection.

When the nonrecurrent, tall parent is a source of simply inherited disease resistance, as is often the case in blast resistance, some of the F_2 seedlings of each selected dwarf F_1 backcross plant are evaluated for disease reaction before the F_2 families are planted. Half of the selected families will carry the resistance gene. The remainder, which segregate

no resistant plants, are discarded and only the families carrying resistance are planted in the field. In a typical example, 100 of the 200 backcross F_1 plants are dwarf. Of these, perhaps 20 are discarded for sterility or poor grain type, leaving 80 plants. About half of those carry blast resistance, giving 40 F_2 families in the field. Thus, an F_2 population of several thousand plants is comprised of families selected in the F_1 for plant type, fertility, grain size, and blast resistance.

PEDIGREE BREEDING

The pedigree method has been the most widely used and successful in rice improvement. Yet pedigree breeding has certain disadvantages. The method requires much time to periodically evaluate lines throughout the growing season and to keep records on which selection at maturity is based. Considerable labor is required because each selection not only must be prepared for field planting but also for laboratory evaluation and for special nurseries for grain quality, disease and insect resistance, and other characters. Of all breeding methods, the pedigree method requires the greatest familiarity with the material and with the relative effects of genotype and environment on character expression.

The many advantages of the pedigree method, however, explain its wide use. Most important, early generations of field-selected plants can be evaluated in special tests for characters such as resistance. This provides a sounder basis for the discarding of undesirable lines and results in the concentration of useful material. The data from these progeny evaluations of single plants become available while the new pedigree lines are growing in the field. Thus, lines that breed true for poor quality, susceptibility, or other defects are immediately eliminated from the field books so that no time is lost on them.

It is not uncommon for one of these tests to fail or to give inconclusive results. The pedigree system of records for prior generations allows the breeder to trace the breeding behavior for the character in question to the rows from which the selections were made. This earlier information gives the breeder some predictive value about the lines in the field nursery.

CHAPTER 3

Operational procedures

REGARDLESS OF THE BREEDING SYSTEMS used, rice improvement programs should be organized in the same basic way, depending somewhat on objectives and scope. Of paramount importance is that a successful plant breeding program be systematic. If not, it will result in confusion.

PROGRAM ORGANIZATION

Experience shows that "extremely promising crosses" seldom result in good varieties. Attempts to force generation advance in such crosses result in inefficient use of supporting staff. More often than not, such materials planted during the off-season are lost to rats and birds. The best approach is to set up and follow an operational system that includes specified procedures for each operation, nursery, and trial to be conducted. This system should, obviously, permit maximum efficiency in screening and generation advance.

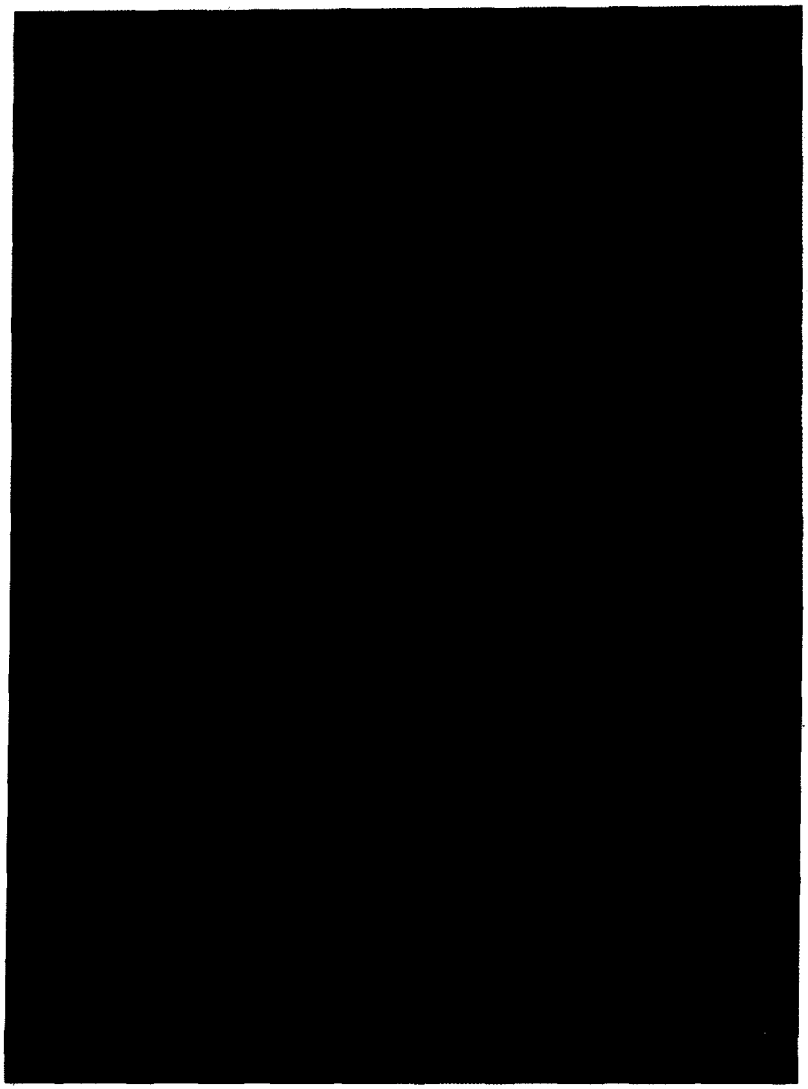
The organization of the IRRI program (Fig. 1) and important variations of it, especially as in the CIAT program, are discussed here. Common considerations of various nurseries and trials such as land preparation, planting methods, and plot care, are covered first.

PERMANENT FIELDS

If experiment station facilities are shared with other crops, the rice breeder should obtain land that is permanently assigned. Experimental plots of rice are not easily rotated with other crops because of special considerations such as soil and plot preparation, the unique problems of irrigation and drainage, and permanent field levees. Direct -seeded programs should have an area large enough so that the same fields are not used for breeding material more than once every 1½ to 2 years. The land should be periodically worked to kill volunteer plants from dropped seed.

Field size

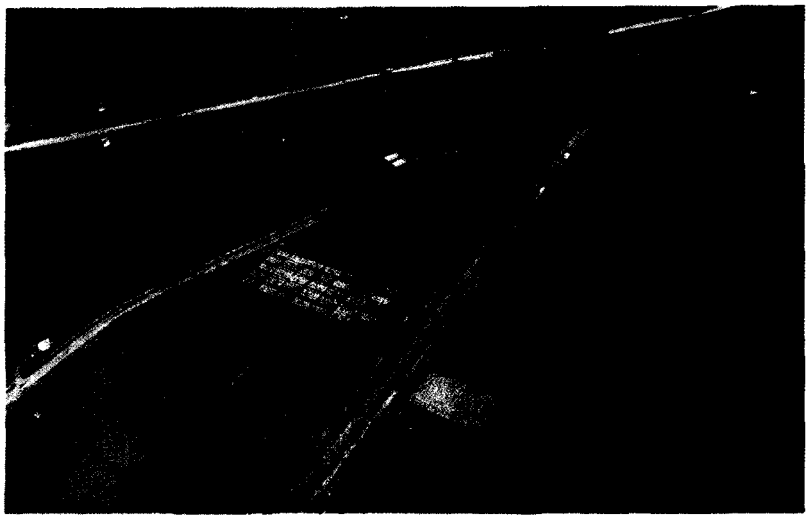
Small fields separated by temporary levees are totally unsatisfactory. Although no single field size is ideal for all circumstances, a useful width is 25 m. This allows for four 5-m blocks of transplanted material separated by 1-m alleys. Transplanted nursery rows are oriented parallel to the narrowest dimension (width) of the field. Rows in directly-seeded



1. Flow of material in the IRRI rice improvement program.

nurseries are usually oriented parallel to the long axis of the field to facilitate row marking. Blocks of 65 rows spaced at 30 cm fit into fields 25 m wide, leaving ample alleys to mark rows at each side along the field levees. Figure 2 shows an aerial view of the layout of experimental blocks at the IRRI farm.

The length of the field depends on the land slope and the degree to which each field can be leveled without exposing the infertile subsoil. Optimum length may range from 80 to 120 m. Shorter fields surrounded



2. Aerial view of a portion of the IRRI research farm. Note the layout of the experimental blocks.

3. F . V. Ramos (left), IRRI farm superintendent, supervises water leveling of the land on a newly developed portion of the farm.

by permanent levees waste space and are difficult to prepare with machinery. In longer fields, water control is often uneven and harvest of materials of variable maturity is hampered.

Substantial amounts of soil may have to be moved to form new fields of about 25 × 100 m. Soil can be moved satisfactorily with machinery (Fig. 3) or by working in water with animals. If power equipment is available, plow the land while it is dry and raise permanent levees. Keep levee size to a mininum to reduce maintenance and weed control. Then flood each field and move mud from the higher to the lower areas. If draft animals

are the only power source and materials are transplanted, plow and move earth in water. Once permanent fields are formed, leveling may have to be repeated every few plantings. Fields are normally arranged in two tiers separated by a central canal so that each field can be flooded and drained independently of the others.

DROPPED SEED

Rice seed can remain viable for several years in tropical soils. Volunteer seedlings from shattered grains of previous crops are a constant problem in directly seeded fields because they develop along with those of the newly seeded nursery. The resulting mixtures are often difficult to distinguish from normal segregation. Frequent plowing and disking of the soil partially control the problem. Burning of dried stubble and plants left in the field is also helpful. Thorough early weeding of all vegetation between rows greatly reduces contamination, although some volunteer plants may still grow within the rows.

When seed multiplication plots are seeded directly, they must be established on land that has not been planted to rice for several seasons. If the seed used to plant the multiplication plots comes from rows known or suspected to contain mixtures, it is important to select panicles individually, observe them in the laboratory, and discard off-types. To ensure uniformity, inspect panicle rows frequently in the first cycle of multiplication.

Volunteer seedlings are rarely a problem in transplanted populations. The final harrowing destroys all field vegetation, giving the transplanted seedlings an advantage in size over any dropped seed that germinates after the last harrowing. Furthermore, the transplanting of single seedlings at a constant spacing facilitates the immediate identification of any plants that are out of place.

PLANTING METHODS

If possible, rice breeders should transplant their material rather than seed it directly. Even workers who develop varieties for directly seeded commercial practice can transplant their breeding plots without concern for any adverse natural selection against desired traits. But severe difficulties arise when a breeding program designed for transplanted rice seeds its material directly.

One problem is that direct seeding seems to favor natural selection of plants of low tillering ability. After many years of such selection in the USA and Surinam, for example, relatively productive varieties have been developed that are not suited for transplanting because their tillering ability is limited. Furthermore, plant evaluation and selection of single-plant hills that are uniformly spaced proceed faster because the breeder does not have to separate plants to be certain that he is harvesting the

panicles of only one plant. Standard spacing results in less interplant competition and more uniform growth within rows. Not only do spaced plants produce more seed, but transplanting rows of segregating materials also requires less seed. Material can be transplanted during rainy periods, but direct seeding requires that weather conditions be ideal to prepare land and make rows. Finally, weeds and volunteer seedlings can be controlled easier in transplanted rice.

Transplanting

Transplanting has three major disadvantages:

1. Transplanting is slower than direct seeding, with an equal labor input, even when well organized.
2. Transplanting requires large amounts of hand labor to prepare and plant the seedbed and to pull, transport, and plant the seedlings.
3. Walking through the soft soil of transplanted plots is difficult and can be a health hazard for barefoot workers.

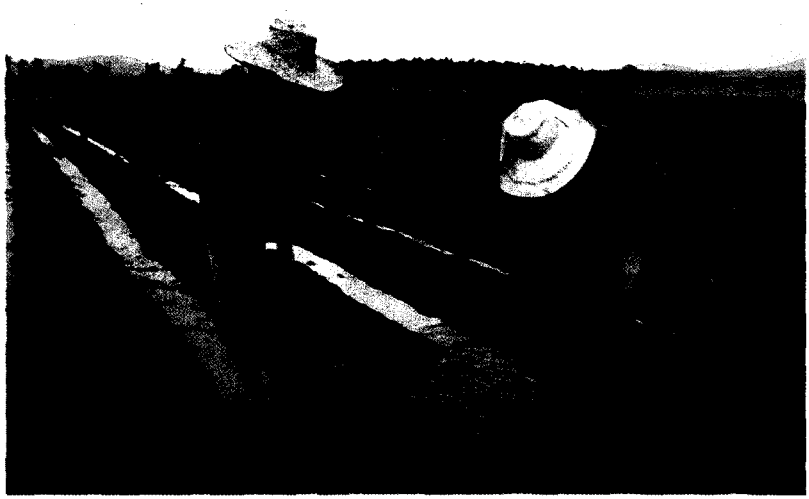
Even though many programs must plant directly because of high labor costs, some could profitably transplant a portion of their material. The F_2 is the most important generation to transplant because it is the most difficult to select. Standard spacing of single seedlings in the transplanted F_2 simplifies roguing and selection. Programs that seed directly can also gain valuable time by transplanting the first seed-multiplication cycles of potential new varieties. One kilogram of seed transplanted at a wide spacing in single-plant hills easily produces a ton or more of seed under normal conditions. But the same amount of seed, if seeded directly at a reduced density of 50 kg/ha, will produce only about 100 kg of seed/ha.

The most convenient row spacing for transplanted material is 30 cm. Closer spacing makes walking within plots and selecting plants difficult. Single-plant hills may be spaced within rows at 25 cm for segregating lines and 15 or 20 cm for yield trials. Extra seedlings are placed at the foot of each row to be used to replace missing hills within 5 days after transplanting. Row tags should be wired and numbered. As each bundle of seedlings is pulled from the seedbed, tie a row tag around it. Stake and tag the pedigree nurseries as they are transplanted. Any seedbed tagging technique may be used that ensures the integrity of each pedigree or fixed line.

IRRI's transplanting procedure uses either a "dry" or "wet" seedbed depending on weather conditions and other considerations, such as the presence of disease inoculum.

For dry beds, a fairly light upland soil is needed, with facilities for flood irrigation. If the area has not previously been used as a seedbed, test the soil for nutrient deficiencies in pots or flats. Make beds about 1 m in width either manually or with a small tractor. Level the beds and remove

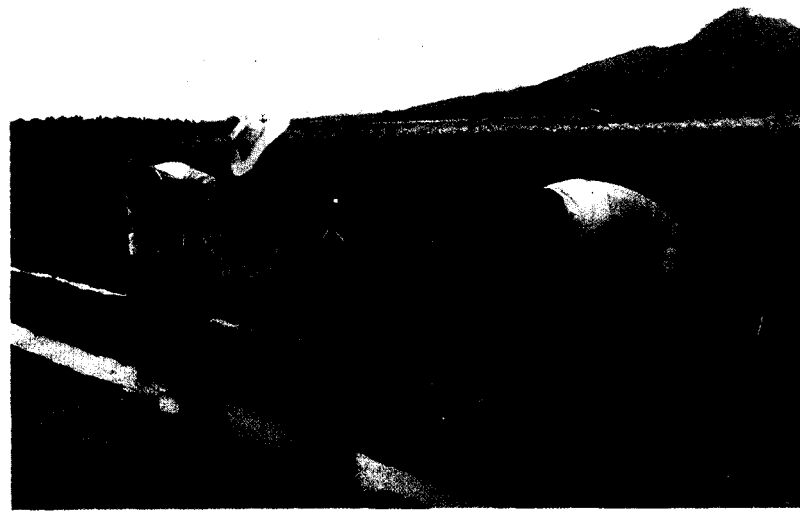
4. Raising and "slicking off" wet seedbeds to give a smooth, firm surface.



5. Making rows on the mud surface of a wet seedbed using a wooden template.

clods, then make rows at 10-cm intervals with a wooden template. Dibble the seed into the rows and cover them. Place identifying stakes at 10-row intervals. When water is needed, flood the depressions between the beds and splash water on the beds with a shovel. Protect the beds from rats and birds until well past seedling emergence and monitor them daily. If seedlings remain yellowish and stunted for no obvious reason, continuous flooding of the beds may remedy the problem.

The wet seedbed technique is conventional in Asian rice culture and is modified only slightly to accommodate breeding material. Puddle the

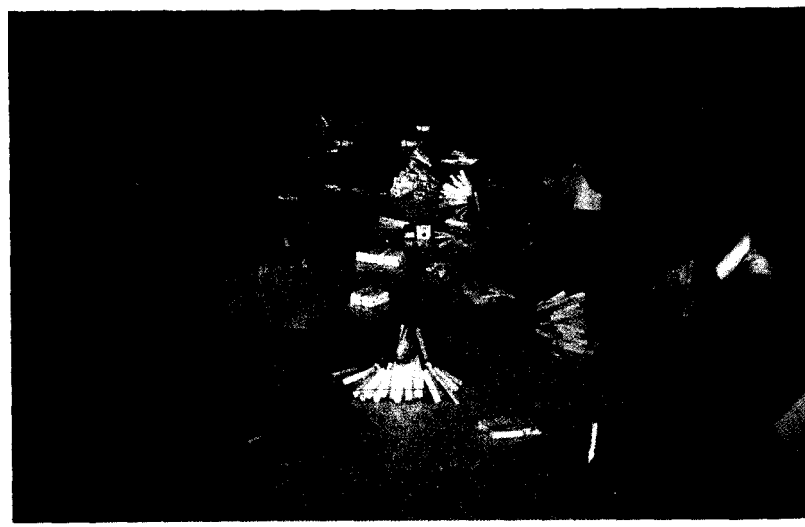


6. After the seeds are dibbled in the rows, they are covered with fine soil.

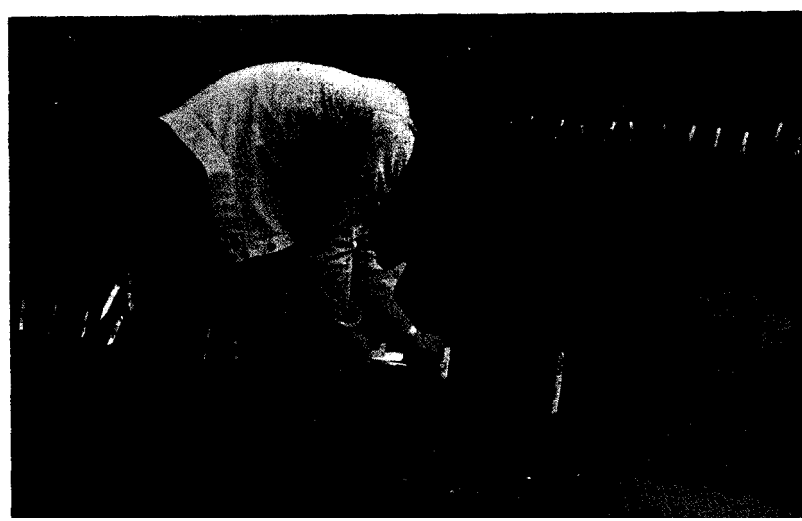
7. The seedbed should be protected from birds (station a person to guard it) and rats (by an appropriate fence).

paddy thoroughly, drain it, and allow it to settle until the mud is suitably cohesive. Then throw the mud up in beds about 1 m wide and "slick-off" to give a smooth firm surface (Fig. 4). Let the beds settle for 1 or 2 days to prevent sticking, then make rows in the mud surface with a wooden template at 10-cm intervals (Fig. 5). Dibble the seed in the rows and cover them with fine, dry soil (Fig. 6). Flood the depressions between the beds, and splash them with water as needed. Mark the rows with stakes at 10-row intervals. Again, the beds must be protected from birds and rats (Fig. 7), and flooding may be required if seedling mortality is high.

8. Preparation of wooden tags.



9. The wooden tags with attached wires are inserted in the mud at the end of each row prior to pulling the seedlings.



Before pulling seedlings, usually 21 days after seeding in the tropics, prepare small wooden tags (Fig. 8) for each row or group of rows that will comprise a plot upon transplanting. Attach a wire about 30 cm in length to one end of each tag. At the time of pulling, place properly numbered tags at the ends of the rows (Fig. 9). Flood the bed to soften the soil and pull the seedlings and tie them in bundles with the wire attached to the tags (Fig. 10). Lay out the field to be transplanted with rows and plots marked by bamboo or other stakes about 1 m in length (Fig. 11). Then place the bundles of seedlings at the base of each stake. Remove the small

10. The seedlings are pulled and tied in bundles in preparation for distribution in the field.

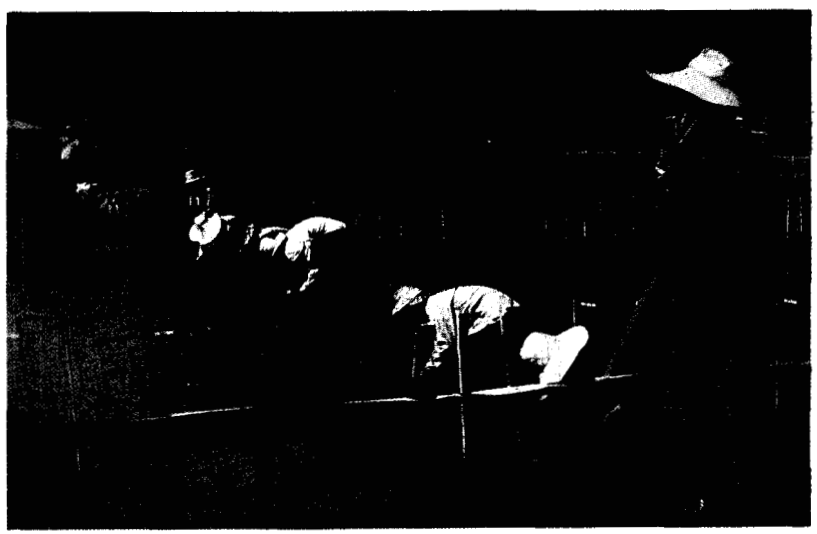
11. The field is laid out by marking each row with a bamboo stake.

wooden tags from the bundles and wire them to the tops of the marker bamboo stakes to identify each transplanted row for the duration of the nursery or trial (Fig. 12). Transplant the nursery using a guide wire to give the proper spacing and alignment (Fig. 13).

Direct seeding

Fields to be prepared for direct planting are mechanically rowed out immediately before planting. Standard spacing between rows is 30 cm because marking of rows, planting, and selecting are difficult at closer

12. The seedlings are placed at the base of the bamboo stakes and the wooden tags are wired to the stakes.



13. The nursery is transplanted using a guide wire to give the proper spacing and alignment.

spacings. At row spacings wider than 30 cm, weeds increase and it is more difficult to distinguish between desirable and undesirable plant types.

Some breeders are concerned about using a 30-cm row spacing because farmers either drill much closer or broadcast their crops. Actually, this is no problem because the preferred higher tillering types, easily identified at a 30-cm spacing, are equally desirable for drilled, broadcast, or transplanted crops. Most experiments show that the highest yielding lines

consistently produce more as row spacings increase to 30 cm. Although low-tillering materials usually yield more at close than at wide spacings, they are less desirable for commercial planting.

When nurseries are planted by hand, the field is mechanically rowed out and is then staked and divided into blocks with twine, leaving 1-m alleys between blocks. To save time, basal fertilizer may be scattered over the soil rather than applied into the row furrows. Use hoes to lightly cover the seeded rows with soil from the ridges between rows. This does not result in mixture of seed from one row to another. Hand planting is remarkably efficient and rapid, and is relatively free of error. A crew of 20 laborers can easily row out, fertilize, plant, and cover 5,000 5-m rows per day.

Flush direct-seeded plots with irrigation water immediately after planting to ensure uniform germination even if rain should fall. Leave at least 5 m between the water inlet and the first block of rows to prevent seed from being washed away. Introduce water at the lowest corner of the field so that it will slowly move toward the highest end.

Yield trials of direct-seeded rice should be planted in rows because results are invariably unsatisfactory when seed is broadcast in small plots. Broadcasting is useful only for large plots, including regional trials conducted on farmers' fields.

Directly planted nurseries are staked as soon as possible after germination so that seedling characters may be recorded. Use stakes to identify every fifth row. (Staking of every 10th row causes confusion in row identity during selection.) Each yield-trial entry is staked. Wooden plot labels should be cut into 5-cm sections. Number the labels on both sides in the seed laboratory (some laboratories have hand numbering machines), coat them with melted paraffin, and wire them to the stakes.

PLOT MANAGEMENT

One of the greatest defects in rice breeding programs is that inadequate attention is paid to the growth and development of breeding materials. When the potential varieties are intended for lowland irrigated conditions, the rice breeder must maintain vigorous, normal growth of his breeding material throughout its life cycle to facilitate the identification and selection of superior plants and lines. Poor growing conditions improve the appearance of undesirable, traditional, tall phenotypes and cause most good plant types to appear undesirable. Observations based on abnormal plants are confusing and invariably result in the selection of inferior material.

Expenditure of labor and herbicides is normally heavy to eradicate weeds during the first month of growth. The application of any selective herbicide against grassy weeds is usually followed by one or more hand cleanings of remaining weeds. There is no excuse for any significant weed

competition in plots from early tillering to harvest.

A common problem in rice plots is nutritional deficiencies, or toxicities from alkaline or strongly acid soils. Deficiencies are best alleviated by applying the essential element before planting, and by thorough leveling of the land followed by careful control of irrigation water. Some toxicity problems are controlled by reducing the organic matter incorporated during land preparation and by draining and drying the soil surface at midseason.

Nitrogen is one of the breeders' best tools to differentiate good from bad plants. Periodically apply enough nitrogen to keep fields dark-green and growing vigorously. The total dose depends on factors such as soil texture, adequacy of water control, or ambient temperature. Nitrogen promotes the lodging of tall phenotypes and weak-culmed dwarfs while allowing sturdy plants to remain erect.

To apply limited nitrogen simply because the commercial use of fertilizers in some areas is low is an error. The trend toward increasing use of nitrogen on farms having good water control will continue as new varieties are developed that respond well to heavy applications. Breeders usually use more nitrogen than the average farmer would apply to facilitate the evaluation and selection of weedless, vigorously growing breeding materials.

Breeders should encourage disease epidemics and insect infestations in their material if the causal organisms are significant farm problems. Heavy disease and insect pressure throughout the growth of the segregating generations in the field is the best possible aid to the identification of resistant lines. Natural or artificial field infection is always preferred over greenhouse or cage tests for resistance. Some workers control epidemics, arguing that otherwise they would lose most of their breeding material. If so, their material has limited farm value. It is preferable to lose susceptible, but otherwise useful, breeding material than to suppress epidemics and run the risk of releasing varieties with inadequate resistance.

Plot management is a special problem for breeders who are developing varieties for rainfed, upland, moderately deep water, or other stressed production areas. Management that is ideal for varietal development of irrigated rice is clearly unsatisfactory for marginal production areas where farmers can use only a portion of the new technology. But weedy, nitrogen-deficient plots are undesirable, regardless of breeding objectives.

For areas with potential plant stress such as rainfed rice areas, varieties should be sufficiently vigorous and well adapted to produce moderate yields when farming practices are less than ideal, but they should respond in grain production to improved practices. Therefore, breeders might alternate degrees of precision in plot management from one seg-

regating generation to the next. For example, the breeder might transplant the F_2 early and provide excellent water control and heavy fertilization. He might transplant the F_3, late, control water irregularly, and reduce fertilizer application. Over several generations this mixture of ideal and rough plot management could provide the wider adaptability required for stress areas without sacrificing high yield potential for the farmer who can employ the full technological package.

But the best procedure for such situations is still open to question. The use of common sense is the only firm recommendation that can presently be made.

CROSSING

A broad-based, high-volume crossing program is essential in any good rice improvement effort. The persons directing such a program must clearly know their objectives and priorities, as well as the characteristics of the more important varieties and lines. Some of these characters are recorded in various field books, but others must be remembered. The scientist who memorizes as much information as possible will be much more effective in comparing and choosing parents.

Unfortunately, predicting the ultimate value of a cross is impossible without prior experience with the parents. Closely related and morphologically similar lines, when crossed with a common parent, often differ greatly in combining ability as measured by the appearance and value of the F_2.

When a breeder lacks previous experience with parents, a sound approach is to increase the number of crosses and to strictly reject inferior F_2 populations. This will greatly increase the likelihood of success. Also, if one parent in a single cross is poor, or if the cross lacks some important characteristics, a topcross, backcross, or double cross will invariably give better results. Such multiple crossing can also speed up the combination of several characteristics in one genotype.

TYPES OF CROSSES

The various types of crosses and the selection of parents are:

- *Single crosses.* Single crosses are the hybridization of one variety or line with another variety or line. Select the female parents considering the objectives of the program and using your knowledge of the available materials. Select as many as possible for each objective, preferably of diverse genetic background. It is advisable to use exotic or unimproved parents as females. Although using the improved parents as females is invariably more convenient, it results in too narrow a base of cytoplasm.
- *Backcrosses.* A backcross is the cross of an F_1 to one of its parents.

PROCEDURES

- *Topcrosses.* A topcross (3-way cross) is the cross of an F_1 to a variety or line.
- *Double crosses.* A double cross is the crossing of two F_1 hybrids.

It is necessary to have notes on the F_1 hybrids as well as knowledge of the various parental varieties and lines. Before crossing begins, note the plant type, maturity, and other characteristics. Most good plant breeders make their decisions in the field while reviewing the F_1's. This requires a thorough familiarity with the parents of the crosses as well as with those available for topcrossing.

Topcrosses and double crosses are used to increase the chance of obtaining desirable segregants from "difficult" materials that are known or suspected to be poor combiners, or to combine desirable traits from three or four different parents, or both. As with single crosses, topcrosses and double crosses should always be chosen for complementary characteristics. For these reasons, backcrosses are normally limited to those cases where the recurrent parent is superior to other rices available for topcrossing. Also, if an essential parent combines poorly, backcrossing offers the best chance to recover a satisfactory type.

It is safer to use the F_1 as a male in a topcross because selling can more easily be detected. But using the F_1 as a female is much more convenient from an operational standpoint because the other parent is probably a better pollen producer. The IRRI procedure is to emasculate all F_1's that flower on a given day and then to decide on the male (topcross parent) that would best complement each F_1, before pollination time the next day.

Double crosses are sometimes useful to combine a large number of desirable traits in a given cross. Double-crossing may also be used where major differences in traits of all four parents are minimal and the aim is to increase variability in the hope of recovering a highly desirable type. Many breeders feel that topcrosses are generally more useful than double crosses.

The following general rules of thumb may be helpful in deciding what type of cross to make:

1. If one parent of the single cross is known or suspected to be a poor combiner, use a backcross.
2. If both parents of the single cross are reasonably good combiners but lack one or more important traits, use a topcross.
3. If both parents of the single cross are reasonably good combiners but lack important traits and no topcross parent can be found with all the needed traits, use a double cross.

MAINTENANCE OF PARENTS

Parents can be grown in large flooded pots that hold from three to five normally developed plants. The pots should have solid bottoms to reduce water loss and nitrogen should be applied sparingly to avoid lodging. Three plants will produce adequate crossed seed for almost all purposes. Three plantings of parents at intervals of from 10 to 14 days should be sufficient to assure simultaneous flowering.

Careful planning of crosses reduces the number of parents used in any one season to about 50 or less and with three planting dates the total number of pots can be accommodated in a small area. Most programs lack the resources to continuously maintain large numbers of lines and varieties in the field for possible future use as parents. A more satisfactory alternative is to request specific parental seed from IRRI or elsewhere as the need arises.

IRRI has adopted specific procedures in its extensive crossing program. Crosses are made throughout the year; during peak periods more than 300 pollinations a day may be made. Maintaining parents in pots would be impossible; instead, they are grown in the field in a hybridization block (HB), which is planted from four to six times each season at 2-week intervals. The HB is organized in groups according to the objectives of the program:

Group I	(General)—IRRI varieties and improved lines
Group II	(International) — varieties and improved lines from national programs
Group III	Agronomic characteristics and grain quality
Group IV	Disease and insect resistance
Group V	Protein content
Group VI	Drought resistance
Group VII	Adverse soils tolerance
Group VIII	Deep water and flood tolerance
Group IX	Temperature tolerance
Group X	Miscellaneous

Parent plants are transplanted into pots immediately prior to crossing and are discarded when the hybrid seed is harvested. Although transplanting into pots is somewhat inefficient in terms of labor, it saves greenhouse space and allows the scientists to first evaluate the parents under field conditions before crossing. Evaluation of a plant in a pot is difficult and unless the breeder took careful notes during the previous season, he may have forgotten the strengths and weaknesses of various parents. Superior lines identified in the yield trials or pedigree nurseries may also be transplanted into pots.

It is essential to maintain purity of parents. Bulked grain from pedi-

gree rows or plots should not be used to produce plants for crosses. The best procedure is to select a few panicles and thresh the grains by hand. Parental plants should be checked repeatedly for purity before crossing.

Parents in pots are identified by pot labels that carry the variety's name — or, for a line, the field number under which it was last planted. Reference to the field books readily gives the parentage and pedigree of the line. It is not necessary to assign a separate numbering system to the parents in pots.

Where to cross

Rice is an easy species to cross if one follows certain basic procedures. Crossing in the field is impractical because of the difficulty in bringing pollen to emasculated panicles, the frequency with which scissors and other tools are dropped in the water, poor footing, and the damage to crosses from diseases, insects, and rodents.

Although greenhouses are ideal for crossing, they are essential only when climate limits the year-around culture of parents. A simple screenhouse is a satisfactory substitute in the tropics, where greenhouses are expensive, often too hot, and space is limited or not available. The sides and top of a crossing facility must be of screen to exclude rodents and birds. The screenhouse should have a gravel or concrete base, with water available for the pots.

EMASCULATION

Emasculation is the process of removing the anthers from the florets. The emasculated plant serves as the female parent. Spikelets are emasculated in several different ways. One technique is to kill pollen by heated air or hot water in a thermos bottle. Individual spikelets remain open for several minutes after the panicle is withdrawn from the thermos bottle; the spikelets are pollinated before they close. This method has many disadvantages. It is slow and seed set is relatively low. The culm often breaks when bent to insert the panicle into the thermos. Pollen must be Immediately available and manually introduced into individual spikelets before their glumes close. If pollen is not available at once, the spikelet must be clipped or forcibly reopened.

The simplest and most efficient emasculation technique is to clip the spikelets and remove the remnant anthers with tweezers or vacuum. Figure 14 shows some of the materials required:

- scissors — small, sharp, pointed, and of good quality;
- fine forceps (not sharp);
- vacuum emasculator (optional);
- apron with pockets or a small box for carrying tags, bags, and marking pencil;
- glassine bags — about 5 × 15 cm;

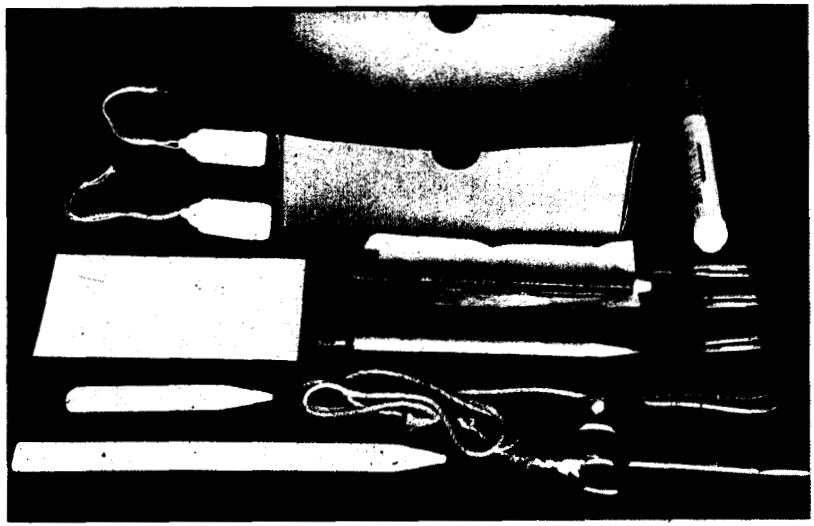
- paper clips;
- pentel pen or wax pencils;
- pot labels;
- tags, and
- stool.

The steps and key points of the emasculation procedure used at IRRI and CIAT are outlined below.

Steps and key points in emasculation.

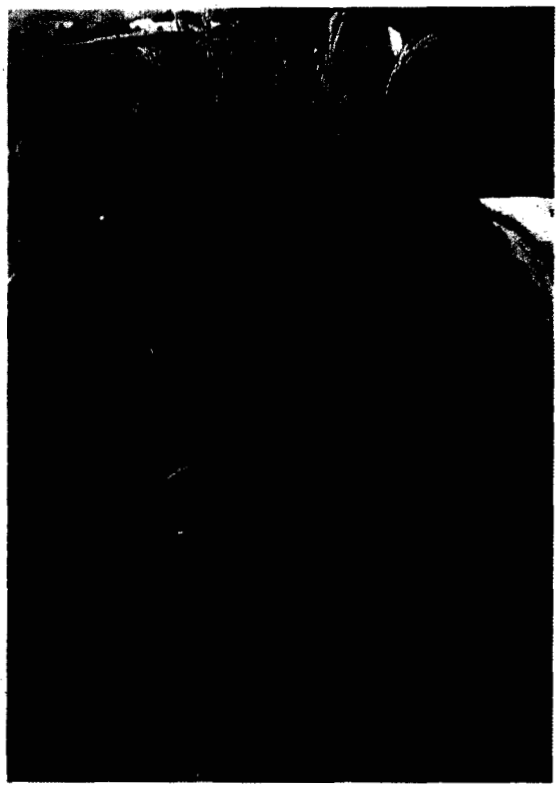
Stem	Key points
1 Select parents.	• Choice depends on the objectives of program. • Make list of rices to be emasculated. • Determine number of panicles: single cross — 2 panicles/cross topcross — 7 panicles/cross backcross — 7 panicles/cross double cross — 11 panicles/cross
2 Select individual plants.	• Each plant should be healthy and representative of the variety or line. • Remove the plant from the plot by cutting the mud around the base with a knife or sickle. • Tag the plant with the designation and plot number. • Pot the plant by adding soil and water as necessary — at least 6 hours before emasculation to permit recovery in case of wilting (Fig. 15).
3 Select individual panicles.	• Panicles should be 50–60% emerged (Fig. 16). • Carefully separate the selected panicle from surrounding ones to make it easy to work on. Remove the leaf sheath. Do not break the culm.
4 Remove upper and lower florets.	• With scissors, cut away all florets from the top that have undergone anthesis (extrusion of anthers). Cut away the young florets from the bottom of the panicle where the height of the anthers is less than half of the floret.

14. Materials required for crossing.



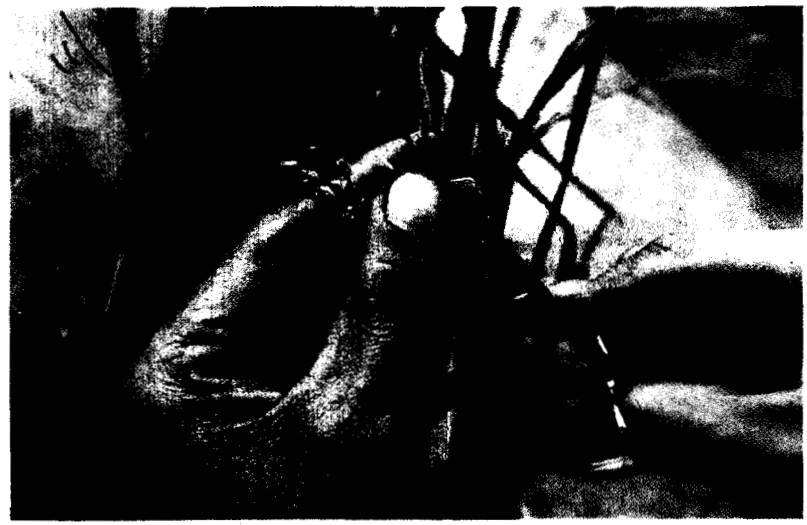
15. Potting a plant for crossing after removing it from the mud with a sickle.

16. A panicle at the proper stage for emasculation (50–60% emerged).



Steps and key points in emasculation continued

Steps	Key points
5 Clip florets.	• With scissors cut away a third to half of the floret obliquely to expose the anthers (Fig. 17). If the anthers are to be removed by forceps you may prefer to cut directly across each floret and through most or all of the anthers. • Do not injure the stigma by cutting too low. • If the cut is too high, emasculation is difficult and pollen may not reach the stigma during pollination.
6 Remove anthers.	*By forceps* • With the tip of one forceps prong, gently press the anthers against the side of the floret and lift them out (Fig. 18). • Use extreme care not to damage the stigma. • Be certain that all six anthers are removed. *By vacuum* • Assemble and adjust the vacuum emasculator (Fig. 19) to give a suction of about 500 mm Hg. Excessive suction may damage the stigma. • Touch the extractor tip to the floret (Fig. 20). Gently jiggle the tip until you hear the airflow interrupted by the extracted anthers. • Be certain that all six anthers are removed
7 Mark bags.	• Mark the glassine bags after all florets on the panicle have been emasculated. • Mark on the bag the date of emasculation and your initials with a pentel pen or wax pencil.
8 Cover panicle.	• Place glassine bag over the panicle. • Fold bottom edge over. • Clip the fold against the peduncle to hold the bag securely in place (Fig. 21).



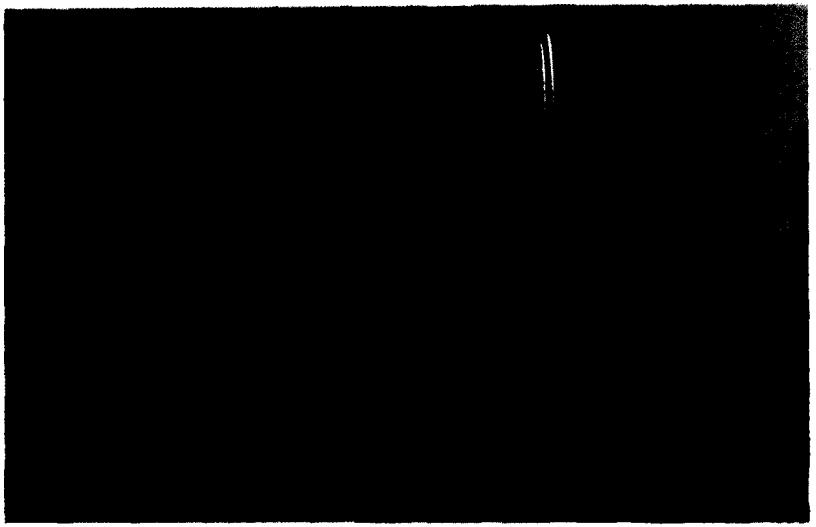
17. Clipping the florets to expose the anthers.

18. Removal of the anthers with forceps.

The vacuum emasculator is a simple apparatus to construct (Fig. 22). It increases the efficiency and speed of emasculation. The components can usually be purchased locally; if not, they are available through IRRI.

POLLINATION

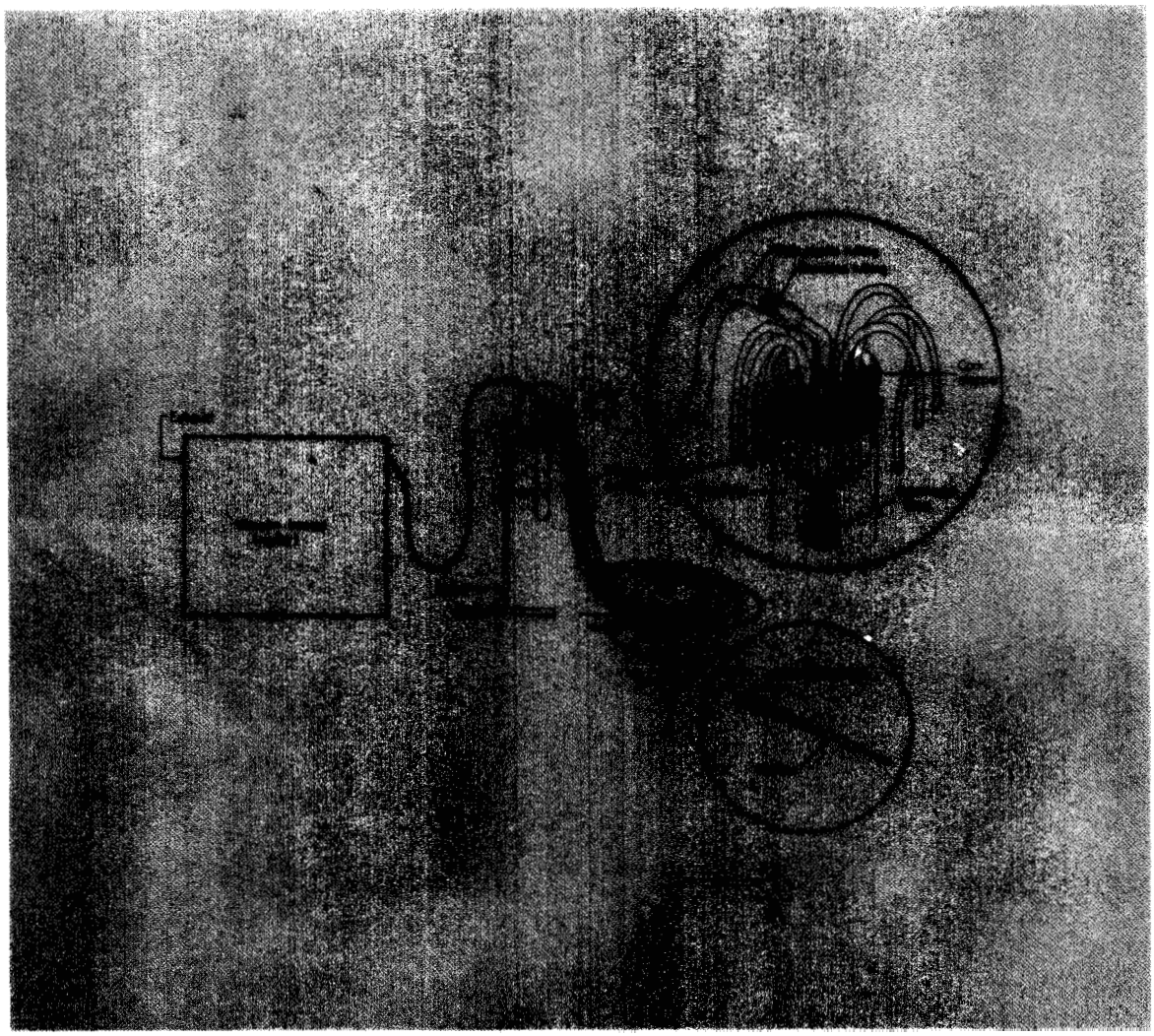
In many areas anthesis, or pollen-shedding, begins 1 or 2 hours before noon and lasts for about 2 hours. In other areas flowers begin to shed pollen shortly after noon. The timing is rather variable, depending on temperature and light. Anthesis is retarded or temporarily impeded on



19. Fully assembled vacuum emasculator.

20. Removal of the anthers by vacuum.

21. After removal of the anthers the panicle is covered with a glassine bag marked with the date and initials of the emasculator.



22. A vacuum emasculator is simple and inexpensive to build. A ¾-hp motor will operate about 6 tubes.

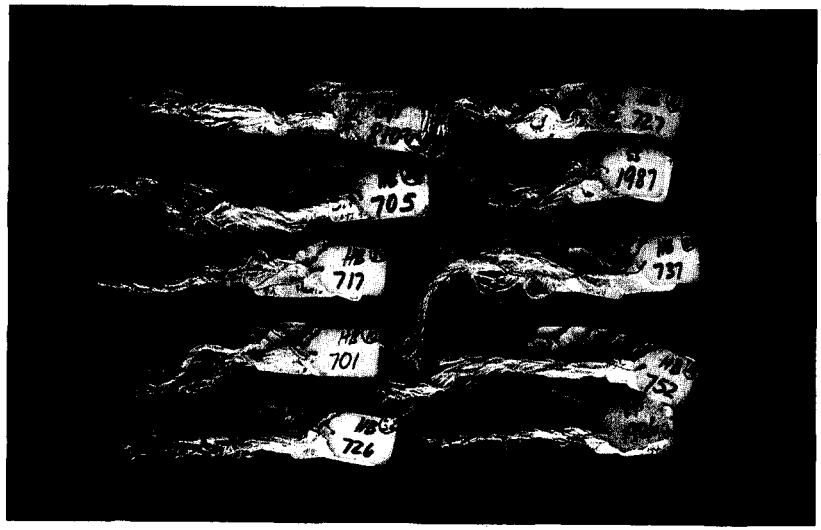
cool, dark, or rainy days. Emasculation is risky in the early morning before pollen is normally shed. Clipping the spikelets in the late afternoon, after the normal anthesis period, is far better because it lessens the possibility that anthers might inadvertently burst during clipping and self-fertilize the plants. The following morning, as anthesis begins, cut a blooming panicle of the staminate (male) parent and carry it to the emasculated panicle. The same materials as for emasculation are needed, plus crossing tags (see next section "Preparation of crossing tags") and a pencil to mark them.

Steps and key points in pollination.

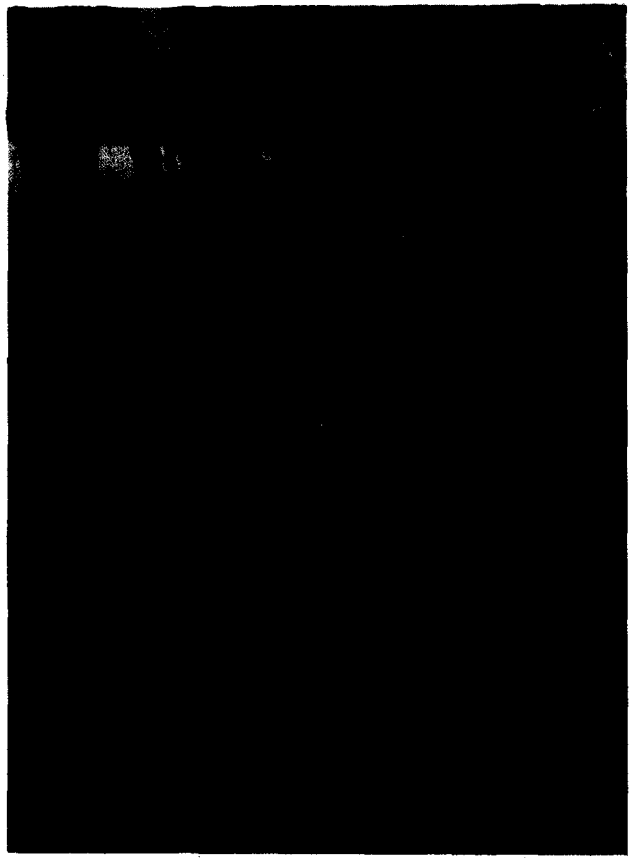
Steps	Key points
1 Organize female parents.	• Arrange the pots for easy access during pollination. A large circle or semi-circle is usually best. • Check the emasculated panicles for any anthers that may have been left and reclip any floret where the opening is small. • If two panicles on the same plant are to be pollinated by the same male, unite the two culms with one of the glassine bags and fasten with a clip. Place the other bag over both panicles.
2 Gather pollen panicles.	• Allow enough time to gather the pollen panicles before anthesis begins depending on the weather and the amount of work to be done. • The crossing tags should have already been prepared and grouped by male parent (Fig. 23). • Take at least one panicle for each tag. • Select panicles from healthy, representative plants. • Select panicles that will have a large number of blooming florets — several florets at the top will have anthers showing (Fig. 24). • Cut the culm at a convenient length below the panicle and cut off the flag leaf.
3 Tie panicles.	• Group all panicles of each male parent and fasten them together with a rubber band. • Attach appropriate tags to each group of panicles. • Clip stems to a uniform length.
4 Place panicles together.	• Bring panicles from field to pollinating area. • Place panicles in pots of water in the center of the circle of female plants where air movement is minimal and access is easy. • Arrange the panicles so that any one can be removed without disturbing the others (Fig. 25).

Steps and key points in pollination continued

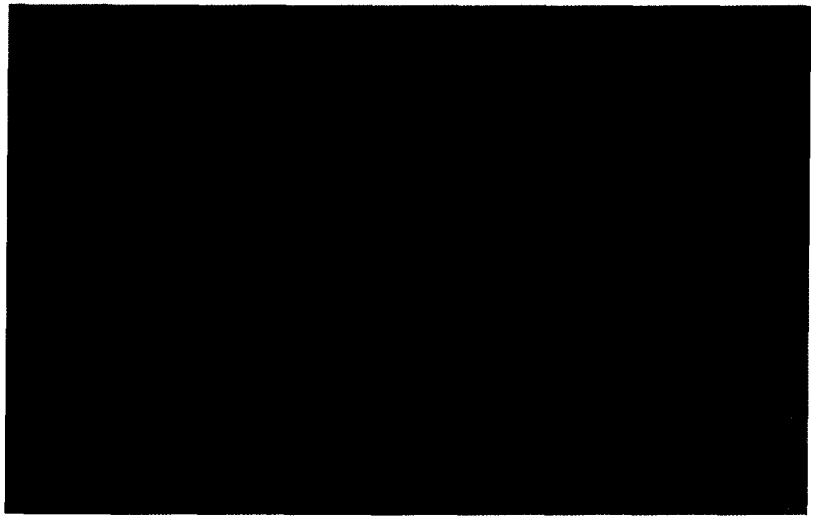
Steps	Key points
5 Observe panicles.	• Watch closely for anther extrusion (Fig. 26). • Begin pollinating as soon as possible and work quickly to take advantage of the period of maximum pollen production.
6 Apply pollen.	• Remove the glassine bag from the female. • Gently lift the blooming panicle from the water and shake it over the emasculated female (Fig. 27).
7 Replace glassine bag	• Place glassine bag over the panicle. • Fold bottom edge over. • Place paper clip on fold against the peduncle to keep bag secure.
8 Attach crossing tag.	• See "Preparation of crossing tags" (next section). • Attach tag string to stem. • Place tag under the paper clip at the bottom of the glassine bag (Fig. 28).
9 Protect pots.	• Pots should be kept out of the wind and rain but with good exposure to sunlight. • Pots should be protected from rodents, birds, and pests.



23. Crossing tags that have been prepared and sorted, by male parent, prior to pollination.

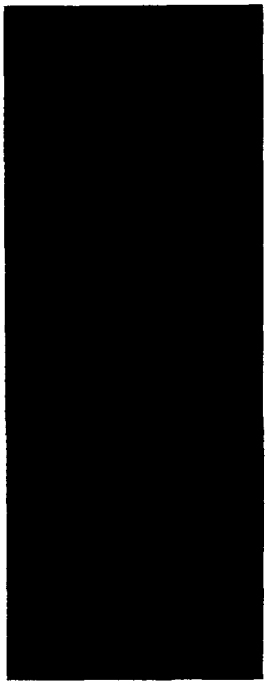


24. A panicle that will have a large number of blooming florets later in the morning. Note the extruded anthers clinging to the upper florets.

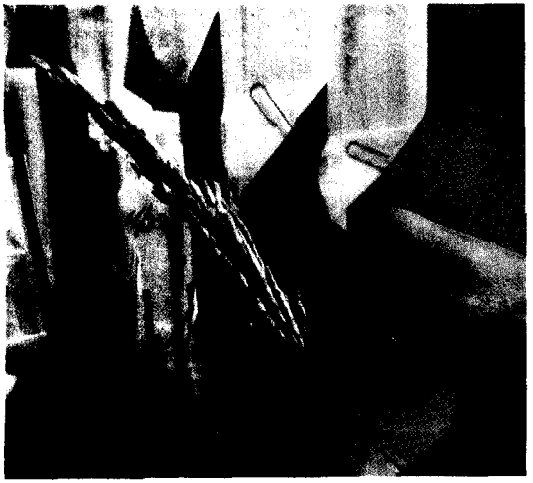


25. The panicles are arranged in pots of water so that any one can be removed without disturbing the others.

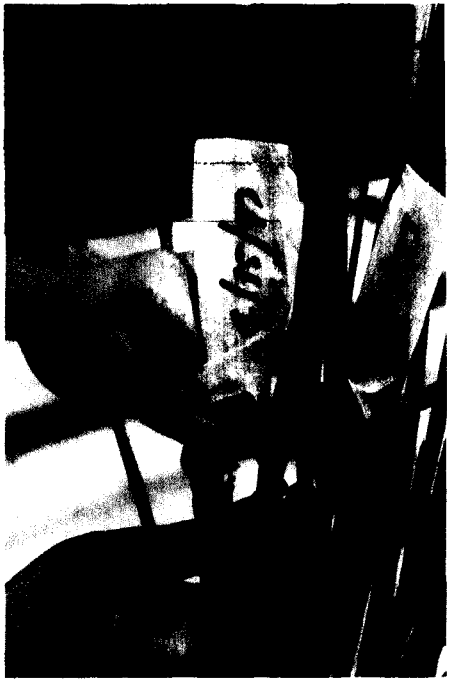
26. When the anthers extrude, a panicle is ready for use in pollination.



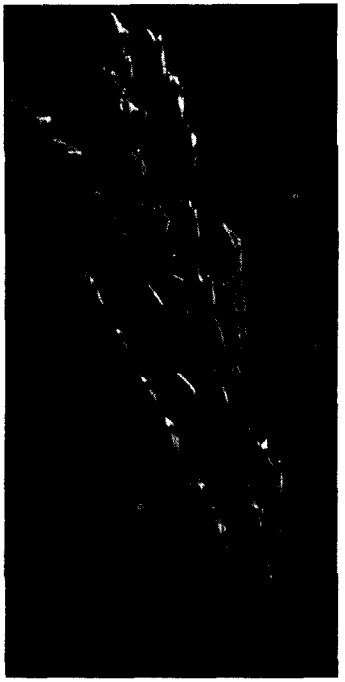
27. The panicle is very gently lifted from the water and shaken over the emasculated female.



28. The crossing tag and glassine bag are fastened securely with a paper clip.



29. The crossed seed is mature when it loses its green color.



The stigmas of emasculated spikelets remain receptive for at least 5 days, so plants may be pollinated on subsequent mornings if no pollen is available or if the quantity appears insufficient. The ability to pollinate an emasculated panicle on successive days, if necessary, is one of the outstanding advantages of emasculation by clipping.

The clipping method of emasculation followed by mass pollination is rapid and efficient. Seed set should reach 50% or higher if the technique is good.

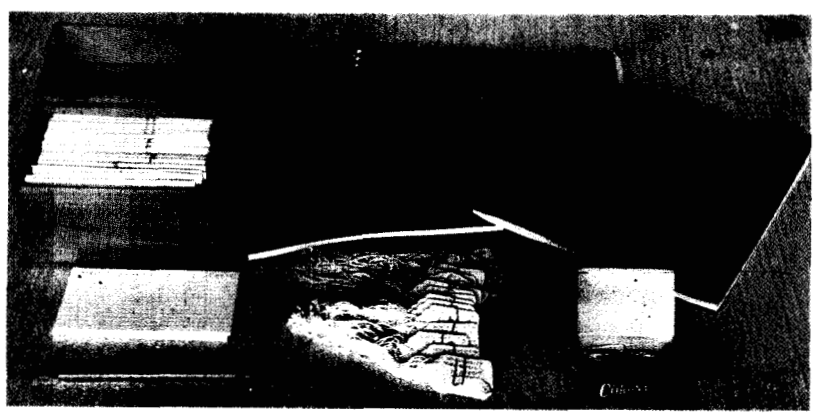
The ovary should begin to swell in 3 or 4 days, indicating successful pollination. The crossed seed is mature when it loses its green color — usually at about 25 days after pollination (Fig. 29). At that time, cut the panicles, thresh the seeds by hand, and remove the glume remnants. Count the naked seeds and place them in small envelopes. Mark the envelops with the names or line identifications of the two parents and the number of crossed seeds enclosed. This is best done by stapling the crossing tag to the envelope.

The developing seeds incompletely covered by the clipped glumes, although viable, are abnormally shaped and often are more strongly dormant than unclipped grains of the pistillate parent. Break dormancy by placing the seed in a dry-air oven for 7 days at from 50 to 55°C, then store the crossed seed in a cold room or refrigerator.

PREPARATION OF CROSSING TAGS

Identify all panicles used for crosses by attaching a tag that stays with each panicle at all times. Avoid duplication by keeping a diary of crosses in a card file. Figure 30 shows the materials needed:

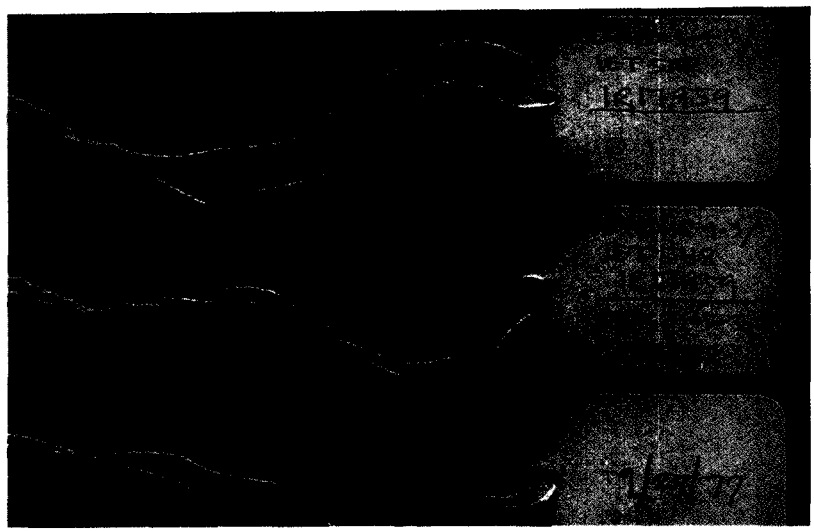
- tags — white or colored, about 3 × 4 cm, with string attached,
- medium pencil — no. 2 or 2½,
- field books, and
- diary of crosses in a card file.



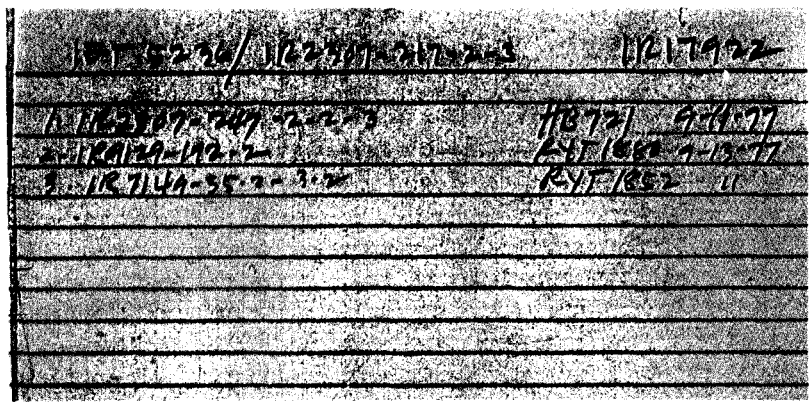
30. Materials needed for the preparation of crossing tags.

Steps and key points in the preparation of crossing tags.

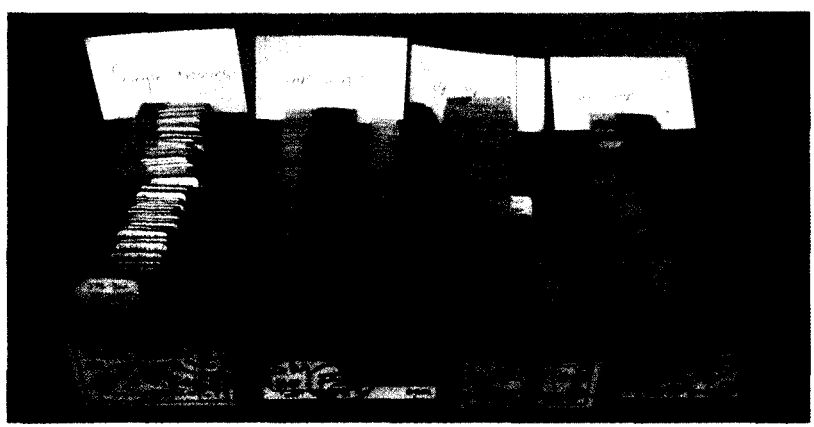
Steps	Key points
1 Assemble and premark tags.	• Have tags on hand well before crossing begins. • On one side identify site, season, and year (if necessary), and stamp or write date of pollination.
2 Identify female parent.	• On the top half of reverse side write the designation and source of the female parent. • Draw a line between the female and male to avoid confusion when both have long pedigrees.
3 Identify male parent.	• It is usually easier to first prepare all of the needed tags for each female and then to add the designation and source of the male on the lower half of the tag (Fig. 31). • Designations must be entered on only one tag for a given cross. The source numbers are sufficient for additional tags.
4 Enter in diary-of-crosses card file.	• See sample card (Fig. 32). • Make one card for each female, enter designation and source at the top. • List all males used on that female and show designation, source, and date of pollination.
Use tags for pollinating.	• Attach crossing tag to glassine bag of pollinated female parent.
6 At harvest.	• Retain the tag with the panicle at all times during harvesting and threshing. Staple the complete tag to the seed envelope (Fig. 33).



31. Steps in the preparation of a crossing tag showing the female parent (top), the pollen parent added (middle), and the date of pollination added to the back side (bottom).



32. Card for the diary-of-crosses file.



33. Packets of F_1 seed. The crossing tags are attached to the packets for identification.

NUMBERING CROSSES

The ideal system of identifying crosses is to number them consecutively and to continue the numbering over the years. This procedure avoids confusion that arises if the numbering is repeated each year. With consecutive numbering, crosses never carry the same number and the pedigree is not complicated with numbers referring to the year or season of the cross. All cross numbers are preceded by a capital letter identifying the program. For example, CIAT uses the prefix P and IRRI, IR. Thus, the identification P752 identifies the cross as the 752nd made since the initiation of the CIAT program.

New cross numbers are given to all backcrosses, whether single or repeated, and to all three-way crosses. Thus, if the single cross P752 is A/B, the backcross A^2/B will receive the next available number. Similarly, a new cross number is assigned if a second backcross is made. Cross numbers are given only after the crossed seeds are harvested, threshed, and placed in small envelopes.

CROSS DESIGNATIONS

The standard practice is to first list the pistillate parent followed by the staminate parent in a cross. Other than this convention, rice breeders use many variations of a basic system of designating crosses. All have certain advantages but some are better than others. Each breeder should select and follow the system he understands best and feels most comfortable with. The following are two systems that have been used to designate crosses at IRRI. The first system was used for a decade but was replaced by the second system, which has greater simplicity.

	First system	*Second system*
Single cross	A × B	A/B
Backcross	A/2 × B	A^2/B
Three-way cross	(A × B) × C	A/B//C
Four-way cross	(A × B) × (C × D)	A/B//C/D
Compound cross	(([(A × B) × C] × D × E)) × F	A/B//C///D/4/E/S/F

The second system replaces the symbol x with the symbol / to chronologically order the crosses as:

Chronological order of crosses	*Symbol*
1	/
2	//
3	///
4	/4/
5	/5/
backcross	exponent

Both systems are reasonably manageable for single crosses through four-way or double crosses. The designations of compound crosses are relatively complex in both systems and can lead to errors in field books. Breeders in the CIAT program, which involves many compound crosses, enter only cross numbers at the head of each page of pedigree lines to reduce the complexity in field pedigree books. For example, if the cross involves a selection of [(A × B × C] × D (= P 1083) crossed with variety E, this cross is designated as P1083 × E in the field books. Similarly, [(A × B) × C] × [(D × E) × F] is simply designated as P1013 × P1381. In these examples the full parentages of P1083, P1013, P1381, etc, are noted on the inside cover of the field book so that the field workers know which parents were used in each cross.

Two other systems of designating crosses are worth mentioning. One is used by the International Center for the Improvement of Maize and Wheat (CIMMYT), and the other by the United States Department of Agriculture (USDA):

	CIMMYT system	*USDA system*
Single cross	A-B	A/B
Backcross	A^2-B	A*2/B
Three-way cross	A-BXC	A/B//C
Four-way cross	A-BXC-D	A/B//C/D
Compound cross	[(A-BXC/D) E] F	A/B//C///D/4/E/5/F

The CIMMYT system is easy to read and write, while the USDA system is compatible with computers.

Because IRRI has recently switched to computerized record keeping it has adopted the USDA system. The new IRRI system differs from the previous one only in the designation of backcrosses:

	Previous IRRI system	New IRRI system (USDA system)
Backcross to pistillate	A^2/B	A*2/B
Backcross to staminate	A/B^2	A/2*B

Note that the dosage numher number of backcrosses plus one) is always placed next to the crossing symbol. This becomes crucial with complex crosses. A/2*B//C means that A was crossed with B, the F_1 was backcrosses to B, and the progeny were crossed with C.

CROSSING BOOK OR HISTORY OF CROSSES

Crossing books arc prepared in triplicate and new pages are added for each group of crosses. Always store the three copies in different places to protect against loss. Record the following information for each cross:

cross number, varietal names or parents and pedigree of both the pistillate and staminate parents, pot identification numbers of both parents, and the number of crossed seeds obtained.

Cross no.	*Parent*	*Parent*	*Source of parents*		*No. of seeds*
P752	CICA 4	× (Col. 1 × IR8) P384–138–3–1–3	6281	6418	31

The same information is kept for backcrosses. If, for example, the cross P752 were backcrossed to CICA 4, the crossing book would show:

P985	CICA 4 × F_1 [CICA 4 × (Col. 1 × IR8)] P752	6281	P752	118

Abbreviate parental names for crosses involving parents with long names and multiparental lines that are derived from several other parents. Thus, Bluebonnet 50 × Century Patna 231 may be written as Bbt 50 × Cp 231.

NUMBER OF CROSSES

Rice workers have traditionally made fewer crosses than breeders of other cereals. A program where 100 crosses/year are made is considered moderately large; IRRI, which probably has the largest program in the world, averaged about 200 crosses/year during its first 10 years. In recent years, the 16 principal breeding stations in Japan have totaled about 800 crosses/year, an average of 50 crosses/station.

Although no specified number of crosses distinguishes a vigorous from a moderately active program, fewer than 20 or 30 per year at one location suggests a need for a re-evaluation of program objectives and activities. Programs that can make only a few crosses might consolidate their breeding programs with those of other stations to form regional crossing tenters. Experiment stations that are severely limited in human or financial resources should consider concentrating exclusively on segregating populations and lines provided by larger centers until their facilities and resources permit more active crossing programs.

It is not entirely clear why IRRI, for example, formerly made far fewer crosses than the wheat team at CIMMYT — perhaps only 10% as many. Nor is it certain that the rice worker's philosophy of fewer crosses and larger populations is entirely disadvantageous. A possible explanation for the basic difference in approach between rice and wheat scientists is that segregation is extraordinary in the F_2 of most crosses. This forces

the screening of large populations to find the relatively few desirable recombinants, which in turn controls the number of crosses that can be handled. Thus, the total number of F_2 plants evaluated in large rice and wheat programs is comparable despite the disparity in the number of crosses. One way to increase crosses, while simultaneously concentrating selection in better rice populations, is to never advance tall F_2 plants into the F_2. Heterozygous, tall F_1 plants will produce a predictable number of dwarf F_2 segregates but, because of competition, the dwarfs are difficult to find and select. Thus, the F_1 of tall × dwarf single crosses might be used only for backcrosses, or for three-way crosses with dwarf parents, to produce a new F_1 that segregates tall and dwarf plants in a ratio of 1:1. Advancing only the dwarf F_1 backcross plants to the F_2 eliminates a vast amount of field labor, thereby allowing an increase in the total number of crosses.

For an example of this approach, take variety B, an excellent source of disease resistance but with poor plant type and grain quality. The resistant B is crossed with an improved but susceptible dwarf A to produce the single cross A × B. This F_1 is used only backcross to A. The F_1 of the backcross A^2 × B will segregate 50% dwarf plants, and only the better ones are advanced to the field to produce F_2 populations. The tall F_1 plants are discarded. Thus, all F_2 families will be uniformly dwarf and most will have acceptable grain. If not evaluated as F_1 backcross plants, these families are tested to determine which carry resistance.

Apart from this technique, the relatively small investment required to make additional crosses suggests that rice breeders should broaden their crossing programs. Increasing the number of three-way and double crosses will increase genetic diversity. Stricter selection in the F_1, and particularly in the F_2, will keep the total volume of material in the field constant while increasing the probability of more desirable combinations.

Two well-recognized principles recently led IRRI to greatly expand its crossing program so that by 1977 some 5,000 crosses per year were being made. The first principle is that linkage is a major impediment to the combination of the many critical characters that differentiate the parents of most rice crosses. High-volume crossing favors the breaking of unfavorable linkages because the frequency in which linkages are broken is proportionate to the degree of heterozygosity in the genotype. Abundant three-way and four-way or double crosses of F_1 hybrids perpetuate heterozygosity, thereby reducing linkages. The second reason for high-volume crossing is the difficulty in predicting combining ability. For largely unknown reasons, some parents combine well in crosses while others do not. The combining ability of a promising parent cannot be determined until several crosses are made and the early segregating generations are evaluated.

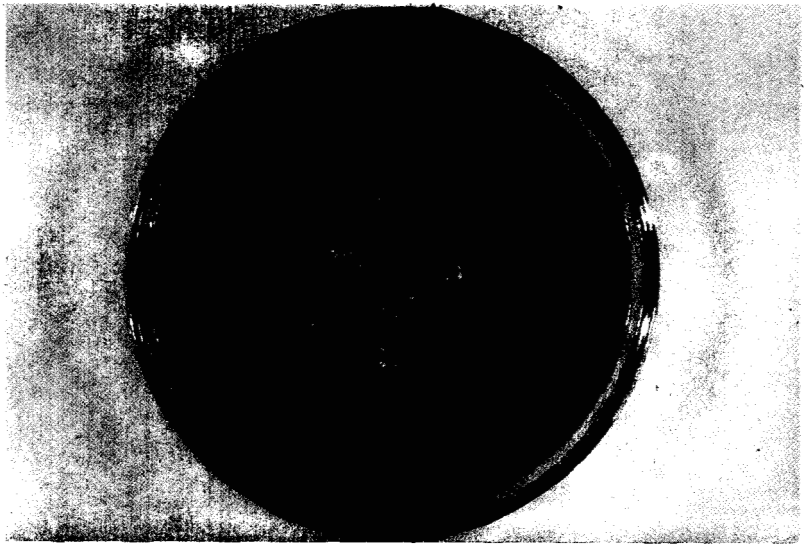
The number of crossed seeds to produce for each single cross depends

on the fertility of the F_1 and the desired size of the F_2. When the F_1 is fertile each plant normally produces at least 10 panicles, each bearing a minimum of 100 seeds. Thus, if the breeder produces from 15 to 20 crossed seeds he will have sufficient F_1 plants to establish a large F_2 population. When the F_1 is partially sterile, a proportionately large number of crossed seeds are required. Backcross or three-way F_1 populations invariably require many many crossed seed than single crosses (see "Backcross breeding," Chap. 2).

CULTURE AND HANDLING OF THE F_1

After dormancy is broken, dust the crossed (F_1) seeds lightly with any standard fungicide except those that contain mercury or that reduce seed viability during prolonged storage. Germinate the seeds on moist filter paper in petri dishes (Fig. 34). When handled in this manner, more than 90% of the naked crossed seeds should germinate. Never sow seeds directly in soil because they lack the protection of the hull. Hold petri dishes at about 30°C in a seed germinator if available; if not, hold them at room temperature on a laboratory bench. If the F_1 populations are to be grown to maturity in pots (which is usually advisable for smaller programs), leave them in the dishes until the one-leaf stage (7–10days), and then transplant them directly in puddled soil in pots. After transplanting, identify the pots with small wooden labels carrying the cross numbers and leave them in the shade for 1 or 2 days to avoid sun scalding.

IRRI's procedure is slightly different. Because so many crosses are made, all F_1 plants are grown in the field. To do that incubate the seed in petri dishes for about 24 hours, or until the hypocotyls are just exserted,



34. Germinated F_1 seed at the appropriate stage for transplanting to soil flats.

and then transplant them end-to-end in rows 10 cm apart in flats having moist soil. Keep the fiats in the shade for about 1 week or until the seedlings are well established and then transfer them to full sunlight in a glass-covered screenhouse: If only a normal, enclosed greenhouse is available it is advisable to move the seedlings outside about 5 days before transplanting. When the seedlings are about 25 days old, carry the flats to the field, pull the seedlings, and immediately transplant them into puddled soil. Choose the soil in the unpuddled flats and in the field with care because hybrids are sensitive to minor nutrient deficiencies (probably because of the reduced seed size).

Inspect the F_1 plants before and after flowering for self-fertilization. Plants that are not true crosses may be identified by expression of any simply inherited characters and by comparison with plants of the pistillate parent of the cross. Once the self-fertilized plants are destroyed, the grain of all F_1 plants of each single cross is usually harvested and bulked to produce a single F_2 population. The integrity of each F_1 plant may be carried into the F_2 by individually threshing and Planting the grain of the F_1 plants. This practice creates planting problems and is not usually worth the added work for single crosses.

Because it is difficult to estimate the value of single crosses by the appearance of the F_1, many breeders advance all single crosses to the F_2 without selecting among the F_1 populations, unless a cross is obviously useless. This common procedure should be carefully re-evaluated. The advantage of discarding F_1 plants that are heterozygous for tallness or are otherwise undesirable, after making backcrosses or three-way crosses, has been discussed. Similarly, wide single crosses give immense selection problems in the F_2. Thus, it is often more advisable to use such single cross F_1 plants only for further crossing. Likewise, there is little reason to advance F_1 plants of relatively narrow single crosses that have obvious defects such as inferior grain or extremely narrow culms.

The F_1 of backcrosses and three-way crosses is handled differently because the plants segregate within each combination. Thus, plants in the pedigree system should not he bulked as for single crosses. The F_1 plants of each backcross or three-way cross are numbered consecutively. Pedigree identifications are assigned, consisting of the cross number followed by individual plant numbers. For example, if cross P985 has 118 F_1 backcross plants, all good ones are retained. Each one is individually harvested, numbered, threshed, and planted as a discrete F_2 family.

Hybrid vigor

Hybrid vigor, or heterosis, is observed in F_1 plants of almost all crosses and is pronounced in many. A few unreplicated experiments on small populations that were transplanted and widely spaced have shown large heterotic values for many plant characters including yield. This has

stimulated sporadic interest in the possible commercial value of F_1 plants. A rather impractical scheme was once proposed to produce sufficient F_1 plants for small-farm use by repeatedly separating and transplanting successive crops of tillers.

In a comprehensive study of heterosis at IRRI, ponlai japonicas were crossed with BPI-76, an improved indica variety. Sufficient crossed seeds of the fertile F_1 population were planted in closely spaced replicated plots with a nitrogen variable. Although plant growth was highly heterotic from tillering through flowering, yield was not. Vegetative vigor increased and yield decreased with added nitrogen. The dense vegetative growth reduced light penetration and increased mutual shading so that grain production was not increased. This suggests that a search for yield heterosis is futile in hybrids that do not have ideal plant type.

But heterosis may have some potential value in rice improvement. Useful hybrid vigor would probably be expressed under improved agronomic conditions in crosses between unrelated dwarf parents. If so, an effective sterility-restorer system could possibly be developed. Male sterility has been reported in rice, but seed set on male sterile plants is poor even when they are surrounded by good pollinators.

F_1 hybrid varieties are grown on a large scale in the People's Republic of China. Cytoplasmic male sterility is employed in hybrid seed production but natural crossing is supplemented by hand pollination.

A realistic appraisal of hybrid vigor for the tropics involves two critical questions. Would an increase of from 5 to 10% in yield potential be a significant contribution? And would hybrid vigor be practical considering the enormous problems in seed distribution and the need to buy new seed each season?

THE F_2 POPULATION

The F_2 is the critical generation in rice breeding because, more than any other, it determines eventual success or failure. Success in F2 selection depends on large populations, spaced plantings, strict adherence to selection criteria, heavy selection pressure, ruthless discard of poor or dubious material, and the ability to differentiate between the effects of competition and inherently undesirable morphology.

One reason that the F_2 is so important in rice is that many characters are fixed early in the breeding cycle. Experience with many traits shows that if the F_2 segregates are not good, chances are remote of finding superior plants in the F_3 or later generations. In practice, this means that continued selection is fruitless if the desired combinations are not found in the F_2. A second problem that emphasizes the importance of this generation is that the typical F_2 progeny from distinct parents is made up of a bewildering array of undesirable segregates, with a sprinkling of good ones. Because of these difficulties, the F_2 populations must be managed

in a manner that will increase the likelihood of finding desirable segregates.

The F_2 handling procedure begins when the F_1 hybrids are harvested. Harvest all single cross F_1 plants in bulk. Plants from segregating F_1's are usually individually selected and harvested but bulks composed of selected plants may also be taken. After drying and threshing, arrange the seed packages by cross number. Decide on the size of each F_2 population to be grown; number the envelopes, continuing after the last number of the previous season; scoop the required seed into the envelopes; and place them in the dormancy oven for about 7 days before seeding.

Pretransplanting selection of seedlings

Selection prior to direct seeding of populations is obviously impossible but the F_2 can often be greatly improved by selecting superior plants in the seedbed as the material is transplanted into the field. The seedlings can be exposed to disease or insect attacks to identify those with resistance. This is especially useful for blast and other diseases which give clear, dependable seedling reactions. The F_2 seedlings of crosses between tall and dwarf parents can be classified for height with fair accuracy at from 20 to 25 days of age. One may select and transplant the dwarf seedlings and discard the tall ones. Short-statured segregates are not selected for seedling vigor because environment has a pronounced influence on this character in the seedbed.

Population size

Although there is no ideal F_2 size for single-cross populations, a useful rule is to make them as large as possible, especially for the wider crosses. Populations of less than 3,000 plants are probably inadequate. Many breeders find that from 6,000 to 10,000 plants per cross are sufficient to find and select an adequate number of useful segregates. The size of the population may be reduced if several crosses are grown with somewhat similar objectives or parentage.

For a given set of objectives, it is probably better to have several smaller populations from several crosses than one large population from one cross. F_2 families from individual F_1 plants of backcrosses, three-way crosses and double crosses should contain from 200 to 400 plants, but the number can be reduced if a large number of families is in each cross or if several similar crosses have been made, or both.

At CIAT, the F_2 plants are grown in 20-m rows. IRRI uses 12-m rows. The number of rows depends on the amount of available F_2 seed. In some programs, a single row of each parent of the cross is planted at the beginning of the F_2 plot. Check varieties are less useful in the F_2 than in later generations, however, because of wide segregation and because competi-

tion in some populations affects plant type so drastically that comparisons with parents are of limited value. Neither IRRI nor CIAT uses check rows in the F_2.

Plant density

Transplanting the F_2 is far superior to direct seeding. Transplanting assures that plants are spaced uniformly with one per hill, thus eliminating the problem of selection of two or more plants together. Competition is somewhat less in transplanted populations and the roguing of undesirable phenotypes is much simpler. Normal spacings for transplanted single-plant hills are 30 × 25 cm, or 30 × 20 cm.

Despite several drawbacks the F_2 must be seeded directly when transplanting is not possible. A good practice is to greatly reduce seed density within each row while retaining a 30-cm spacing between rows. In the CIAT program, about 5 g of seed is planted per 20 m of row. Care is taken to plant single seeds by band at about 10-cm intervals. If seeded more densely, plants grow close together, which complicates roguing the selection of individual plants.

Making selections

The F_2 populations are repeatedly observed from the early tillering through flowering stages to decide whether to select within or to reject them. Many F_2 populations have so few useful segregates that they are rejected outright. The risk of losing a few valuable plants should not deter the breeder from eliminating the least promising crosses and thus saving valuable time. A recommended practice is to make many crosses and reject some in the F_2, thereby increasing the time available to select the remainder that segregate favorably.

If the F_2 population of a tall × dwarf combination appears promising, a thorough removal of tall, competitive plants is essential. Populations of single-cross or backcross families that are segregating talls and dwarfs are extraordinarily difficult to select without roguing, especially for directly seeded materials and for populations that have been moderately to heavily fertilized with nitrogen. The F_2 families of single backcrosses to the dwarf parents are easier to handle than single crosses. If all F_1 plants were selected and advanced to the F_2, only 50% of the families would segregate for height and require roguing of the tall plants. Crosses between parents of similar morphology do not segregate appreciably for plant type and are not rogued.

The number of plants selected in the F_2 varies enormously and can seldom be predicted on the basis of the objectives of the cross. If the parents combine exceedingly well, from 400 to 300 selections might be made from a single-cross population of 8,000 plants. Bur the percentage of outstanding segregates is usually much lower. In backcross or three-way

cross material, selection is first practiced among families and many are discarded entirely. From promising families of about 400 plants each, the number of selections can range to 100 or more but usually averages from 20 to 40. The number of selections made in each family or single cross is recorded in the field book.

Exercise care to select only one plant at a time in directly seeded material. Two or more plants of similar height often grow so close together that the breeder must carefully examine the grain or other characters to separate them.

Despite the removal of undesirable tall and leafy plants at early flowering, competition profoundly alters the morphology of desirable segregates in tall × dwarf crosses. Typically, these plants are low tillering, weak, and partially sterile, although grain characters are not affected much. The more valuable segregates generally appear undesirable so identifying them is a challenge to the breeder. The deleterious effects of early competition often make it difficult to evaluate the culm and leaf characters of the dwarf plants. In these cases, useful field observations for selection are good grain type, freedom from diseases or insect damage, and time to maturity. Selection for differences in plant-type characters among the dwarfs is more successful in the F_3 pedigree nursery.

PEDIGREE NURSERIES

The pedigree nurseries are the heart of a rice improvement program. It is here that promising material is first identified with any degree of certainty. It is also here that useless material may accumulate, stifling the entire program. Good management and good judgment are more essential in handling pedigree nurseries than in any other phase of the operation.

Frequency of planting

If climate permits and water is available throughout the year, it is better to plant smaller pedigree nurseries several times rather than to plant two large nurseries at 6-month intervals. At CIAT the breeding material is planted in small nurseries every 45 to 60 days, spreading the work load over the year. Furthermore, a team of 2 or 3 workers cannot efficiently evaluate and select nurseries of more than 5,000 pedigree rows when only 30 or 40 days separate the earliest from the latest segregates. But once harvesting of smaller nurseries is completed, a small team can dry and prepare seed, break dormancy, write the new field books, and replant the selected material in from 45 to 60 days. Thus, by use of staggered plantings, a small team can handle six or more smaller nurseries each year.

By planting smaller nurseries more frequently, the breeder has material at various stages of development in the field at any given time. This eliminates the slack periods characteristic of programs where nurseries

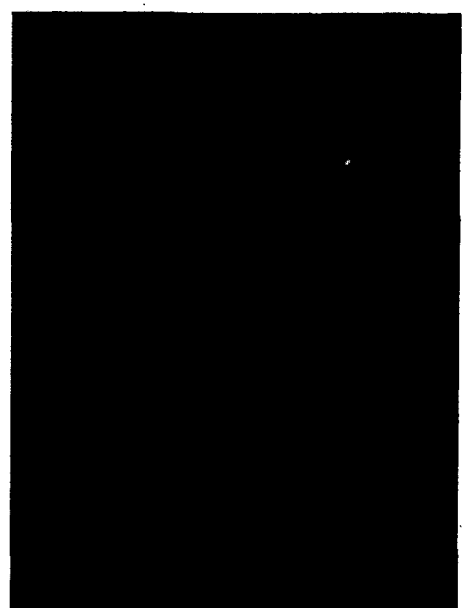
are planted every 6 months, and forces the habit of working in the field daily. Visitors, students, and in-service trainees can join the program at any time and find all stages of work in progress from planting to harvesting.

Preparation of seed for planting

Panicles of plants selected in F_2 populations or pedigree nurseries in the field are brought to the laboratory in manila envelopes. There, they are conveniently stored in wooden trays and shelved until eventual cold-room storage. The panicles selected each day must be dried rapidly to avoid spoilage or deterioration of quality. In many areas the panicles in envelopes are sun-dried on patios but this practice has several drawbacks, especially increased grain breakage during milling for quality tests.

Breeders should insist on a dryer as an indispensable part of their program. At CIAT, a small electric-heated air dryer was built that holds four wooden trays, each containing about 300 single-plant selections. The air temperature is regulated not to exceed 40°C. The grain is usually dried to 14% moisture or less within 24 hours. Although drying longer or at a higher temperature does not affect viability, it can cause seed to crack. The cracked seeds then break when milled for quality evaluations.

Thresh panicles only after the grain is dry — never before. Since no satisfactory single-plant thresher is available for rice, one of the most efficient procedures is to thresh the dried panicles by hand over grain pans. Clean the threshed grain by blowing lightly to remove sterile spikelets and light grains and then return it to its envelope. If small head threshers are used, an additional pass through a mechanical blower is generally necessary for suitable cleaning (Fig. 35).



35. Cleaning seed of a plant selection with a mechanical blower.

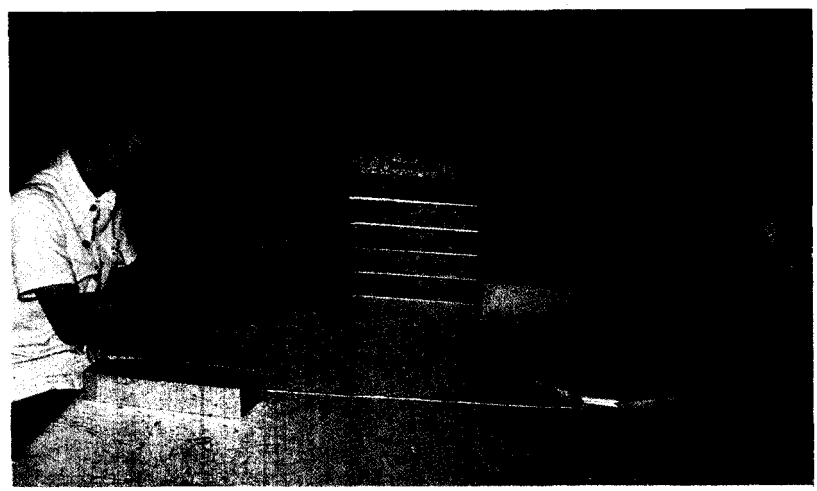
After all selections are threshed, arrange the envelopes numerically according to the field numbers of the selected rows and check the number of plants against the number recorded in the field at the time of selection. Correct discrepancies in the book and determine the total number of selections.

Carry field row numbers, as well as cross numbers, forward continuously for several years to eliminate any possibility of duplicate row numbers in consecutive seasons or years. The first number of the new nurse ry, therefore, should follow the last previously assigned field number. It is preferable to skip a few numbers when necessary so that the first row number ends in 1. Thus, if the previous nursery terminated at 38,692, the new one should begin with 38,701.

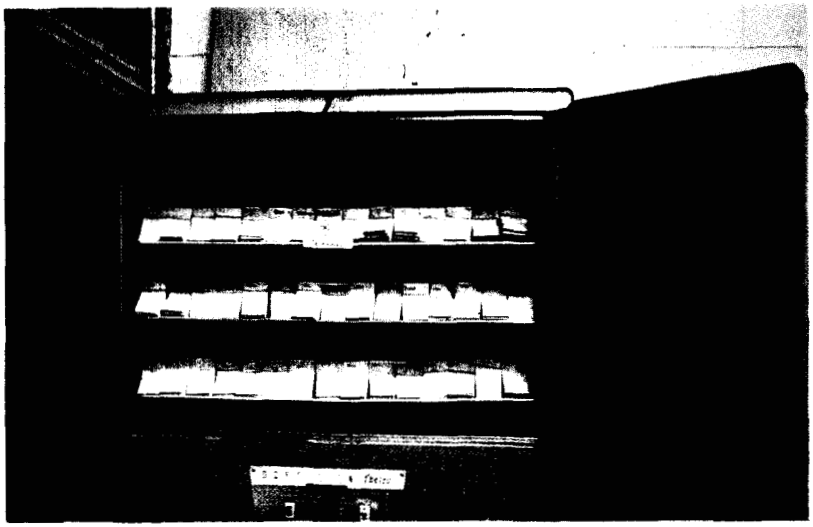
Number the manila envelopes of threshed grain consecutively with a hand numbering machine, skipping all numbers that terminate in 20, 40, 60, 80, and 00. These numbers are reserved for seed of the check varieties, which are planted every 20 rows in pedigree nurseries.

While one worker numbers the envelopes, another prepares the new seeding list. Record the new row numbers in the first column. In the last column list the source-of-origin numbers that correspond to the selected rows in the previous nursery. In the intermediate columns record the cross, pedigree, and generation of each selection. To avoid mistakes, check the numbering of the new seed list frequently against the numbering of the manila envelopes.

The next step is the numbering of small envelopes for each selection (Fig. 36). Three coin envelopes are needed for each selection if each is to be planted in the field, evaluated for quality, and tested for resistance to a single disease in a separate nursery. As selections are given new field



36. Numbering of coin envelopes prior to scooping of seed of the plant selections.



37. Dormancy is broken by placing the seed in an oven for 5 to 7 days at 50° to 55°C.

numbers, place the coin envelopes in triplicate in manila envelopes containing the grain. Set aside coin envelopes ending in 20, 40, 60, 80, and 00 for seed of the check varieties.

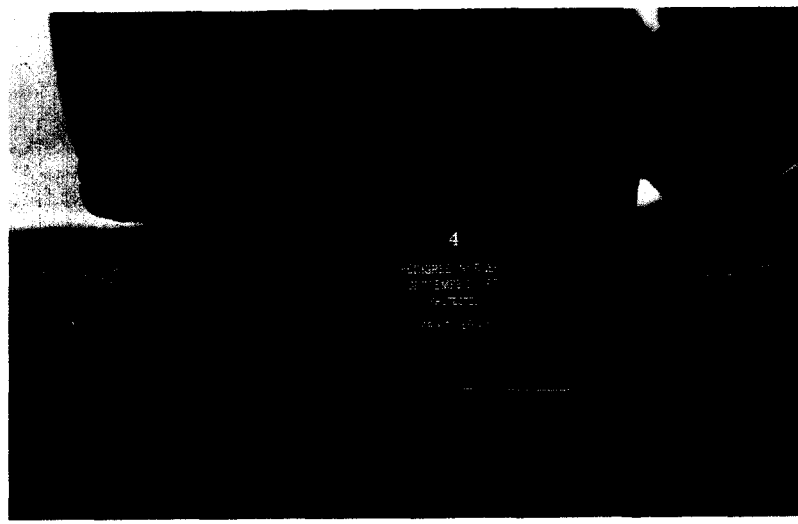
Next place the grain in the coin envelopes. Any small, shallow cap or tube can be used to deliver the appropriate amount of grain to each coin envelope, leaving a small quantity in each manila envelope for reserve to be held in cold storage until the new planting is well established. Then seal the coin envelopes and separate them into the field, quality, and disease nurseries. Prepare and insert the seed of the check varieties into each field nursery and then place the coin envelopes in consecutive order in cardboard boxes marked to indicate their contents.

Place the prepared seed (except that to be evaluated for quality) in controlled-temperature ovens and hold them at 50 to 55°C for 5 to 7 days to break dormancy to permit immediate planting (Fig. 37).

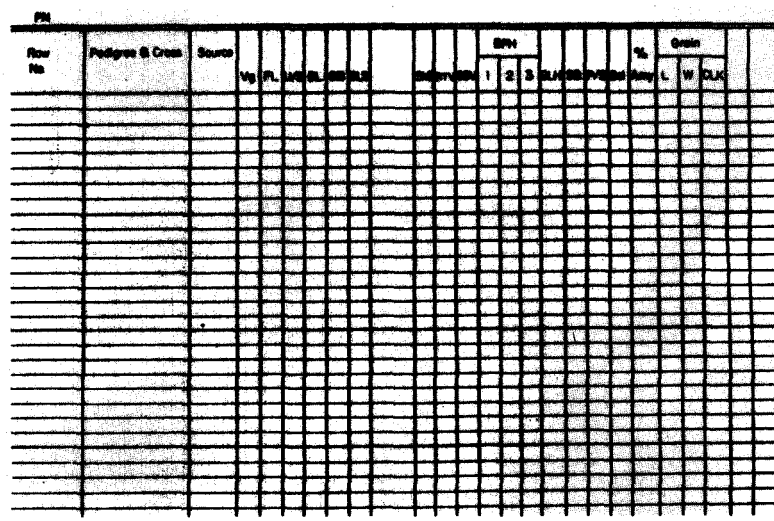
Pedigree books

The paramount requirement of a field book is that it be easy to handle in the field. The book should be small enough to fit into a pocket so that hands will be free (Fig. 38). Larger books are more difficult to handle in the field. However, IRRI has switched to larger field books so that pages can easily be photocopied and distributed to the several scientists involved in the program.

The covers of the books should be hard and waterproof. The CIAT books are 12 × 23 cm and contain about 100 pages, each of which provides space for 16 pedigree lines. Pages are lined horizontally and are divided into vertical columns. On the left-hand page, record the row



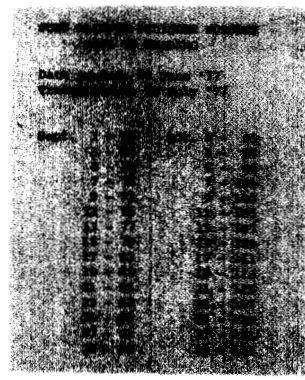
38. Field books should be of a convenient size for use in the field.



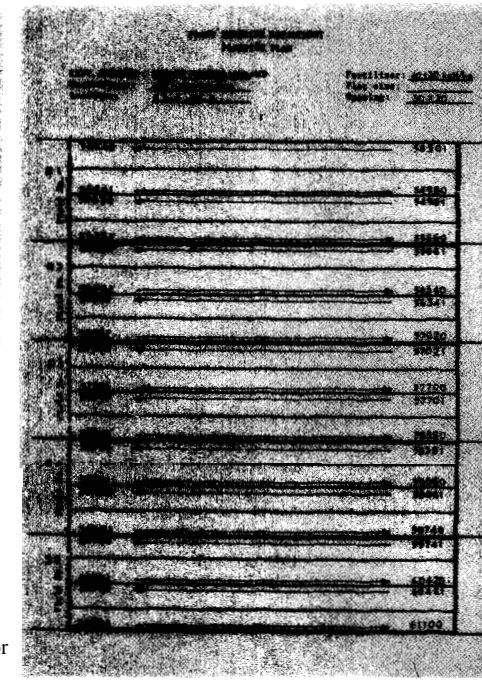
39. Sample pages of a field book for pedigree nurseries.

number, cross, pedigree, source number, and plant generation. On the right-hand page, record quality, disease reactions, and field notes (Fig. 39).

Once the seed list is completed and checked for accuracy, prepare the pedigree books from it. For years at CIAT, the original of each book was copied by hand to protect against loss and field notes were not entered into the copy. Later CIAT suspended the tedious process of preparing copies because a replacement could be prepared from the seed list in the unlikely event that the original book was lost.



40. A calendar is placed in the front of the field book.



41. A field map is prepared prior to transplanting.

A nursery of 6,000 rows requires four pedigree books. This allows four workers to simultaneously record notes in the field and is far preferable to having the entire nursery recorded in a single large book.

Books should never include materials from more than one planting, even if considerable space remains in the last field book or if the second planting closely follows the first. This practice avoids the problem of having to use one book in separate fields.

Mark the hard outer covers of the books to indicate their contents, the beginning and ending row numbers, and the planting date. On the inside cover, place a calendar, starting with the date of planting. Base all notes on the number of days following planting, not on the actual date itself. Thus, the calendar should consist of one column of dates and another column that gives the equivalent numbers of days since planting (Fig. 40). Upland rice breeding nurseries may germinate 2 or 3 weeks after planting if rains are not timely. In such cases, the calendar should begin with the date of seedling emergence.

Prepare a field map in the seed laboratory before planting, showing the first and last row numbers in each block in each field (Fig. 41). Check the distribution of seed envelopes on the map before planting and then staple it into the field book for future use.

Row planting and labeling

Pedigree lines from the F_3 to F_6 or F_7 are customarily grown in 5-m rows, separated by 30 cm. Transplanted rows usually contain single plants spaced at 20-cm intervals, giving 26 plants per row. From 2 to 3 g of seed are sufficient to plant one line. Stake each row before or during transplanting and wire the numbered tag that identifies the seedling bundle to a stake at the foot of the transplanted row.

Directly seeded pedigree nurseries require about 5 g of seed for each 5-m row. This seeding rate is considerably higher than that used for the F_2 because competition of contrasting plant types is not a problem after the F_2 and vigorous, normal densities and growth are important beginning in the F_3. Soon after seedling emergence, stake the plots to record the notes on seedling vigor and tillering. Place a slender bamboo stake at the foot of every fifth row. Wooden pot labels or tags should be cut to 5-cm length, numbered on both sides, and dipped into melted paraffin. They are then wired to the bamboo or wooden stakes. It is too expensive to stake every row in the field. The staking of every 10th row gives inadequate coverage. Collect the stakes after every harvest and reuse them until they deteriorate.

To avoid difficulties of duplicate numbers, run the row numbers consecutively for several years instead of returning to a common starting point each season or year. It is convenient to reserve the numbers from 10,001 to 20,000 for F_2 populations and 20,001 to 99,999 for pedigree rows, while using lower numbers for observation plots and yield trials.

Check rows

Check varieties should be planted at fixed intervals, usually every 20 rows, in pedigree nurseries for comparisons. It is impractical to use the numerous parents of all the crosses in the field as check varieties. Instead, a few varieties should be used that contrast in expression of the major breeding objectives. Thus, the varieties may be changed every few seasons. In the CIAT program, three checks are alternated throughout the nurseries. Bluebonnet 50 is representative of a tall, low-tillering plant type; it has excellent grain quality and is susceptible to both hoja blanca virus disease and its vector. IR8 represents a late-maturing semidwarf that is sensitive to low temperature. CICA 4 combines desired plant type with tolerance for low temperature and resistance to the hoja blanca virus-vector complex. Although blast resistance is a major objective, no resistant varieties are included among the checks because the disease does not occur in the field at the CIAT program headquarters.

Recording notes

Essential to the selection process is a record of frequent field observations, along with quality and resistance data from duplicate nurseries.

Obviously, the efficiency of selection is directly related to the accuracy and completeness of the observations recorded in the field book. Because pedigree lines segregate for many important characters, observations should be expressed as numbers or letters so that a concise array of information can be entered in the field book. Many characters can be conveniently coded on a scale of from 1 to 9, with the number 1 indicating the most desirable expression of the trait.

During the growth of the pedigree nursery additional information is also accumulated from the quality laboratory, and the nurseries for diseases and other factors. Unsatisfactory lines can be eliminated from further consideration by striking out their row numbers in the field books.

The number of days to first flowering or 50% flowering is recorded for each pedigree line in many programs. But flowering notes are not recorded at CIAT because the great amount of work involved is not considered justifiable. This frees time to evaluate more important characters. By stopping plant selection at a predetermined date after planting, the breeder automatically discards unacceptably late lines and ensures that all plants selected fall within an acceptable maturity range. At CIAT, precise data on flowering and maturity are recorded only for material in yield trials.

Selection in pedigree lines

The selection process for pedigree lines is much like that in the F_2, except that selection pressure is stricter because considerably more information is available on line behavior. Selection is highly subjective among and within segregating rows and is more of an art than a science. The ability to efficiently select is aided by a functional system of field book records comprising as many field and laboratory observations as possible. As the data are compiled, many lines will be found unacceptable in one or more major characters. Once identified, eliminate these by crossing out their line numbers in the field book. Since most of the lines in large field nurseries will flower at about the same time, prior discard of inferior lines allows the breeder to concentrate his attention on the field characters of the most promising material during the peak work period from late flowering to maturity.

Field evaluation is initially made among families of related lines. As the lines approach maturity many will be found unacceptable and crossed out in the field book. Remaining lines are individually evaluated by observing plants within the rows for traits not easily seen from the alleys at the foot of the rows. Normally only three, but occasionally as many as six plants per row, are selected. Selection is made from the best row of the family; the other rows are usually discarded. Only rarely are plants selected from all lines of a family.

It is essential to practice a philosophy of strict selection. The first rule of efficient selection is to reject lines that are unsatisfactory in one or more major characters. Breeders must not weaken in determination and select within undesirable rows, justifying the act by saying that the plants might continue to segregate or perhaps be useful in future crosses. This rarely occurs in practice. Most important characters are fixed early and selection within doubtful lines seldom improves the following generation. The weakening of selection pressure inevitably leads to a steadily increasing accumulation of useless material.

A good example is grain shape, which seldom segregates appreciably after the F_3 and is often essentially fixed in the F_2. This means that borderline grain types in the F_2 or F_3 seldom produce more desirable types in the following generation. If desired segregates are not found by the F_3, the material should be discarded. Every bad plant selected consumes valuable space, time, and money in seed preparation, replanting, and evaluation. To err by selecting too rigorously (and, thus, to be able to handle more crosses and larger populations) is far better than to relax selection criteria.

Selection is easier in transplanted than in directly seeded nurseries because there is only one plant per hill and the hills are evenly spaced. As one moves down rows having acceptable plant type, the eyes first focus on grain types. With experience, one can spot plants with good grain at a distance of about a meter. Grasp the panicles of a promising plant in one hand and pull them to the side to check tillering and culm thickness. If satisfactory, cut the panicles with a sickle and pass them to a laborer carrying manila envelopes or bags marked with the row numbers (Fig. 42). The envelopes or bags should be large enough to hold several panicles and

42. Cutting and bagging plant ssselections.

must have ungummed flags. Note the number of selections taken from each row in the field book.

Follow a similar selection procedure for directly seeded nurseries. But because the plants grow closer together there is always a danger of cutting panicles from two or more plants. It is imperative to harvest only panicles of the selected plant. Grasp the panicles with one hand and with the other hand separate the culms of the plant from those of its neighbors at the water level.

It is impractical to avoid mixtures by selecting only one panicle per plant because a large grain sample of each selection is needed for replanting, reserve seed, quality evaluation, and pest-resistance nurseries. A minimum of 10 to 15 g of grain per selection is required, equivalent to 4 to 6 normal panicles.

In active tropical programs several large pedigree nurseries are handled throughout the year so that one nursery is being selected while others are being evaluated. Begin selection as soon as the earliest lines are mature and the pertinent field, quality, and resistance data are available in the field book. Continue at weekly intervals until all of the promising lines are selected. If plants have hard but greenish and immature grain, delay selection until the grain is fully mature. Green grain germinates satisfactorily but breaks excessively when milled for quality studies and is difiicult to evaluate for endosperm appearance.

Assigning pedigrees

Many systems have been developed to record pedigrees. The ideal system combines simplicity with completeness of information. The following system used at CIAT is a synthesis of many systems modified by many workers.

The pedigree begins with a capital letter or letters designating the station where the cross was made. Thus, IR, P, and B indicate crosses made at IRRI, CIAT (Palmira), and Beaumont, Texas, respectively.

The capital letter is immediately followed by the cross number with no dash or space separating them. P6 indicates the sixth cross made at CIAT. Cross numbers are assigned consecutively over a period of several years and are not repeated. Following the cross number with designations of the season or year that the cross was made is not desirable. This information is rarely needed during field operations and is easily obtained by referring to the crossing record book or by counting the number of selections in the pedigree.

Seed of single cross F_1 plants is usually bulked, or is occasionally planted individually, to form an F_2 population that carries only the cross number, such as P752. The next numerical addition to the pedigree is assigned after the F_2 plants are selected, threshed, and counted. The harvested F_2 plants are then numbered consecutively. The F_3 pedigree

numbers are separated from the cross number with a dasn. If 200 plants are selected from the F_2 of cross P752 then the F_3 book will have 200 entries designated as P752-1, P752-2, P752-3 . . . P752-200.

The F_3 rows are evaluated and selections are made from the better ones. If lines P752-1 and P752-2 were discarded and three plants were selected from line P752-3, the selections would be entered in the F_4 pedigree nursery and field book as P752-3-1, P753-3-2, and P752-3-3. Their pedigrees show that all three came from the same F_3 line. This procedure is followed until the selection of individual plants is terminated, usually in the F_6. For example, P752-187-2-3-1 indicates an F_6 line that traces back to the 187th F_2 plant selected from cross P752.

Populations derived from one or more backcrosses or from three-way crosses are assigned pedigrees in the same manner except that one additional number is inserted into the pedigree to identify the F_2 families. For example, the backcross of P752 to one of its parents might receive the new cross number P985. The grain from each selected backcross F_1 plant forms an F_2 family. These families are numbered consecutively in the F_2 field book as P985-1, P985-2, P985-3, and so forth. Selections in following generations are assigned pedigree numbers by the same procedure as for single crosses. Thus P985-18-3-2-1-3 is an F_6 line. Its pedigree carries one more selection number than does an F_6 line from a single cross. This difference causes no problems because single crosses are immediately distinguished from backcrosses by reference to the cross parentage in either the field book or the cross history book.

YIELD TRIALS

Grain yield is a function of yielding ability, resistance to insects and diseases, adaptability to environmental conditions, agronomic practices, and other factors. Although rice workers can readily estimate yielding ability, it is important to have yield data under specific testing conditions and early data on comparative yields.

Early testing

Early estimates of yielding ability are useful. Some workers with other crops begin preliminary yield testing with F_3 or F_4 material that is still segregating. They retain and purify the higher yielding lines and discard the rest. IRRI often yield-tests early generation material but only if it is relatively uniform. Most such testing at IRRI is done with protein work where yield data are necessary to compare lines for protein content. If programs have limited resources, it is better to rely on the plant breeder's judgment of yielding ability in early generations. The causal relationship between plant morphology and grain yield, often known as the plant type concept, allows breeders to observe a few plants of a line or variety and to estimate yielding ability with fair accuracy.

Yield testing can begin with grain from F_5 or F_6 rows, despite continuing minor segregation until the F_6 or F_7 in such characters as awns, pigmentation, maturity, and certain endosperm traits. Select and bulk enough panicles from each promising row to establish an unreplicated observation plot. Also, harvest three superior plants from each promising row to plant in the next pedigree nursery. Determine yield from the observation plot and discard harvested grain after recording the yield data. If the yield is satisfactory, one or all three fixed pedigree rows are available as sources of grain for continued yield evaluation. This practice of early yield testing while the pedigree lines are being stabilized is a valuable aid to the early selection of advanced lines.

Yield testing philosophy

Line evaluation begins long before yield tests. With the pedigree method, strict selection can begin with the F_2 of single crosses. By the time homozygosity is approached, the surviving lines have been repeatedly evaluated for resistance, grain characters, cooking quality, maturity, plant type, and other traits. Haphazard or weak selection in the early generations eventually results in the yield testing of largely useless material.

Yield tests are conducted to confirm preliminary evaluation of characters that are difficult to handle in pedigree lines, such as grain yield, grain-to-straw ratio, lodging resistance, resistance to shattering, milling quality, and adaptability to environmental stresses.

Preliminary and advanced yield trials are assigned various names and are organized differently in distinct rice programs. More variation and controversy is related to the design and management of yield trials than to any other phase of rice improvement. Nevertheless, all yield testing programs have two common paramount objectives:

- Rapid screening of numerous lines to eliminate obviously undesirable ones, and
- Critical assessment of a few highly promising lines to identify potential new varieties.

An active program produces a large volume of promising fixed lines for yield evaluation every few months. This requires efficient preliminary screening and a rate of discard equal to the rapid production of new fixed lines. The rapid screening of hundreds of lines at this stage is more critical than the prolonged, detailed evaluation of a few lines, which follows at the next stage. In the system described next, many new lines are rapidly screened and a few elite materials are critically scrutinized.

Observation plots

The most preliminary yield evaluations are in the observation plots. Seeds for the observation plots come from individually selected panicles from the better F_5 to F_7 lines. About 30 panicles are needed for each line

and each testing site. Carefully inspect the panicles for uniformity in the seed laboratory before bulking their grain. If lines are still segregating slightly, simultaneously plant and purify them in the pedigree nursery and evaluate them in the observation plots.

Observation plots usually have four, or occasionally six, rows, each from 5 to 10 m long. To facilitate the roguing of off-types, space the transplanted plots at 30 × 15 cm, or 20 × 20 cm, with only one plant per hill. Directly seeded plots require about 8 g of seed per 5-m row and are spaced at 30-cm intervals. Observation plots are unreplicated. Scatter check varieties throughout as points of reference to partially compensate for soil heterogeneity and other nongenetic sources of variation.

Use optimum husbandry for those factors that farmers can adequately control. Treat factors that farmers in large areas cannot completely control, such as water depth or transplanting date, as better farmers would handle them. Encourage disease and insect infestations. Observations of line development are recorded in field books every 7 to 10 days from early tillering to flowering. These should be terse evaluations rather than lengthy descriptions. Pay special attention to vegetative vigor, or the rate at which lines close the space between rows and increase in leaf area. Use numerical scales to record notes on traits such as flowering date, spikelet sterility, plant height, leaf condition at maturity, lodging, grain shattering, and resistance. Periodically rogue off-type plants from the observation plots.

As many as several hundred observation plots may be grown each season. Plots that are found inferior before and during harvest should not be harvested. Often, from 10 to 40% of the observation plots are left unharvested. Cut the central rows of the more promising plots that remain, leaving one border row standing on each side. Individually select about 100 panicles from the border rows of uniform plots and check them for uniformity to provide seed for the next cycle of yield trials. Do not use bulked grain from the harvested rows for laterplanting because it is often contaminated during harvesting, threshing, drying, or handling in the seed laboratory.

After drying, cleaning, and weighing the harvested grain, convert yield to kilograms per hectare and record it in the field book. Although it is desirable to correct yields to a standard 14% moisture content, accurate moisture meters are not always available. This potential source of error, however, is small compared with many others and can be ignored if samples are dried with reasonable uniformity.

Milling quality may be determined from samples of 1 kg or smaller and lines that produce a low percentage of head rice can be eliminated. A few grams of milled seed of each harvested line placed in shallow glass-covered seed trays are useful for constant reference to grain size, shape, and endosperm appearance.

Once all of the data are entered in the field book, compare each har-

vested line with those in neighboring plots and with check varieties. The basic criteria for discarding lines are field notes on growth throughout the growing season at various testing sites, along with data on grain yield, disease resistance, and quality. Generally, no line is retained unless it is superior to commercial varieties in one or more major characters and roughly equal in the others. Typically, only from 10 to 25% of the observation plots are superior enough to continue to evaluate in yield trials.

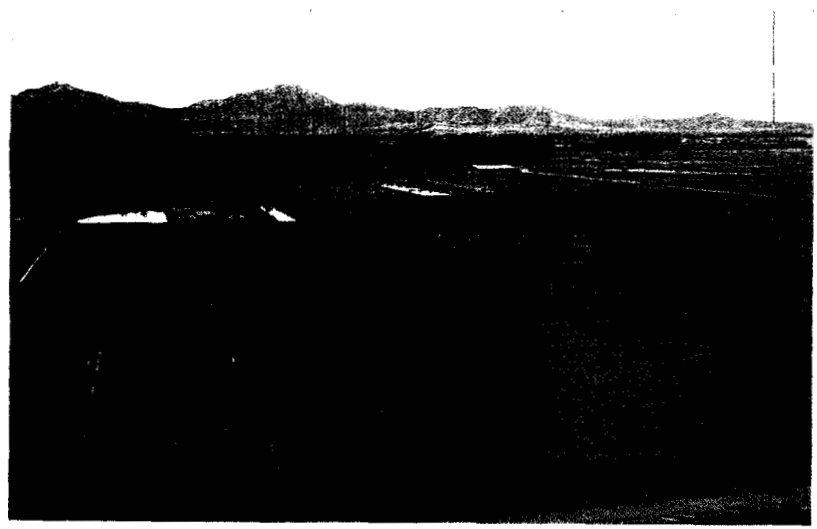
Replicated yield trials

The better lines selected from observation plots are advanced to replicated yield trials for continued evaluation (Fig. 43). These are known as advanced yield trials in some programs, as distinguished from preliminary yield trials or observation plots.

Replicated yield trials differ from observation plots in several respects. They have only from 20 to 40% as many entries. Plots in replicated yield trials are larger, often comprising eight rows, each 10 m long. At CIAT, only two or three replications of larger plots are used. At IRRI and in most programs, the more conventional four replications are used for each set of entries.

The only statistical design that CIAT uses is randomization of the entries within the replicates. The entries are fairly uniform in maturity and essentially all are of dwarf or moderate stature so little attempt is made to group the entries by maturity classes or plant height. But lines must be grouped into maturity classes in some temperate areas where very early maturity is desired for production of a ratoon crop.

IRRI's flexible system of yield testing permits almost any type of comparison, yet is extremely simple. Yield trials are uniform in size and are



43. Replicated yield trials at IRRI.

composed of four replications of 25 entries (including two checks). The plot size is 2 × 5 m, spaced 20 × 20 cm (10 rows, including 2 border rows at each side; harvest area is more than 5 sq m). One yield trial covers exactly half an irrigation block. The design is a partially balanced lattice but it may be analyzed as a randomized complete block. The number of trials formulated is dependent on the number of lines to be tested. There are two check varieties or lines common to each trial, which allows an LSD to be computed and statistical comparison to be made among all entries in all trials. Using this method, IRRI sometimes tests as many as 500 entries (20 trials) per season. Table 1 shows the randomization for the standard trial.

Table 1. Randomization for replicated yield trials at the International Rice Research Institute.

Entry no.	Plot no.				Entry no.	Plot no.			
	I	II	III	IV		I	II	III	IV
1	24	27	58	98	14	13	49	61	85
2	21	39	64	86	15	11	42	74	95
3	23	32	75	82	16	10	26	71	90
4	22	50	52	92	17	07	38	53	83
5	25	41	69	79	18	08	34	68	91
6	02	29	67	84	19	06	46	56	80
7	05	40	60	93	20	09	45	62	00
8	03	35	63	77	21	19	28	65	94
9	01	48	72	96	22	20	37	73	76
10	04	43	55	88	23	18	33	54	99
11	15	30	51	78	24	17	47	70	87
12	14	36	66	97	25	16	44	59	81
13	12	31	57	89					

Details of the analysis are available from the IRRI Statistics Department. Complete standardization of yield testing enables IRRI, within 30 days, to harvest the yield trials, analyze the data, decide which lines are to be further evaluated, and plant the next set of trials.

CIAT does not statistically analyze yield data and that is probably not worthwhile for most programs. Statistical analysis of yield differences at the last minute is too often substituted for constant visual evaluation of the yield trial entries throughout their growth stages. Breeders in temperate areas harvest once a year and have all winter to analyze yield data. But workers in the tropics are under constant pressure to replant as soon as possible after the last harvest. In tropical areas, continuing yield testing without delay is more important than taking the time to analyze yield data. Workers who argue that they have reached a yield plateau and the yield variation among their trial plots is so limited that analysis is required to determine differences would be better off spending their time and energy to identify and overcome yield-limiting factors.

A final major difference between yield trials and observation plots is that yield trials should be replicated over diverse locations while observation plots are usually conducted at only a few breeding stations because of seed limitations and the large number of entries. In the Colombian program, for example, yield trials are conducted at the headquarters and at three widely separated substations within the country. Seed is also provided to cooperators in several other Latin American countries. Replication over several areas is more valuable than an increase in replicates at one location.

Workers at the Colombian headquarters visit all of the plantings at least once each season. After the harvest, the local workers responsible for each trial meet to review each entry. In almost every trial, many lines that perform well at the program headquarters and at certain stations show limiting defects at other sites. This clearly illustrates the need to identify and discard inferior material through wide testing and continuous field observation before they reach commercial use as named varieties. The greatest weakness of yield trials throughout the world is inadequate testing of advanced lines over many distinct environments. Not only is prolonged testing at one location a poor substitute for wide testing, it also forms a bottleneck that limits the entire program's progress and leads to the release of narrowly adapted varieties.

Notes taken in yield trials are identical to those recorded in observation plots except that essentially all entries are harvested. Otherwise, entries are rejected for the same reasons as in observation plots. Grain yield is usually recorded from the central four rows of the eight-row plots. From 150 to 200 panicles are individually harvested from the border rows to provide seed for continuing yield trials. Lines are seldom evaluated more than twice in yield trials before they are either discarded or advanced to regional trials.

Regional trials

The most promising lines identified from one or two series of previous yield trials are tested in regional trials at experiment stations and on rice farms. The average number of entries tested is about 10, although it may reach 15, including 1 or 2 check varieties. Plots of each entry range from 100 to 1,000 sq m, and are normally replicated only once if at all.

The objectives of regional trials are to evaluate potential new varieties on farms and to provide sites for off-station field days. For regional trials, select cooperating farmers who will provide plots with uniform soil and water, and will care for them throughout the growing season. Regional trials should be selected in cooperation with local extension workers and located along main roads so that they are highly visible to local farmers.

Regional trials are difficult to manage because daily supervision is usually impossible. If possible, well-trained extension specialists in the

immediate area should be assigned to one or more trials. The highly visible regional trials must receive optimum care because poorly managed trials reduce the credibility of researchers in the eyes of farmers. The person in charge should not identify the trial with signs until he is certain of success. Field days should be scheduled only if the plots are in good condition and if at least one line is so outstanding that it will probably be released as a new variety.

It is remarkable how often lines that passed successfully through the pedigree nurseries, observation plots, and yield trials are found to have major weaknesses in regional trials. Therefore, the breeder should conduct as many regional trials as possible, concentrating on areas that differ from the experiment stations.

Regional trials are difficult to harvest and thresh because the plots are large and often far from experiment station facilities, and no satisfactory high-volume, self-cleaning threshers are available for these purposes. The best procedure is to carefully select the sample areas in each plot, harvest by hand, and thresh them in the field by beating the cut plants against empty fuel drums placed over large cloth or plastic sheets. The bagged grain is then transported to the experiment station for drying, cleaning, and calculating yield.

INTERNATIONAL TESTING

Participation in the International Rice Testing Program (IRTP), headquartered at IRRI and CIAT, offers an excellent opportunity for rice improvement programs to have their best materials tested in a wide range of environments. The information gained in one year can be more useful than several years of data from one location or even several locations within a region. The stability of resistance to diseases and insects can be assessed better because materials are simultaneously exposed to a complete spectrum of strains, biotypes, and races.

Further, cooperating rice workers have routine access to the best improved materials from all programs. This valuable influx of diverse material prevents stagnation and reliance on narrow genetic bases. This is often a problem in smaller programs where the scientists lack the resources and opportunities to travel and therefore have limited exposure to other scientists and programs.

BREEDERS' SEED

Two years of yield trials and regional and international tests in several locations are normally adequate to decide ifadvanced lines should be discarded or multiplied for possible release as new varieties. Breeders are then often faced with the problem of having identified several excellent lines without bring certain which should be named as a variety. The breeders' seed procedure allows the breeder to simultaneously multiply

seed of the leading candidates and narrow them to the best one or two.

For this procedure, assume that six lines have been outstanding during two series of yield trials and one of regional trials. Select 600 panicles of each line individually from either yield or regional trials. Inspect them for uniformity of grain types in the laboratory and thresh each one separately. To speed seed multiplication, transplant the material if possible.

This first cycle of multiplication, conducted on the main experiment station, should coincide with the second series of regional trials on private farms. Transplant the material in single-plant hills to facilitate roguing. Inspect each row frequently during crop development and destroy occasional off-type plants in otherwise normal rows. Distinct rows are eliminated.

Constant evaluation of the six lines in the regional trials and multiplication plots results in the identification of the one or more lines most worthy of being named as a variety. To avoid mixtures, use extreme care when the field seed is bulk harvested, dried, cleaned, and bagged. Under normal conditions, 1,000 kg of seed is harvested from the 600 panicle rows. About 300 kg of seed of the line is stored in an air-conditioned room as breeders' seed, to be used for subsequent production of foundation seed in future years. The seed usually retains its viability for 5 years or longer when held at moderately low temperature and relative humidity. The breeders' seed is carefully separated and labeled to prevent mixture with other seed lots. If questions are raised about varietal characters, the breeders' seed is the ultimate source.

Once dormancy is lost, all or part of the other 700 kg of breeders' seed is replanted in a final series of regional trials and on the experiment station to produce foundation seed. The area planted depends on the volume of grain needed for distribution to producers of registered seed in the following season. The 700 kg will produce from 10 to 20 ha of foundation seed, depending on the planting method. Twenty hectares should produce 100 t of foundation seed, enough to transplant 2,500 ha or to directly seed 800 ha for production of registered seed.

The breeder does not normally produce foundation seed, but he is responsible for periodic inspection of the fields. The final decision to name the outstanding line as a variety is the result of field inspections and data from the simultaneous regional trials. Once this decision is made, the harvested foundation seed is turned over to normal channels for distribution to authorized growers of registered or certified seed. In areas where there is no system to produce registered or certified seed, the foundation seed may be distributed directly to commercial farmers. This was how IR8 was first distributed in the Philippines.

The amount of seed released to growers depends on the land area used in previous multiplication steps. For larger fields of breeders' and foundation seed, start with more panicle rows. Transplanting throughout the

process greatly increases the rate of seed increase. Tillers of 30- to 40-day-old seedlings are sometimes separated and retransplanted to increase the area of seed production. One can expect an increase of at least from 1 to 50,000 kg in less than a year when the field of breeders' seed is transplanted and the foundation seed field is directly seeded. Transplanting at both stages easily doubles that rate.

Breeders' seed is produced by more sophisticated and involved methods in some temperate areas to ensure stricter varietal purity. But minor residual segregation in noneconomic characters is rarely an issue in developing countries where seed is often of questionable quality. The method outlined above produces an adequate stock of seed in a minimum of time. The number of panicles selected at the beginning of the procedure can obviously be varied to regulate the volume of breeders' seed produced.

To summarize the length of time required to produce a new variety: observation plots are begun with the F_6, yield and regional trials in the F_7 and F_8, breeders' seed production and continuing regional trials in the F_9, and foundation seed production and the final regional trials in the F_{10}. Therefore, a program that advances at the rate of two generations a year should provide seed of new varieties to farmers about 5 years after crosses are made.

VARIETAL DESCRIPTIONS

Once a new variety is named, the breeder customarily prepares a varietal description to register it. These descriptions are usually perfunctory and simply list the more important distinguishing and economic characters of the variety. The breeder, nevertheless, should be cautious on two aspects of the varietal description.

First, he should not ignore varietal weaknesses while emphasizing the virtues. For example, if the variety is susceptible to a disease or tends to shatter when allowed to overripen in the field, this should be declared in the varietal description and in any printed information that accompanies the seed. This alerts farmers and processors and gives them time to take remedial action. It is also infinitely easier to honestly describe the variety at the time of its release than to explain defects after they appear on farms or in mills.

Second, the breeder should use care in describing traits, even unimportant ones, that are markedly or subtly influenced by environment. In some cases, he can give a range in expression of the character. In other cases, he may have to resort to ambiguity to avoid future difficulties. For example, when the varieties CICA 4 and IR22 were released in Colombia, they were described as awnless on the basis of numerous observations of yield and regional trials. Although both had produced a few tip awns in seed certification fields in one small area, neither variety had produced

awns in any subsequent experimental plantings. Because the varieties were originally described as awnless, several seed fields were initially rejected for certification on the basis of having a few awned plants. The problem was resolved only after lengthy debate and progeny tests showing that the awned plants were not mixtures. Yet the entire difficulty could have been avoided by including in the varietal description: "may occasionally produce a few small tip awns." Other cases have been reported of finding an occasional gold hull segregate in a straw-colored variety or a pigmented segregate in a colorless cultivar.

Reporting of yields in official varietal descriptions should be handled with care. Comparisons of yields of the new variety and several standard commercial varieties should be included. However, a specific yield level should never be claimed for any area or set of conditions. Such a statement as "variety A yields 6 t/ha in Shangri-La during the wet season" is an obvious target for any farmer who harvests less because of poor weather or inadequate management.

CHAPTER 4

Setting breeding objectives

SUCCESS IN PLANT BREEDING depends on three major factors:

- a clear definition of specific objectives,
- satisfactory genetic sources of desired traits, and
- adequate tests to identify superior plants.

Vague objectives such as "breeding for high yield" result in frustration and failure. The pertinent question is "what factors limit yield?" Such factors could include weak culms and lodging; inadequate tillering; mutual shading due to poor leaf morphology; inappropriate growth duration for the climate; sensitivity to low temperature; disease or insect susceptibility; or combinations of these and other factors. Once the basic problems are understood, specific breeding objectives can be set.

If new varieties are to be commercially accepted, varieties of improved plant type must have the specific grain characteristics preferred in each consumer area. It is paradoxical that consumer preferences for grain appearance and cooking quality are so pronounced in areas that are chronically deficient in food. But such preferences exist and changing quality traits is easier than altering human preferences.

The first improved semidwarfs released by IRRI and other programs were relatively inferior in milling and cooking quality, which affected their rates of adoption. In extreme cases, farmers who were heavily penalized for quality defects returned to the low-yielding traditional varieties. The press publicized these early problems, leading some workers to conclude that the dwarf plant type could not be combined with superior grain quality. Fortunately, that is not true. There are no barriers to the union of improved plant type with any combination of grain size, appearance, or cooking quality.

Excellent sources of almost all important plant and grain characters are available within the enormous varietal diversity of rice or will be found through further screening. Breeders have not generally used species closely related to *Oryza* to improve cultivated rice, except in the case of resistance to grassy stunt virus disease.

It is fashionable to propose the induction of mutations as a source of character variability, especially among workers who are not aware of the existing natural diversity. A review of the literature on mutation breeding of rice shows that the bulk of the work has been in the inducement of

such common and naturally abundant characters as short culms, earliness, grain size, nonshattering, or high tillering. There is no reason to induce mutations for additional sources of characters at the expense of conventional breeding practices when most natural sources have not yet been exploited. A realistic evaluation of breeding priorities based on the needs of the rice industry and rice consumers would show that mutation breeding is normally more detrimental than beneficial during the first several years of improvement programs in both temperate and tropical regions. The use of induced mutations should be limited only to an established program that is highly productive and has exhausted most natural sources or characters. Nevertheless, the induction of solid culms, yellow endosperm, or fragile glumes such as those of wheat would be an extraordinary valuable contribution to rice breeding.

Although excellent sources of needed characters are available, the best often are not used because breeders are not aware of their existence. Breeders should recognize their obligation to make available information concerning newly discovered sources of important characters. IRRI maintains a massive world collection of such rices, most of which have been evaluated for many characters. Detailed information is available to any breeder on request.

Rice has been the subject of considerable genetic study, much of which has been useful to rice breeders. But unfortunately too much time and money have been spent on study of characters of little or no economic value. Furthermore, the genetics of several important characters have not been thoroughly studied, including total protein, amino acid distribution or content, amylose content, gelatinization temperature, endosperm chalkiness, low temperature tolerance, and resistance to many diseases, insects, and soil problems.

But breeders do not generally have time for genetic studies. When working with a character of unknown inheritance, they cannot wait for genetic analysis before beginning their crosses and selection. Genetic information is not indispensable to breeding success. Examples include the splendid improvement of rice made by primitive man as well as improved varieties recently developed by scientists. Nevertheless, information on modes of inheritance and heritability estimates makes selection procedures more effective.

Rice breeders are particularly fortunate because many important characters are simply inherited and major genes seem to play an unusually prominent role in quantitative inheritance. Despite this, unfavorable genetic linkages have never prevented the recombination of any important characters — donors have always been found without linkage problems. Another common and peculiar feature of rice is that many quantitatively inherited characters are fixed rapidly, emphasizing the need to test for character expression on large populations in the F_2 and F_3.

Most tests presently used for specific objectives adequately differentiate between good and bad plants. But any test can be further improved. Evaluation of a few important characters remains unsatisfactory because the available tests are expensive, delicate, time consuming, unreliable, or inefficient to apply to large numbers of individual plants. Examples include photosynthetic efficiency, amylose content, milling quality, shattering, and resistance to sheath blight and many pests. Rice breeders have great opportunity to increase the efficiency of these and other tests.

The following chapters treat the more critical aspects of specific breeding objectives for the tropics: characters, sources, inheritance, testing techniques, and difficulties in handling characters.

CHAPTER 5

Breeding for agronomic and morphological characteristics

HEIGHT, LODGING RESISTANCE, AND NITROGEN RESPONSE

SHORT AND STURDY CULMS, more than any other character, determine lodging resistance, favorable grain-to-straw ratio, nitrogen responsiveness, and high yield capacity. Early lodging of long, thin culms disturbs leaf arrangement, increases mutual shading, interrupts transport of nutrients and photosynthates, causes sterility, and reduces yield. Short and thick culms resist lodging and reduce respiration loss from the culm.

The most outstanding advance in rice breeding in recent years was the discovery of the significance and usefulness of the Chinese dwarfs Dee-geo-woo-gen, I-geo-tze, and Taichung Native 1. These varieties and several other less known natural and radiation-induced dwarfs carry the same recessive major gene for short culms. They are unique in that their dwarfism does not affect the panicles or spikelets. The Dee-geo-woo-gen gene for dwarfism has been introduced into an array of improved indica varieties and lines and, more recently, into japonicas. These improved materials are more useful as parents than the three original Chinese dwarfs because short stature is combined with many other desirable characters.

A limited number of useful sources of short, stiff culms is available, including both polygenically inherited short varieties and Mendelian dwarfs. A few varieties with quantitatively inherited short culms such as Century Patna/SLO 17 are known. They are less useful than some of the monogenic dwarfs because when crossed with tall genotypes, they segregate widely and continuously for plant height. Most simply inherited dwarf mutants have abnormal panicles and grains. They have not been useful as parents because of the difficulty of recombining short culms with normal inflorescence structures. No dwarf useful in breeding programs has been found with a dominant single gene that controls short stature.

The heritability of dwarfism is high and it is easy to identify, select, and recombine with other traits. Dwarf segregates can be identified with fair accuracy among seedlings pulled from seedbeds, so many tall seedlings can be discarded in transplanted populations. In later stages of development, dwarfs are easily identified in the field. They always have short culms with short leaves, often of a deep bluish-green cast. Dwarfs usually, but not always, tiller profusely.

Dwarf segregates have a fairly narrow range in height, presumably from minor gene action. Although a few are so short that they are undesirable, the great majority fall within the useful range of from 80 to 100 cm with some reaching 120 cm under certain conditions.

But not all dwarf plants have sturdy culms — some lodge. Although principally related to short stature, lodging resistance also depends on other characters including culm diameter, culm wall thickness, and the degree to which leaf sheaths wrap internodes. The breeder in the field cannot evaluate anatomical traits or leaf sheath wrapping but he can use high levels of nitrogen and observe culm height and thickness. It is almost impossible to identify and evaluate dwarf segregates in nitrogen-deficient populations. One way to estimate a plant's culm strength is to bend it about half-way over and then release it. The speed and degree to which it regains its upright position is a reliable indicator of culm strength and lodging resistance.

Direct measurement of plant height takes too much time to practice in segregating generations. Start it in observation plots by measuring about five plants per plot from ground level to the tip of the tallest panicle. Although both panicle length and culm height may be measured, panicle size varies relatively little among lines. It is never practical to measure only the culm height from ground level to the base of the panicle.

Line rejection based on lodging must be judicious in observation plots and yield trials. For example, the variety IR20, which has rather thin culms, consistently lodged more than IR8 and other lines when it was being evaluated in experiment station and regional yield trials at high nitrogen levels.

But IR20 usually lodged late, which did not affect yield much. Despite some concern about its lodging, IR20 was released because of its superior disease and insect resistance. IR20 immediately became commercially important in the transplanted-rice areas of tropical Asia where it seldom lodges because farm use of nitrogen is low.

During the 1960's breeders made excellent progress in the development of other dwarf varieties that responded to heavy applications of nitrogen. These varieties rapidly covered the tropical areas where farmers had good soils and water control and could risk investment in nitrogen. Heavy doses of nitrogen paid off because of the relative prices of fertilizer and grain. But application of massive levels of fertilizer to breeding material almost certainly prevented the selection of segregates with the ability to perform well under low-nitrogen stress.

The recent discovery that anærobic bacteria fix substantial amounts of nitrogen in flooded rice soils opens a fascinating, totally new area related to nitrogen response. These bacteria appear to use root exudates and debris as energy sources. It seems logical that varieties would differ both quantitatively and qualitatively in the production of these energy sub-

strates. If so, then varieties may be selected that can grow and yield better at moderate levels of natural soil nitrogen. In other words, perhaps varieties can be bred for tolerance for nitrogen deficiency.

Although farfetched at first glance, this possibility would have immense economic value for the huge rainfed areas where rice production is so dependent on weather that farmers cannot risk cash for fertilizer. Furthermore, fertilizer costs are increasing as fossil fuels are being depleted, and the public is increasingly concerned with water pollution. These factors suggest that rice breeders and microbiologists should investigate the feasibility of breeding for low-nitrogen tolerance.

This subject is so new that no breeder had begun to develop a methodology to evaluate parents and progeny for differences by mid-1977. But one procedure might be to eliminate the addition of nitrogen to at least some of the segregating generations, since added nitrogen could inhibit its bacterial fixation. A return to the unimproved, tall, leafy plant type would probably be a step backward. A better plant type might be of moderate height with short leaves.

ELONGATION ABILITY

Certain rice areas in tropical Asia and Africa (and potential areas in Latin America) are subject to prolonged and deep flooding at depths ranging from 1 to 5 meters. In such areas, farmers grow floating rices with internodes that elongate as the water rises and with adventitious roots at the upper nodes. Such varieties are low yielding; little plant breeding has been directed to the development of improved varieties for such extreme conditions. Presently, rice production in the deepwater areas can be increased only by constructing costly drainage and water control systems or by developing techniques to harvest in deep water before the fields drain naturally and plants lodge.

But in large rice areas of Asia and in huge areas of potential rice lands in Latin America, fields flood no deeper than from 40 to 100 cm, often for short periods. The genes that control the floating character are also valuable for improved varieties for these water areas of moderately deep water.

Through cooperative programs with Thailand and Bangladesh, IRRI has crossed deep-water varieties with improved dwarfs and has selected lines in which the floating habit is combined with dwarfism, sturdy culms, erect leaves, and high tillering ability. Plants with both floating and dwarf genes may be superior to the traditional floating or the nonfloating tall varieties for areas of limited flooding. The hybrids remain short in shallow water but elongate as water rises. Scientists are working to develop an array of these deep-water dwarfs with weak to strong photoperiod sensitivity and a range of maturity and grain types. Selections from the IR442 cross have many good traits but they lack

photoperiod sensitivity and adequate disease resistance. IR442 lines are particularly promising as parents in future crosses. The floating genes in IR442 are from Leb Mue Nahng and the dwarf genes are from a selection of Peta*2/Taichung Native 1. Many more unimproved sources of floating genes are available from the IRRI collection or from national programs in tropical Asia. Apparently, all of the floating varieties are photoperiod sensitive and most have poor grain quality.

Several genes probably control the floating habit, although early work has reported duplicate and triplicate factor inheritance. Dwarf floating segregants are difficult to identify; special testing conditions are required that are not available at the international centers. To test for deep-water tolerance, the water level is raised gradually after the plants pass the tillering stage and is then maintained at a depth of from 60 to 100 cm. Such tests are usually conducted in level fields with high levees or in flat areas that are invariably subject to natural deep flooding. A better technique might be to plant on sloping fields so that line performance could be evaluated at different water depths.

Segregates that emerge through water but do not elongate excessively should be selected for continued testing if they tiller well and produce normal yields. Such traits may best be handled by a modified bulk system featuring large populations, strict selection for elongation in moderate depths beginning in the F_2, and intercrosses of the better-adapted dwarf segregates.

VEGETATIVE VIGOR

Plants with early vegetative vigor (that rapidly fill in the space between plants and rows) are desirable if such vigor does not carry through to excessive growth and mutual shading after panicle initiation. Early vigor is as important for directly seeded as for transplanted crops because it decreases weed competition, compensates for missing plants and low seeding rates, and helps ensure that the crop achieves its critical leaf area at flowering. Vigor is associated with various combinations of rapid seedling emergence and development, early and heavy tillering, moderately long and initially droopy leaves, and early and rapid increase in seedling height. Vegetative vigor is poor in moderately short types that tiller poorly, including varieties from the USA and Surinam as well as most upland and japonica varieties. A few tall, low-tillering varieties adapted to direct seeding are strongly vigorous during early growth. Early vigor is usually strong in unimproved tropical varieties, but their vegetation is usually excessive at flowering. Furthermore, they are too tall and lodge. Several dwarf, indica types, including CICA 4 and other selections from the IR930 cross, have excellent vegetative vigor combined with initially droopy leaves, erect adult plant habit, and a slow growth rate after reaching the critical leaf area. Although dwarf lines vary

greatly, their early vigor is usually less than that of tall, traditional varieties.

Material should be rated when clear differences in the early vigor are observed in the pedigree nurseries — at about 40 to 50 days after seed germination, although it may be later in cool areas or if nitrogen is deficient. Vigor cannot be accurately rated in seedbeds prior to transplanting. Evaluating individual plants for vigor is difficult, so notes are first taken on a line basis in the F_3, and are continued through yield trials. Material is rated on a 1–9 scale.

When vigorous dwarfs are crossed with low-tillering, nonvigorous varieties, a single backcross to the vigorous parent greatly increases the probability of finding useful F_2 families and F_3 lines. Although inheritance of early vigor has not been critically studied it is obviously quantitative. Unfortunately, strong early vigor has not yet been combined with very early maturity, but early vigor combines easily with other important characters such as short stature, intermediate maturity, and photoperiod insensitivity. Although the heritability of early vigor is low, evaluation and selection can definitely result in measurable breeding advance.

TILLERING ABILITY

A combination of high tillering ability and compact or nonspreading culm arrangement is desirable for all rice farmers. Compact culms that are moderately erect allow increased solar radiation to tillers — less mutual shading per unit of land area. In improved plants, heavy tillering is preferred over medium or low tillering. Because dwarfs do not have an optimum leaf area index, heavy tillering does not result in excessive plant size or mutual shading.

Some scientists argue that a single tiller is best for maximum yield potential in some cereals. At heavy seed or seedling densities, which are necessary for high rice yields, profusely tillering varieties will form few culms per plant but still produce more in total than low-tillering varieties. Heavy tillering compensates for missing plants at low densities, but varieties with limited tillering capacity lack this plasticity. Thus, heavy tillering is desirable for maximum productivity with both moderate and dense populations. We note with interest that the newer japonicas from Japan show a continuing increase in tiller number in association with higher yielding ability.

Developing good plant types with high tillering capacity is rather simple. Many sources of heavy tillering are available in traditional tropical rices. When their culms are shortened, their tillering ability generally does not decrease — and may increase. Crosses that include one high-tillering parent have a high frequency of segregates that tiller heavily.

Tiller number is quantitatively inherited. Its heritability is low to intermediate depending on the cultural practices used and the unifor-

mity of the soil. Although often associated with early vigor in short-statured materials, tiller number is inherited independently of all other major characters. In many crosses, tiller erectness or compactness is recessive to a spreading culm arrangement.

Field evaluation of tiller number and compactness is relatively simple, even in directly seeded material, if breeding plots are located on uniform soil, weeds are thoroughly controlled, and nitrogen and other nutrients are adequate. Visually estimating the tiller number is much faster and almost as accurate as counting the culms of several plants. Selection of individual F_2 plants for tiller number is possible but the rating of lines beginning in the F_3 is more accurate. The undesirable spreading arrangement of culms is easily detected in individual plants after flowering.

Heavy tillering as a breeding objective requires particular care in direct-seeded rice programs. There is strong empirical evidence that direct seeding of populations slowly but progressively results in natural selection against heavy tillering and eventually produces relatively low-tillering materials. For example, this appears to have occurred over many years in direct-seeded rice programs in the USA and Surinam. Breeding materials that are transplanted do not seem to suffer natural selection against tillering ability. This loss of tillering may be counteracted by seeding at low rates in the F_2 to facilitate identification of profusely tillering plants; by strictly selecting for high tillering; and, when possible, by periodically transplanting the F_2 and observation plots.

LEAF CHARACTERS

Leaf erectness

Erect leaves after panicle initiation is the most important leaf character associated with high yielding capacity. Erect leaves permit greater penetration and more even distribution of light into the crop and, thus, higher photosynthetic activity.

All progeny of the Chinese sources of dwarfism have moderately to strongly erect leaves after panicle initiation. Leaves of some lines are excessively erect; this trait is often associated with low tillering, resulting in a loss of light interception. Leaves of a few dwarfs, including IR930 selections, are rather lax during vegetative growth but become erect after panicle initiation. These are probably more desirable than leaves that are erect throughout the life cycle because they contribute to early vegetative vigor.

The erect leaves seem to be the result of a pleiotrophic effect of the dwarf gene. Therefore, this trait follows a simple recessive mode of inheritance. The erect-leaf trait is highly heritable, is easily observed at early flowering, and is easy to visually rate in pedigree rows or fixed lines. At CIAT and IRRI, notes on leaf erectness are usually not recorded in the

field books but tall selections with drooping leaves are automatically discarded before and after panicle initiation. Lines that have lax leaves before panicle initiation and erect leaves afterward are especially valued.

Leaf length, width, and thickness

Leaf length is extremely variable in rice. Because leaf angle is directly associated with leaf length, short leaves are more erect than long ones. Short leaves are more evenly distributed throughout the canopy so mutual shading is reduced and light is more efficiently used.

All dwarf varieties have short leaves. Tall varieties usually have long leaves, although some are relatively short. These strong associations suggest that leaf length in both dwarf and tall types is a pleiotrophic effect of genes for plant height.

Leaf width is less variable than length but obvious differences are found within both dwarf and tall materials. Although little attention has been paid to width in relation to yielding ability, field observations suggest that leaves that are narrower than those of varieties such as IR8 are desirable. Several newer lines have combinations of narrow leaves, early vigor, heavy tillering, long panicles, and exceptional yielding ability. The extent of genetic association among these characters is unknown. Narrow leaves are assumed to contribute to higher yields because they are more uniformly distributed than wide leaves and cause less shading within the canopy. Little is known about the inheritance or breeding behavior of leaf width. Leaf width is difficult to estimate visually in individual plants although segregates with narrow leaves can be identified on a row basis.

Leaf thickness has been related to high yielding ability through increased photosynthetic rate per unit of leaf area. Some highly productive varieties, however, have relatively thin leaves when either transplanted or directly seeded. This suggests that the character does not have an important, direct relationship to yield potential. Leaf thickness may have value for some areas because it is directly associated with leaf toughness. Leaf thickness is not presently evaluated in breeding programs because it is impossible to rate visually with consistent accuracy.

Notes are seldom recorded on leaf length of breeding lines until harvest because the trait is so easy to evaluate visually. Short leaves are automatically recovered in dwarf selections because of the pleiotrophic effect of the dwarfing gene on leaf length. For intermediate-statured types for rainfed areas, somewhat longer leaves may be desirable to enhance competition with weeds.

Leaf toughness, color, and senescence

Leaf toughness is desirable only for areas where intense winds shred and break leaves. Toughness seems to be directly associated with leaf thick-

ness and lignification of the leaf tissues. Most japonica varieties and many from the USA are good genetic sources for tough leaves. No artificial technique has been developed to test this character; toughness can be evaluated and selected only when strong winds cause damage.

Dark green leaves were formerly associated with high yielding ability because they enhanced the absorption of light. Although leaf color may eventually prove to affect yield, several high yielding dwarf varieties, including CICA 4, have pale leaves. This suggests that leaf color has little practical importance in selection for yielding ability.

Some breeders feel that slow senescence of the upper two or three leaves is desirable because, theoretically, it allows active photosynthesis and grain filling until the grain is fully mature. Although this thesis is not supported by either conclusive physiological evidence or breeding effort for delayed senescence, field observations suggest that delayed leaf senescence may be important. Rices vary considerably in rates of leaf senescence. Some rices, including most japonicas, retain functioning green leaves at harvest while leaves of others begin to deteriorate before grain maturity. Delayed senescence and leaf toughness are often found in the same varieties, which may indicate a common physiological or anatomical cause. Slow senescence of the upper leaves is easy to evaluate visually at grain maturity.

Breeders lack accurate information on the inheritance, heritability, or breeding behavior of leaf toughness, color, and slow senescence. It is doubtful that any program presently considers these traits as major breeding objectives or makes a concerted effort to select for them.

Glabrous leaves

The leaves and spikelets of most rice varieties are pubescent, but those of a few are glabrous or smooth with few or no bicellular trichomes. No varieties have pubescent leaves and glabrous glumes, or vice versa. Glabrous rices do not irritate workers' skin during harvesting, threshing, drying, and milling. Thus, glabrousness is fairly desirable, particularly where rice culture is highly mechanized. It is doubtful that any tropical program places much emphasis on glabrousness. Smooth plant parts are probably not associated with yielding ability or reaction to insect or disease attack.

All important varieties in the southern USA, some in Surinam, and a few other indicas are glabrous. Apparently all japonicas are pubescent. The USA varieties are good parental sources of glabrousness because they also have several other desirable traits. Good glabrous dwarfs would be preferred to the USA material and some are now available at IRRI.

Glabrousness is controlled by a single recessive gene and environment does not affect its expression. Because glabrousness is exceptionally easy to evaluate in individual plants, selection can begin in the F_2 as soon as

seedlings are growing rapidly, although larger plants are more convenient to work with. To evaluate, pass the fingers lightly over the surface of any leaf from the tip toward the base of the leaf blade. Glabrous leaves are smooth to the touch; pubescent leaves are rough. The leaf reaction always characterizes the condition of the spikelets. Despite its simple inheritance and ease of evaluation, CIAT has had considerable difficulty in combining glabrousness with excellent plant and grain types. This is probably a temporary problem.

Flag leaves

The flag leaves are important to yielding ability because they are primary suppliers of photosynthate directly to the panicle. Flag leaves also help to stabilize yield because erect, moderately long flag leaves, such as those of CICA 4, help protect ripening grain against bird damage. Because the panicles of dwarf rices are normally within the canopy, the length of the flag leaf determines the amount of protection. The flag leaves of tall varieties rarely, if ever, extend far past the panicles.

Length and erectness of flag leaves are variable. Many dwarfs, such as IR22, have short and erect flag leaves that provide little panicle protection. Other dwarfs have long, drooping flag leaves even though interior leaves are short and erect. Thus, the size of flags seems independent of that of lower leaves.

Many breeders discard lines with unusually long flag leaves — extending 30 cm or more past the panicles — because they suspect that this trait encourages mutual shading. No modern varieties have unusually long flag leaves. For areas subject to bird damage, the protection provided by moderately long, erect flag leaves would outweigh any possible losses from shading. But where bird damage is insignificant, small, erect flags may be preferrred.

Little is known about the inheritance of flag leaf length or angle although it is apparently independent of the dwarf gene that controls the length of culms and other leaves. Flag leaves are shortened by nutritional deficiencies, particularly nitrogen, and heavy seeding rates. Such factors seem to affect the length of flags more than that of other leaves.

Length and angle of flag leaves are relatively simple to evaluate on a line basis but not on a single plant basis. Therefore, selection for desired flag leaves should begin in the F_3 of pedigreed material and should continue for several generations.

PANICLE CHARACTERS

Panicle size

Many workers are unduly concerned about panicle size as a breeding objective, probably because early work loosely divided rice varieties into two types: low-tillering with large panicles, and high-tillering with small

panicles. This clearly is not an inevitable association because some high-tillering dwarfs have intermediate-to-large panicles and high yielding ability. But there is generally a compensatory association between panicle size and tiller number; as one increases the other decreases (unless plant type or photosynthetic efficiency is concurrently improved).

But panicle characters do not strictly cause or determine yield. Such traits simply permit yield to be divisible into subunits called yield components. Unlike the inflorescences of other cereals, rice panicles contribute little photosynthate to grain filling. The routine measurement of panicle length as a selection criterion for yield is probably not productive.

Lines that combine heavy tillering with large panicles would be expected to yield higher. Recent field observations suggest that narrow leaves and exceptional early vigor in dwarf backgrounds are often associated with heavy tillering, long panicles, and higher yielding ability.

Compact panicles

Spreading panicles are universally considered undesirable, although rices with the character do not necessarily have fewer spikelets. The inheritance of open panicles is reported to be controlled by a single recessive gene in some cases, but it appears to be polygenic in others. Little is known about which combinations of parents tend to produce the abnormality or about how environment affects its expression. Selection for the normal compact inflorescence is easy and effective in segregating populations.

Panicle exsertion

Panicles should emerge completely from the flag leaf sheath, so that part of the internode below the panicle base is exposed. The lower panicle branches often remain enclosed because the upper internode is short. Such enclosed spikelets are sterile or only partially filled and are often blackened by secondary pathogens, resulting in moderate grain losses.

The fully exserted panicle is supposedly dominant over the partially enclosed one, but air temperature and, possibly, shading drastically modify the expression. In many lines, panicles exsert completely if the weather is warm after panicle initiation but exsert incompletely if the weather is cool.

Incomplete panicle exsertion is a major breeding problem in some areas. The trait does not appear to be associated with either plant or grain types, but it may be related to short flag leaves. Exsertion is not easily evaluated because of the influence of environment, the wide range of character expression, and the partial covering of panicles by flag leaves in dwarf material. In unusually cool areas and seasons, poor exsertion may appear suddenly in otherwise promising advanced lines; almost all plants

show the defect in such cases. This emphasizes the importance of strict selection for complete exsertion in the early generations.

Although the work is tedious, individual F_2 plants can be bent slightly into the space between rows to expose the panicles for visual inspection. It is best to do this when grain is mature so that lines can be simultaneously evaluated and selected. More advanced pedigree lines are easier to rate on a row basis. Undesirable plants can be identified by a black, pathogenic discoloration of leaf sheaths of incompletely exserted panicles. If panicle exsertion is an important character, evaluate the observation plots and yield trials routinely. Rate the completeness of exsertion by any simple numerical scale and record the results in the field book.

DURATION OF THE GRAIN-FILLING PERIOD

A prolonged period of grain filling has repeatedly been observed to be associated with increased grain yields, although no one has proved that extended duration causes high yields. The period from flowering to maturity often ranges from 45 to 60 days in temperate areas where yields are usually high. This long grain-filling period is clearly an effect of temperature, and is not a varietal character. In the tropics, the time from flowering to maturity averages about 30 days. Maximum varietal range is about 25 to 35 days. The grain-filling duration of japonicas is often slightly longer than that of indicas. Breeders shouldnot be too concerned with this character at present because the known variability is limited and the evaluation of segregating material is difficult. But the discovery of tropical varieties with longer grain-filling periods would be of great value.

SPIKELET FERTILITY

Fertile spikelets are an obvious prerequisite for high yield. With good crop management and growth, high yields are obtained with normal spikelet sterility of as much as 10 to 15%. Higher sterility is cause for concern. Sterility is common in rice breeding materials and has three major causes: extreme temperatures, lodging, and hybrid sterility or genetic incompatibility.

An important symptom of temperature damage is partial-to-complete spikelet sterility. Partial sterility is also found in rices of poor plant type that are characterized by excessive growth, mutual shading, and early lodging.

Hybrid sterility is a major problem in rice breeding. Rice breeders and geneticists have focused more attention on hybrid sterility than on any other aspect of varietal improvement; it remains a controversial subject.

Intervarietal hybrids of the three major varietal groups of cultivated rice — indica, japonica, and javanica — normally have appreciable F_1 sterility. Sterility is generally higher from crosses of varieties of any two

groups than from crosses of varieties in a single group. Hybrids from crosses of tropical indica and japonica or javanica varieties are almost always partially to completely sterile, but sterility also occurs in some wide indica × indica hybrids. This intervarietal hybrid sterility is more pronounced in rice than in other cultivated crops. Although F_1 hybrids commonly have 20 to 80% spikelet sterility, some are completely sterile.

Breeders first became interested in sterility when they attempted to improve indicas by crossing them with japonica varieties. A few indica × japonica and indica × javanica crosses are still made although they generally result in poor plant type, weak or sparse culms, and undesirable grain characters. Interest in the improvement of indicas with japonica characters declined when breeders discovered the significance of the Chinese dwarfs as sources of good plant type, lodging resistance, and nitrogen response. But the situation has recently reversed and many japonica breeders are looking to indicas as sources of desirable characters. This may stimulate renewed interest in hybrid sterility.

Some breeders still argue about whether hybrid sterility is caused by gene action or by structural differentiation in the chromosomes of parent varieties. This argument should not concern the practical breeder because hybrid sterility, whatever its cause, is highly heritable. F_2 populations derived from partially sterile hybrids segregate widely and continuously from highly sterile to fertile; many plants are more sterile than the F_1. The degree of fertility in successive generations is associated so that F_1 fertility, for example, may be used to predict F_2 breeding behavior.

Some workers have postulated serious consequences of hybrid sterility that could slow advances in breeding. Claims have been made that segregation ratios are abnormal and that F_2 recombinants from partially sterile hybrids have lower fertility and propagation rates than parental types. Careful analysis of F_2 populations, however, shows that recombinants and parental types are equally fertile and that hybrid sterility does not cause a deficiency of recombinants. Sterility does not disturb the normal F_2 segregation ratios for monogenic and quantitative characters.

Sterility has been reported to cause a progressive loss of recombinants and japonica plant types in segregating populations of partially sterile crosses between japonica and unimproved indica varieties. This does occur but not as a consequence of sterility. The dominance of the indica-type segregates simply reflects their greater competitive ability. The same phenomenon occurs in any cross between distinct plant types, even if fertile, unless the less competitive plants are protected.

But sterility is a problem for breeders even though it does not upset segregation ratios or the number of recombinants. Many F_1 hybrids are so sterile that they do not produce enough seed for the F_2. For example, crosses of dwarfs with the variety Mudgo (a good source of leafhopper

resistance) are often more than 99% sterile in the F_1. In such extreme but fairly common cases, it is obviously impractical to produce enough F_1 plants to harvest sufficient seed for the F_2. The solution is to make a single backcross to the parent with the greatest number of desirable characters and to discard the F_2 seed of the single cross. Use the highly sterile F_1 plant as the pistillate parent, with the recurrent parent supplying abundant pollen; when the sterile F_1 is used as the pollen parent, seed set is never satisfactory. Because segregation for fertility is wide, one should produce more backcross F_1 plants and discard the highly sterile ones. The single backcross technique greatly increases fertility in the backcross F_2 families and it also reduces the extreme F_2 segregation for 211 characters typical of wide crosses.

Because of the close parent-progeny association for fertility, strong and early selection for fertility rapidly reduces sterility in segregating populations. Begin selection in the F_2 of single crosses, or the F_1 of backcrosses, and reject the highly to moderately sterile plants regardless of their other characters. The degree of sterility in each plant is usually easy to observe in mature material although borderline cases may be difficult to evaluate on exceptionally bright days. This problem can be overcome by shading the panicles with a field book or hat, or by hand threshing a representative panicle, throwing the grain into water, and estimating the percentage of sterile spikelets that float on the surface.

MATURITY AND PHOTOPERIOD SENSITIVITY

The prevailing climatic and agronomic practices largely dictate the ideal number of days from rice seeding to harvest. Germplasm varies greatly in maturity, so breeders can tailor rices suited to local conditions and farm practices. In the tropics the maturity period of photoperiod-insensitive varieties ranges from about 90 to 160 days.

Maturity is strongly affected by air temperature and, to a lesser extent, water temperature. When directly seeded, IR8 matures in 120 days along the hot Ecuadorian coast and 175 days on the cool Peruvian coast, even though both areas are geographically contiguous. Less drastic but common factors that influence maturity period are planting methods and nitrogen fertilization. Directly seeded crops usually mature a few days earlier than transplanted ones. Nitrogen deficiency hastens maturity somewhat and heavy application delays it slightly.

Varieties that mature in about 110 to 135 days usually yield more than those that mature earlier or later under most agronomic conditions, although very early maturing varieties give excellent yields in the southern USA if cultural practices are perfectly timed. Late-maturing varieties are usually required for areas where heavy rain or deep water during the growing season hinders the harvest of early varieties. Varieties that mature very early — in 105 days or less — are desired for subtropical

areas where ratooning is practiced such as the southern USA, for tropical areas where water is only available for short periods, and to fit into intensive crop rotations.

Most modern varieties are intermediate in maturity. A few sources of very late maturity are available, especially from Surinam. Good sources of very early maturity for the tropics (90–105 days) include photoperiod-insensitive japonicas and several rices from the southern USA and IRRI. The USA materials are better than the japonicas as sources of very early maturity for the tropics, despite their low tillering and inadequate vigor, because they combine better with tropical indicas.

The maturity period is generally controlled by polygenes so transgressive segregation is common for both earliness and lateness. The very early maturity of Belle Patna, Blue Belle, and related material from the USA appears to be controlled by a single dominant gene, making them elite sources of earliness when used as nonrecurrent parents in single backcrosses to tropical indicas.

In almost all programs notes on first or 50% flowering are recorded for all pedigree rows beginning with the F_3. The recording of flowering date gives an accurate measure of total maturity period, as the period from flowering to grain maturity is relatively constant among lines.

But recording flowering date requires much time and repeated observation, and is an example of a routine practice followed without question of its usefulness. CIAT has abandoned the practice in pedigree material and records flowering dates only for observation plots and yield trials. The time saved is spent on more critical work with no loss of effectiveness of selection for distinct maturity classes. All field books include a calendar indicating the days from seeding at any given date. Select for very early material at the appropriate period after seeding when it is the only material with mature grain. If lines that mature later than 140 days are undesirable, for example, suspend field selection at that date.

In general, intermediate and late maturity recombine readily with other desired characters. A far more difficult breeding objective is the recombination of very early maturity (less than 105 days) with high yield and causal morphological characters (early vigor, heavy tillering, short and sturdy culms, and erect leaves). The USA sources of extreme earliness are low tillering and moderately tall. The panicle neck nodes and the spikelets differentiate about 30 to 20 days before flowering, respectively. From flowering to harvest takes another 30 days, so a 100-day variety has only from 40 to 50 days of vegetative growth before panicle initiation. Therefore, the problem is to develop in that short period sufficient leaf area to support high yields. Furthermore, precise timing of fertilizer topdressing and control of water and weeds become critically important for high yield in very early varieties.

So, high yield in very early tropical varieties is generally expected only

in plant types that are exceptionally vigorous in terms of early leaf-area development per unit of time. Heavy tillering appears to be an ideal trait for greater plasticity and rapid covering of space among plants, especially for transplanted crops. To some extent, increasing the planting density in direct-seeded rice supplements early vigor and increases leaf area and yield in very early varieties.

No highly productive varieties with very early maturity are presently available for the humid tropics. The early USA varieties such as Belle Patna and Blue Belle mature in about 100 to 105 days in the American tropics but rarely produce as much as the improved dwarfs. But at higher, cooler altitudes, their maturity is delayed and they yield considerably better. By comparison, the improved dwarfs, which mature from 15 to 20 days later, often yield twice as much as the USA types in the tropics. Even discounting their greater pest susceptibility, the low tillering ability and weak vigor of the USA varieties in the hot tropics combine to limit foliar development prior to panicle initiation and, therefore, yield. The combination of their earliness with the tillering, vigor, and yielding ability of improved tropical dwarfs remains a fascinating challenge. IRRI has developed relatively productive lines that mature in from 100 to 105 days. They yield about 5 t/ha in the wet season and from 6 to 7 t/ha in the dry season.

Photoperiod insensitivity is a major reason that many of the modern dwarf varieties are so widely adaptable. The trait is increasingly preferred in many tropical areas because it permits cultivation of any one variety over a wide range of latitude, offers flexibility in planting dates, and allows double- or triple-cropping.

All important varieties in tropical Latin America are insensitive or weakly sensitive. In Asia, sensitivity to photoperiod is required in large areas of relatively deep water such as in Bangladesh, Burma, Vietnam, and Thailand. In these areas, varieties must ripen after water recedes and before the dry-season water shortage. In areas where rice can only be dried in the sun, photoperiod-sensitive varieties are often preferred to ensure that the crop is harvested after the rainy season.

Strongly sensitive rice varieties are required for most areas subject to deep flooding while weakly sensitive varieties are desired for areas where flooding is shallow to moderate. Strongly sensitive varieties will not flower when days are long. Weakly sensitive rices will flower under any natural day length but long days extend their maturity period. Long days do not delay flowering in completely insensitive varieties such as CICA 4, but such varieties are relatively uncommon.

Improved dwarf lines that are strongly sensitive, weakly sensitive, and insensitive to photoperiod have been developed at IRRI and in other programs. These rices are available to all breeders as parental materials. If a strongly sensitive variety needed for crossing will not flower under

local photoperiods, the breeder may force flowering by exposing the plants to several consecutive long nights of about 14 hours each in a dark chamber.

Photoperiod sensitivity is thought to be controlled by one or, occasionally, two dominant genes, although the weakly sensitive response may be under multigenic control. Photoperiod response is easily recombined through hybridization with all important plant and grain characters including grain dormancy. In unimproved materials that evolved through natural selection, photoperiod sensitivity is often associated with characters that offer advantages in traditional farming systems, such as tallness, long leaves, and grain dormancy.

Evaluation of pedigree lines for photoperiod reaction is simple in programs where two crops a year are grown at latitudes 5° or more north or south of the equator. Plants are evaluated on the basis of differences in flowering in consecutive plantings. At IRRI, for example, homozygous photoperiod sensitive lines flower from 40 to 70 days earlier when planted in December than in May. But the maturity period of uniformly insensitive lines is longer when planted in December because temperatures are lower until March. At either date of planting segregating lines show a two class segregation for flowering date.

Individual segregating plants in F_2 populations are somewhat more difficult to classify. At locations north of the equator, insensitive or weekly sensitive plants generally flower earlier when planted in May and later when planted in December. The trend is reversed in areas more than 5° south latitude.

Selection for photoperiod insensitivity at or near the equator is easier because few strongly sensitive plants or lines will flower under existing day lengths at any time of the year. The maturity of weakly insensitive material may or may not be extended under such conditions. Advanced lines can be clearly separated into insensitive and weakly sensitive material only by planting at higher latitudes.

PIGMENTATION

No character has received as much attention, with so little justification, as the pigmentation patterns of different plant parts. Many varieties have no obvious anthocyanin pigmentation. Among those that do, the pigmentation varies in intensity and in location. Pigmentation in any of its possible combinations does not appear to be related to crop development, pest resistance, grain yield, or any other important growth or quality character. Most workers discard heavily pigmented lines despite the fact that the trait is not clearly disadvantageous. A minor exception involves parboiled grain because a pigmented apiculus or hull may stain the endosperm. Pigmentation patterns and their inheritance remain a plaything of some geneticists who should concentrate on more important

characters. Localization of pigmentation can be useful in varietal identification, but remember that the color is often weakly expressed if the plant part is heavily shaded.

The background color of rice is straw or gold. Gold hull, recessive to straw colored hull, is fairly common in commercial varieties. Breeders often arbitrarily discriminate against gold hulls. presumably because the endosperm of the grain might be stained if parboiled. Hull color does not affect grain yield or any other important characters and deserves little attention. Because of its simple inheritance it is useful for checking F_1 plants for self-fertilization in crosses where a gold-hulled variety is the pistillate parent.

AWNS

Most breeders select awnless grains because the awns are tough, persistent, and objectionable in threshing and milling. Lines with partly awned panicles, having a few small awns on the tip grains present no problem and should not be discarded because of that character alone. The awn does not contribute significantly to grain filling, is not important in protection against bird damage, and apparently serves no useful function.

Two or three dominant genes control the presence of awns. Partly awned × awnless crosses differ by one gene. Unknown environmental factors often influence the presence of tip awns and the degree of awning. Awns often appear in a ratoon crop whose original planting was completely awnless.

Most varieties are awnless or have only a few tip awns, so the character is rarely a problem in breeding. Rejection of fully awned individuals in the F_2 and F_3 eliminates most of the difficulty in the occasional cross involving a fully awned parent. There is no evidence that complete or partial awning is linked to any other economically important grain character.

THRESHABILITY

Grain shattering or shedding, which depends on the strength of spikelet attachment to its pedicel, is of great economic importance and is a major breeding consideration. The ease of spikelet attachment is loosely classified as tight, intermediate, or shattering. The degree of shattering that is permissible in a particular area depends largely on the environment and the prevailing system of harvesting and threshing.

Varieties grown in areas where winds are strong at grain maturity must resist shattering. Nonshattering is especially important for stiff-culmed, nonlodging varieties whose erect culms, unlike those of lodged plants, are not protected from severe shaking. Varieties that are harvested, shocked, and temporarily stored in the field before threshing, a common prac-

tice in Japan, require strong resistance to shattering.

Intermediate-shattering types can be threshed more thoroughly with less grain loss when mechanically harvested. Farmers who use a combine to harvest and who grow easily shedding varieties should begin harvest while the grain has a high moisture content to avoid excessive grain loss. But this results in a high percentage of incompletely mature grain with chalky endosperm, which greatly reduces milling quality and increases drying costs.

In many parts of the world rice is harvested by hand and threshed immediately by beating the panicles against oil drums, logs, or other solid objects. In these areas, intermediate to shattering types are preferred to reduce threshing time.

Japonica varieties are highly resistant to shattering; so are some indicas. Red rice is most susceptible. Most indica varieties are intermediate between these extremes.

Shattering is believed to be controlled by one gene, usually considered dominant to tightness, although the reverse condition has sometimes been reported. Whatever its mode of inheritance, the degree of shedding is markedly influenced by the stage of grain maturity and by the environment although the latter factor is not well understood. The various degrees of shattering are genetically independent of all other important characters and may be combined with any of them.

Of more practical concern to the breeder is the impossibility of evaluating and selecting segregating material for the desired degree of shattering at a uniform stage of grain maturity. The breeder often selects plants with slightly immature grain because he is reluctant to return at a later date to evaluate only a few remaining late-maturing lines. Similarly, segregation for maturity period within lines renders impossible the evaluation of shattering and the selection of plants of uniform physiological maturity. Although immature grain is usually resistant to shattering, this may not be related to its behavior at complete maturity. Grains overripen in pedigree lines when breeders fall behind in their field work. Such rows tend to shatter easily but again this may not reflect their performance at ideal maturity.

Furthermore, breeders have no efficient method to evaluate shattering ability. The best technique, although it is far from ideal, is to enclose the panicles of a plant loosely in one hand, squeeze slightly with the fingers, and estimate the number of grains in the hand. With practice a worker learns to apply about the same pressure for each evaluation. Despite its drawbacks, the method is rapid and reasonably accurate, and requires no special tools.

The squeezing method is not satisfactory for evaluation of single plants, and trying to classify individual plants in the F_2 is generally useless. The test should be repeated with three or more plants per row to get

a satisfactory estimate of the degree of shattering within a line. Thus, lines are normally evaluated on a family basis, beginning with the F_3 and continuing through all subsequent generations. Several people usually work together to select plants in large pedigree nurseries. Therefore, the amount of pressure applied to each line varies and so does shattering. Nevertheless, if lines that shatter excessively, or lines that hold grains tightly, escape detection in one generation they will be identified in the next.

Only one worker should evaluate threshability in observation plots and yield trials, and entries should be at comparable stages of ripeness to increase the uniformity of evaluation.

GRAIN DORMANCY

Grain dormancy refers to the low germinability of viable, freshly harvested grain. Like shattering and profuse awning, dormancy is a primitive trait that favors survival in nature. Dormancy is also desirable for most agronomic environments because it protects grain from sprouting on panicles before harvest. Sprouting is a chronic problem if rains are frequent during grain ripening or if the crop lodges into water. Thus, dormancy is an important breeding objective.

Japonica varieties as a group have little or no grain dormancy. Most indicas have some dormancy and many, especially those from tropical Asia, are strongly dormant. Rices vary widely in percent germination of grain at harvest, in duration of dormancy, and in the difficulty of breaking dormancy.

Under normal conditions of grain development, dormancy is controlled largely by the lemma and palea and somewhat less by the pericarp and the embryo. Its mode of inheritance is multigenic. Dormancy is strongly to partially dominant over nondormancy. Little is known about the genetic association, if any, between the strength and the length of dormancy. Environment strongly affects the trait. Grains that mature during sunny, dry weather are less dormant than grains that ripen during humid weather. Thus, a single variety may be rated as weakly to strongly dormant depending on environment.

Dormancy is inherited independently of and combines readily with early maturity, photoperiod insensitivity, a range of grain types and cooking qualities, important panicle characters, and all desirable culm and leaf traits.

Most crosses in tropical programs involve dormant parents. Essentially all segregating material is dormant. Such material presents no problems other than the breaking of dormancy. Their progeny need not be evaluated until preliminary yield trials. But crosses that involve one nondormant or weakly dormant parent are a special problem if two or more generations are produced per year. In programs where seed is harvested,

prepared, and replanted within 50 days, dormancy must be broken to ensure that the dormant seed will also germinate. If dormancy is not broken, the desired dormant segregates are rapidly eliminated because only the nondormant or weakly dormant seed germinate. Seed may be held until dormancy disappears naturally, but this is not practical in programs that wish to advance material rapidly.

A dramatic example of the consequences of not breaking dormancy occurred in Colombia when, accidentally, a box of several hundred recently harvested selections was not treated to break dormancy. Other selections, which had been treated before planting, germinated normally, but essentially none of the highly dormant nontreated material germinated. Stands were normal in the check rows, prepared from old seed.

The simplest way to break dormancy of freshly harvested material when only a few grains are involved is to remove the hulls and treat the seed with a fungicide before planting. This is not practical, however, for breeding nurseries. Similarly, some liquid chemicals break dormancy effectively but can not be used practically for large numbers of selections.

A practical and efficient heat treatment breaks dormancy in large numbers of breeding selections. Maintain envelopes of recently harvested seed in a dry-air oven at 50 to 55°C for 5 to 7 days. No seed viability is lost if material is inadvertently exposed for longer periods or if temperature reaches as high as 65°C. A maximum of 2 kg of seed can be treated in paper bags left open to facilitate rapid moisture loss. The treated grain may be planted immediately after removal from the oven.

Dormancy is sometimes exceptionally strong in hull-less crossed seed that result from the clipping method of emasculation. The clipped seed of hybrids crossed with ICA 10, for example, are so intensely dormant that the normal technique does not satisfactorily break it. In such rare cases, leave the seed in the oven for 10 days and then hold it for a month or so before germinating.

Dormancy is relatively simple to determine in single-plant selections or in fixed lines, but it requires much hand labor and time. Place 100 fungicide-treated grains of each freshly harvested selection or line on moist filter paper in clean petri dishes and add distilled water as needed. If no germinating oven is available, store the petri dishes on a laboratory table. The percentage of nongerminated seed after 7 to 10 days is the initial dormancy. Determine the length of the dormancy period by repeating the test weekly until 80% germination is reached.

The evaluation of the strength of dormancy requires so much labor, time, and space that it should be performed only when absolutely necessary. Crosses between two dormant parents segregate into so few weakly dormant individuals that evaluation is not necessary until fixed lines are selected. But crosses between dormant and nondormant parents segregate an array of dormancy classes. Whenever possible, use F_3 seed from

CHAPTER 6

Grain quality

ENDOSPERM APPEARANCE

THE APPEARANCE OF MILLED RICE is important to the consumer, which makes it also important to the producer and the miller. Thus it is a major breeding consideration.

The consumer prefers rice with a clear endosperm and pays a premium price for it, even though opacity disappears during cooking and does not alter eating quality. Grain with opaque areas in the endosperm, caused by the loose packing of the starch and protein particles, breaks more readily than clear grain during milling, greatly reducing the market value.

A few varieties have almost totally opaque endosperm. Other varieties are clear or have only minute traces of white belly. The milled grains of these varieties also often have an attractive translucency or brilliance; this is simply a visual preference character and does not affect nutritional or cooking quality. In all rice markets the ideal type of endosperm is free of opaqueness and is strongly translucent.

The opaque areas are known as white belly, white center, or white back, depending on the location of the spot within the endosperm. For evaluation of breeding material it is most convenient to group them together as white belly rather than to individually rate each one. Opacity should not be confused with the superficially similar appearance of glutinous or waxy rice, or with that of immature, chalky grain harvested at a high moisture content.

The presence and degree of white belly are partially under genetic control although certain environmental factors markedly affect their expression. The individual grains of a single panicle may differ in opacity. Some varieties such as IR22 are often free from white belly in all environments while others, such as CICA 4, have clear endosperm in some environments but considerable opacity in others. But IR8 and other varieties are severely affected with white belly in almost all environments.

The major environmental factor affecting opacity appears to be temperature immediately after flowering; high temperature increases white belly while low temperature decreases or eliminates it. This presents special problems for programs headquartered in cool areas that serve farms in hot areas. In such cases, materials with clear endosperm selected in the cool area must be critically checked in warmer environments. Soil fertil-

ity and water management are also suspected to affect the degree of white belly in unknown ways.

Although white belly is reportedly controlled by a recessive gene, experienced breeders have questioned so simple an inheritance in most materials. But a fair percentage of clear grains is found in progeny of backcrosses to parents with some white belly, indicating that the inheritance of clear endosperm is not highly complex.

As with other grain traits that are fixed early in the segregating generations, it is important to evaluate and begin strict selection with the F_3 grain from F_2 plants in single crosses or with the grain of F_1 plants from individual backcrosses or three-way crosses. Because this trait is difficult to handle and its heritability is low, the breeder must reject all questionable selections. A separate test is not required for evaluation because one can rate the endosperm appearance of seed milled for analysis of cooking quality at the same time that he measures their length. If a small sample mill is not available and cooking quality tests are not performed, dehulled or brown rice may be used to rate endosperm appearance with fair accuracy at best. Record the average score of 5 or 10 grains/plant or panicle selection, using a scale of 1 to 9 with 1 representing a completely clear endosperm.

Translucent grain with little or no white belly can be combined with any desired grain type, amylose content (except waxy), or gelatinization temperature. Translucency is inherited independently of all important agronomic characters.

GRAIN LENGTH, SHAPE, AND MILLING QUALITIES

Standards for evaluation of grain length and shape of breeding material vary among countries and marketing areas. Table 1 gives a reasonably useful classification for routine breeding evaluation:

Table 1. Classification of grain length and shape of milled rice.

Designation	Length (mm)	Scale	Shape	Length-width ratio	Scale
Extra long	7.50+	1	Slender	3.01	1
Long	6.61–7.50	3	Medium	2.1–3.0	3
Medium	5.51–6.60	5	Bold	+1.1–2.0	
Short	–5.50	7	Round	–1.1	9
Extra short		9			

Preferences for grain length vary enormously from region to region. Those who prefer japonica rices almost always like short grain although Europeans prefer some japonicas with medium to medium-long grain. In tropical Asia most rice is medium to long with some extra-long types preferred in Thailand and elsewhere. In the Americas, long or extra long (Surinam-type) grain is generally preferred except where low tempera-

ture requires that japonica-derived varieties be grown.

Width and thickness, or shape, are less variable and less important than length, although the highest quality markets usually demand a slender to medium width (Table 1). Bold grain is often discriminated against because it breaks in milling. An exception is the Brazilian upland rices, which have long and bold grain, a heavy 100-grain weight, and good milling quality. Grains of short to medium length usually, but not always. break less than long grains during milling. Thus, grain size and shape are closely related to yields of head rice or unbroken grain.

But total milled rice (head rice plus broken grain) of intermediate or bold grain is usually slightly higher than of slender types. The grain of IR8, for example is considered excessively bold, which contributes to low yields of head rice but high yields of total rice. Breeders should give more emphasis to head rice improvement than to total rice yield because it is more important commercially, it varies more, and it is easier to improve.

Length and shape of grain arc independently inherited and can be combined as desired with the possible exception of the extra long and bold characters. Furthermore, there are no barriers to recombination of any expression of grain length and shape with other quality traits such as endosperm appearance or amylose content, or with plant type, dormancy, or maturity period. However, consumer preferences and prolonged human selection have resulted in nongenetic associations of grain types with cooking behavior. Thus, long-grained rice usually cooks dry and fluffy and short grains usually cook moist and sticky. The once prevalent feeling that short-grained varieties have a higher yielding ability than long-grained types is not valid. This belief, like so many others, arose because short-grained japonica varieties received more breeding attention for years in Japan and elsewhere, and because they are often grown in temperate areas that have more favorable environments.

Some workers in tempcrate areas have indicated that it is difficult or impossible to recombine dwarfism and heavy tillering with long grains of slender or medium width. Fortunately, this is not true. Scientists in tropical rice breeding programs have developed many selections with typical dwarf plant characters and excellent grain suitable for international commerce, by intercrossing superior lines for several cycles and strictly selecting for grain type.

Nevertheless, grain size and shape are relatively difficult traits to handle. The most important consideration is for the breeder to know which grain types are desired in the markets he serves and to stringently reject all segregants that do not meet those requirements. It is futile to spend years developing high-yielding, disease-resistant lines only to find that farmers, millers, or consumers discriminate against them because of unacceptable grain measurements.

Improved dwarf plant types with essentially all possible combinations of grain shape and length are becoming increasingly available for use as parents in crosses. Thus, it is no longer necessary to use unimproved plant types as donors of good grain. One combination not yet developed for parental use, however, is long, slender grain in a dwarf background with sufficient cold tolerance for the temperate areas. But several promising new IRRI selections are under evaluation in the 1978 International Rice Cold Tolerance Nursery (IRCTN).

Grain length and shape are quantitatively inherited. The F_1 is typically intermediate between its parents in size; transgressive segregation for longer or shorter grain is common in the F_2. Grain size is highly heritable in most environments although low temperature after flowering can slightly reduce grain length. Despite the apparent complexity of their inheritance, grain length and shape appear to be fixed exceptionally early in the segregating generations. If the desired expression is not found in the F_2, the chance of finding better types in the F_3 is almost nil. Conversely, when excellent grain is selected in the F_2 it rarely segregates much in subsequent generations. This indicates the extreme importance of putting strong selection pressure on the F_2 of single crosses and on the F_1 of backcross, three-way, or double-cross populations. If good types are not found in any generation or population it is advisable to discard the material and look elsewhere.

Length and shape are not easy to evaluate in the field, although with practice types that are obviously good or bad can be spotted without much difficulty. To save time in the field, take all selections that appear to have satisfactory grain to the seed laboratory for drying. Then carefully inspect the grain of all plants in the laboratory either before or after threshing and discard the many questionable types.

A relatively minor grain trait to keep in mind both in the field and the laboratory is the completeness of seed enclosure by the lemma and palea. The grains of some plants show a gap between the glumes. This is undesirable because pathogens may enter and spoil grain during humid conditions in the field or in storage.

The preliminary visual evaluations of grain appearance in the field and laboratory are based on rough rice and are supplemented with more accurate measurements of milled rice. Because all field selections should also be tested for other quality factors that require dehulling and milling, a routine practice is to measure the length of from 5 to 10 representative milled grains and to record this information in the field book. Some scientists measure only the larger grains at the tips of the panicles to reduce variability because the lower grains are usually shorter. Do not record grain shape of the selections from pedigree nurseries because of the difficulty and time required to measure width and to calculate the 1ength:width ratio. Most undesirable shapes in segregating material are

eliminated by visual inspection of the panicles in the field and laboratory and during the measurement of milled grain for length. The tedious direct measurement of grain shape can be reserved for fixed advanced lines, or skipped without great loss.

Careful evaluation of milling quality, particularly percentage of head rice, is critical in all rice breeding programs even for areas where the harvest is partially or largely parboiled to reduce grain breakage. Unfortunately, there is no simple, accurate technique to directly measure the milling quality of individual selections in the segregating generations. Most breeders attempt to estimate the milling behavior of pedigree selections on the basis of grain length and shape and on the endosperm appearance. Grain traits that contribute to increased breakage, singly and in combination with other traits, include long or extra long grain, excessively slender or bold shape. partially flattened grain. and appreciable white belly.

Direct measurement of milling quality usually begins with the bulked grain of elite F_5 or F_6 lines tentatively selected for entry in preliminary yield trials. The evaluation should include well-known check varieties and should continue through all successive cycles of yield testing and multiplication. A commonly used procedure is to dry 1-kg samples of grain to less than 14% moisture content. Dehull the samples and mill with laboratory equipment, carefully following the manufacturer's recommendations for time and the weight applied to the mill. Double-check lines with unusually low yields of head rice and discard all lines confirmed as unsatisfactory. The correlation between results obtained from the 1-kg laboratory mill and from large commercial mills is generally satisfactory. Results from smaller laboratory mills that use much smaller grain samples are less accurate.

After milling, separate the whole and the broken grains in a sizing device for two important evaluations. The first is the percentage of head rice, or unbroken grain, based on the initial kilogram of rough rice. The other is the percentage of total rice, or the sum total of head rice and all classes of broken grains. Determination of the head rice yield is more critical as it varies considerably more than total rice yield.

It is imperative to run at least one evaluation of milling quality, preferably more, in a well-adjusted commercial mill before releasing a new variety. Because evaluation requires from 2 to 4 tons of rice, it is done with the grain produced in the first stage of large-scale seed multiplication. Whenever possible, this test should be repeated after from 3 to 4 months of storage because storage maximizes grain hardness and head rice yield.

AMYLOSE CONTENT

Amylose is the linear fraction of starch in the nonglutinous varieties. Amylopectin, the branched fraction. makes up the remainder of the starch. Amylose content has a major influence on the characteristics of

cooked milled rice. It correlates negatively with taste panel scores for cohesiveness, tenderness, color, and gloss of the boiled rice. Rice varieties are grouped on the basis of their amylose content into waxy (1 to 2% amylose), low amylose (8 to 20%), intermediate amylose (21 to 25%), and high amylose (more than 25%).

Glutinous or waxy rice is the staple food in a few small areas in Asia. It is also used to prepare rice cakes, desserts, sweets, puffed rice, and parboiled rice flakes. Its volume expansion and water absorption during cooking are low. After preparation glutinous rice is very moist, sticky, and glossy. A single recessive gene controls the glutinous trait but modifying genes apparently affect the processing characteristics.

The nonglutinous or nonwaxy varieties, which make up the bulk of the world's rice, range from 8 to 37% in amylose content, although most are from 13 to 32%. Low-amylose varieties are moist, sticky, and glossy when cooked, and readily split and disintegrate when overcooked. Rices with a high-amylose content, such as IR8, cook dry and fluffy but become hard upon cooling. Intermediate types, such as Pelita I from Indonesia, C4-63 from the Philippines, CICA 4 from Colombia, and Basmati 370 from Pakistan have the fluffiness of high-amylose types but retain a soft texture when cool.

Japonica varieties have low amylose content and are sticky when cooked. Indica varieties vary widely in amylose content according to regional quality preferences. Intermediate amylose content is preferred in the major consuming areas of Indonesia and the Philippines, probably because the cooked rice is soft when it cools. High amylose rices are widely grown in Asia but intermediate amylose content would probably be equally preferred. Intermediate types are generally preferred by Latin American consumers and in the world's major import markets.

Although the inheritance of amylose content is not well understood, high- and low-amylose types appear to differ by control of a single gene. The heterozygote has intermediate amylose content but this cannot be stabilized. If intermediate amylose content is desired, one or both parents must be intermediate.

Amylose content is partly modified by environment in largely unknown ways. High temperature during grain ripening lowers amylose content. A variety can vary as much as 6% in content from season to season.

Determination of amylose content

Although breeding for any specific amylose content is not difficult, direct amylose determination is difficult because the procedure is expensive, slow, and delicate, and requires advanced capability in chemical analysis. Many programs lack the resources to determine amylose content. As a limited solution, such programs can substitute the simple al-

kali test for gelatinization temperature. That will provide a partial and preliminary screening for amylose content on the basis of association of the two traits. For areas where low amylose (sticky cooking) is not preferred, the high-gelatinizing types, which are always associated with low amylose, can be discarded. Similarly, rices of intermediate gelatinization temperature are rarely low in amylose and, therefore, should be retained.

Unfortunately, gelatinization temperature cannot be used to predict other possible combinations with amylose content. Low gelatinization temperature can be associated with low, intermediate, or high amylose content. Intermediate-gelatinizing rice can be intermediate or high in amylose. These cases usually represent the bulk of the breeder's material and presently can be determined only by direct analysis of amylose content.

Amylose can be measured by the starch-iodine blue test. This test is claimed to be useful for identifying low-amylose varieties with high gelatinization temperature at 77°C because the amylose extraction for such varieties is minimal. Yet it seems simpler to identify such types by the alkali estimation of gelatinization temperature. At 100°C the extracted amylose correlates with the amylose content of the rice regardless of the gelatinization temperatures. One limitation, however, is that the high amylose rices give low values that are similar to those of intermediate amylose rices. Thus, the starch-iodine blue test is useful only if the amylose value does not exceed 27%.

Amylose content is more often determined colorimetrically with iodine after defatting with methanol, gelatinizing the starch for 2 days at 4°C, titrating the solution to obtain a final pH of from 9.8 to 10.0, and reading the color at 590 nm.

IRRI recently developed a simpler, faster, more accurate method using a pH of 4.5 to 4.7 and a wavelength of 620 nm. This test may be conducted manually and 100 unreplicated samples per day may be analyzed in an efficient laboratory. The test has also been adapted to an autoanalyzer to screen breeding lines faster — about 200 samples/day can be run with the autoanalyzer — but its drawback is its expense.

The basic procedure is to prepare a standard curve using solutions of purified potato amylose employing the standard method. In this curve, the light-transmission values of the colored solution are plotted against amylose concentration. Next, standard rice samples with a range of amylose content are treated using the standard method, and the light transmission values are determined. The plotted curve is then used to determine the amylose content of the samples. Their percentage of amylose is plotted against light transmission values to form a second curve. Finally, the unknown samples are treated with the use of the simplified method, and the light transmission values are determined. By referring to the second standard curve, the percentage of amylose of the

unknown samples is determined. The second curve is made to account for the effect of the amylose that is present in rice but not in the purified potato amylose.

The materials and reagents needed are:

- analytical balance
- colorimeter
- boiling water bath
- tripod support for bath
- gas burner
- 100-ml volumetric flasks
- pipettes (1-5 ml)
- 1-ml and 10-ml automatically dispensing pipettes
- absolute methanol
- hydrochloric acid, 0.05 N
- sodium hydroxide, 1 N
- acetic acid, 1 N
- ethanol, 95%
- stock iodine solution (0.2% in 2.0% KI)
- amylose, purified potato

Procedure for determining amylose content.

Steps	Key points
1 Prepare standard rice samples (standard method)	• Make certain that all samples to be used have been stored in the same room for at least 2 days to ensure equal moisture content. • Choose a range of rices representing low, Intermediate, and high amylose content for the standard samples. • Grind 8- to 10-grain lots of each sample to a fine powder in a Wig-L-Bug amalgamator or similar device for 40 seconds. A UD cyclone mill with 60- mesh sieve may also be used for grinding.
2 Weigh samples	• Weigh 40 mg of potato amylose into a 100-ml volumetric flask. • Weigh precisely 100 mg of the ground rice samples into 100-ml volumetric flasks.

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Procedure for determining amylose Content continued

Steps	Key points
3 Dissolve samples	• Add 4 ml of absolute methanol, carefully washing down any sample adhering to the sides of the flask • Let stand for 2% hours. • Carefully pipette or suck out the methanol. • Add 1 ml ethanol • Add 9 ml of 1.0 N NaOH without disturbing the sample. • Heat for 10 minutes in a vigorously boiling water bath. • Cool and make up to volume (add water until exactly 100 ml is in each flask and mix well).
4 Prepare solution to read transmittance values	• Place 1-, 2-, 3-, 4-, and 5-ml aliquots of the purified amylose solution and 5-ml aliquots of each of the standard rice sample solutions in 150-ml beakers containing 50 ml distilled water. • Titrate each solution with 0.05 N HCL to a pH reading of 10.5 (between each solution, wash the electrodes of the pH meter with neutral distilled water). • Transfer the contents of each beaker to a 100-ml volumetric flask. rinsing the beaker well with distilled water. • Add 2.0-ml iodine solution • Make up to volume with neutral water and mix. • Let set for 20 min.
5 Read transmittance values	• Warm the colorimeter for at least 30 min. • Set wavelength to 590 nm • Prepare a "blank" solution (follow the same procedure as step 3 but do not use a sample). • Adjust meter reading to 0% transmission • Select a colorimeter tube, fill with blank solution, insert, and adjust meter reading to 100% transmission. • Select a second tube that matches (i.e. gives a reading of 100% transmission when filled with blank solution).

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Procedure for determining amylose content continued

Steps	Key points
	• Place sample solution in one tube and record percentage of transmission. • Adjust meter reading, using blank solution after each sample has been read.
6 Calculate amylose content of standard samples.	• Plot the transmission values of the purified amylose solutions against the concentration of amylose (mg/ml). • Referring to the curve, determine the amylose content of the standard rice samples. Take into account that the rice samples were diluted by 20 times.
7 Prepare unknown rice samples (simplified method).	• As in Step no. 1 • Include three or four standard samples of known amylose content as a check.
8 Weigh samples.	• As in Step no. 2, point 2. • Weigh duplicate samples.
9 Dissolve samples.	• Add 1.0 ml of 95% ethanol. • Swirl the flask to wet the powder. • Add 9.0 ml of 1.0 N NaOH. • Heat for 10 min in a vigorously boiling water bath. • Cool and make up to volume.
10 Prepare solutions to read transmission values.	• In 100-ml volumetric flask containing 50 ml of distilled water, place 5 ml aliquots in each of the sample solutions. • Add 1 ml of 1 N acetic acid and mix. • Add 2 ml of iodine solution. • Make up to volume with distilled water and mix. • Let stand for 20 min.

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Procedure for determining amylose content continued

Steps	Key points
11 Read transmission values.	• As in step no 5, except use 620 nm and as blank solution 2 ml of I_2 KI solution and 1 ml of 1 N acetic acid in a 100-ml volumetric flask diluted to volume.
12 Prepare a second standard curve.	• Plot transmission values of the standard sample obtained in step no. 11 against their amylose contents obtained in step no. 6. point 2.
13 Determine amylose content.	• Use the standard curve prepared in step no. 12.

GEL CONSISTENCY TEST

Amylose content is the major factor that determines taste panel scores for cohesiveness, tenderness, color, and gloss of cooked nonwaxy rice. Varietal differences in gel consistency exist among varieties of similar high amylose content (more than 25%). Gel consistency of rice with less than 24% amylose is usually soft. The gel consistency test is based on the consistency of the rice paste and differentiates among varieties with high amylose content. The test was developed to complement the amylose test in breeding programs for rice quality. This test separates high-amylose rices into three categories:

1) *very flaky rices* with hard gel consistency (length of gel, 40 mm or less);
2) *flaky rices* with medium gel consistency (length of gel, 41 to 60 mm); and
3) *soft rices* with soft consistency (length of gel, more than 61 mm).

The materials needed for the gel consistency test are:

- vortex Genie cyclone mixer,
- boiling water bath,
- tripod support for bath,
- gas burner,
- wire test tube holder,
- analytical balance,

- glass marbles (1.27 mm or $\frac{1}{2}$ inch in diameter),
- Wig-L-Bug amalgamator,
- 13 × 100-mm culture tubes (Pyrex no. 9820),
- graph paper or ruler, and
- one - and two-ml repipets.

Steps and key points of the gel consistency test.

Steps	Key points
1 Grind samples.	• Make certain that all samples are stored in the same room for at least 2 days so that the moisture content will be equal. • Place from 8 to 10 milled grains in the Wig-L-Bug amalgamator. • Grind for 40 seconds to give a fine flour (100 mesh).
2 Weigh samples.	• Weigh 100 mg (± 1 mg at 12% moisture) of powder, in duplicate, in the culture tubes. • If moisture level varies from 12% make an appropriate adjustment because the concentration of starch is critical
3 Dissolve samples	• Add 0.2 ml of 95% ethanol containing 0.025% thymol blue (alcohol prevents clumping of the powder during alkali gelatinization, while thymol blue imparts color to the alkali paste to make the gel front easier to read). • Add 2.0- ml of 0.2N KOH with a repipet. • Mix using a Vortex Genie mixer with speed set at 6. • Cover the tubes with glass marbles (to prevent steam loss). • Heat in a vigorously boiling water bath for 8 minutes, making sure that the tube contents reach 2/3 the height of the tube. • Remove from the water bath and let stand for 5 minutes. • Cool in an ice water bath for 20 minutes

(continued on opposite page)

Steps and key points of the gel consistency test continued

Steps	Key points
4 Prepare tubes for reading.	• Lay the tubes horizontally on a table • Do not disturb for 1 hour.
5 Record consistency.	• Measure the total length of the gel (mm) from the bottom of the tube to the gel front.

GELATINIZATION TEMPERATURE

As mentioned earlier gelatinization temperature is partly associated with the amylose content of the starch, the major determinant of cooking behavior. This limited association is important because in certain cases it allows the breeders to use the simple gelatinization temperature test to estimate the amylose content, which is considerably more difficult to measure directly.

The gelatinization temperature of the endosperm starch, a useful test of cooking quality, refers to the cooking temperature at which water is absorbed and the starch granules swell irreversibly with a simultaneous loss of crystallinity. The gelatinization temperature ranges from about 55 to 79°C and is divided into three main groups: low (less than 70°C), intermediate (70 to 74°C), and high (more than 74°C).

The physical cooking properties of rice are more closely related to the gelatinization temperature than to the amylose content of the starch. Rice with a high gelatinization temperature becomes excessively soft and tends to disintegrate when overcooked. Under standard cooking procedures rice with higher gelatinization temperature tends to remain undercooked. Rices of high gelatinization temperature require more water and time to cook than those with low or intermediate gelatinization temperature. Thus, gelatinization temperature correlates positively with the time required to cook rice.

Soaked milled rice of high gelatinization temperature elongates less during cooking than low- and intermediate-gelatinizing rice.

The gelatinization temperature may reflect the hardness of the starch granule and the endosperm; thus it may influence insect and fungus attack of rough rice and its field and postharvest deterioration in humid weather. There is some evidence that rices of intermediate or high gelatinization temperature are damaged less by such problems than low-gelatinizing grain.

The gelatinization temperature directly affects the physical properties

of the starch granule, which in turn influence the quality ratings of cooked rice. Rices of high gelatinization temperature seem to be uniformly undesirable in all breeding programs. Consumers in all major markets discriminate against high gelatinization temperature.

Most, if not all, japonica varieties are low in gelatinization temperature while the vast majority of tropical indicas are intermediate or low gelatinizing. The desirable low and intermediate classes that are equal in amylose content cook similarly. Thus, there is little reason to prefer one over the other.

The inheritance of gelatinization temperature is not entirely clear, but it appears to be fairly simple, involving one or two major genes. Gelatinization temperature is reasonably high in heritability, although it may vary by as much as 10°C within a variety in exceptional cases, depending on environment. High air temperature after flowering raises the gelatinization temperature (which lowers grain quality) and low air temperature reduces it.

When crossed with tropical indicas, many japonica (low gelatinization temperature) and some USA (intermediate) parents produce a moderate proportion of high-gelatinizing segregates. Crosses in which one parent has high gelatinization temperature always produce many high-gelatinizing F_2 segregates. Scientists at CIAT have observed that F_2 selections (F_3 seed) rated as high in gelatinization temperature are essentially homozygous for that trait and seldom segregate further. Thus, all high gelatinizing segregants should be immediately discarded. Some F_2 segregants that are low in gelatinization temperature, and most that are intermediate, will continue to segregate for all three breeding classes of temperature reaction. The F_2 selections that segregate as high, intermediate, and low temperature usually require several generations of selection before they become homozygous.

Gelatinization temperature is not associated with other important plant or grain traits except for certain useful correlations with amylose content. Thus, the preferred low or intermediate gelatinization temperature reactions are readily recombined with improved plant type, favored maturity, dormancy, and a wide range of desirable grain length, shape, and cooking qualities.

Varieties with high gelatinization temperature appear to have low amylose content, which makes them cook sticky. The only known exception is BPI 76, which has high to intermediate gelatinization temperature and intermediate amylose content. No varieties are known that have high gelatinization temperature and high amylose content. Because intermediate to intermediately high amylose content is preferred in most major indica areas, breeders can immediately discard high-gelatinizing segregants without determining their amylose content. High gelatinizing segregates have inferior cooking quality and are undesirable even in

indica areas where moderately low to intermediate amylose content is preferred, such as the Philippines and Indonesia. Similarly, high gelatinizing types should be discarded from japonica breeding programs, where low amylose is preferred — because of the detrimental effect of high gelatinization temperature on the physical properties of the starch. Interestingly, the reverse correlation does not hold — rices with low amylose content can be either low or high in gelatinization temperature.

A second apparent correlation concerns intermediate gelatinization temperature which apparently has never been recombined with low amylose content. All varieties that have intermediate gelatinization temperature are either intermediate or high in amylose content. Thus, where low amylose is undesirable, as in most indica programs, an intermediate gelatinization temperature indicates that the starch does not have a low amylose content. Such intermediate segregants do not need to be analyzed for amylose in the early generations, although an amylose determination is eventually necessary to distinguish between intermediate and high content.

The low gelatinizing class has no strict association with low, intermediate, and high amylose contents. Low gelatinization temperature is readily recombined with the three amylose levels.

The following associations of gelatinization temperature with amylose content are unknown or rare: high temperature and intermediate amylose; high temperature and high amylose; intermediate temperature and low amylose. Table 2 shows observed combinations and examples of each.

Table 2. Observed combinations of gelatinization temperature and amylose content and examples of each.

Gelatinization temperature	Amylose	Example
High	Low	Century Patna 231
Intermediate	Intermediate	CICA 4
Intermediate	High	Peta, IR5
Low	Low	japonicas
Low	Intermediate	many breeding lines
Low	High	IR8

Unlike amylose determination, which requires complex equipment and is comparatively difficult, the evaluation of gelatinization temperature is simple and rapid. Gelatinization temperature is estimated by the extent of the spreading and clearing of milled rice treated with a 1.7% solution of potassium hydroxide for 23 hours at 30°C. The grains with low gelatinizing temperature dissolve completely; the endosperm of the

intermediate class spreads partially; and the rices with high gelatinization temperature are essentially unaffected by the alkali.

The materials needed to determine gelatinization temperature are:

- plastic boxes 4.6 × 4.6 cm square and 1.9 cm high
- KOH (1.7 ± 0.05%). Dissolve 19.54 g KOH pellets (85%) in 1,000 ml of recently boiled and cooled distilled water. Store for at least 24 hours before use.
- repipet (optional).

Steps in determining the rice gelatinization temperature.

Steps	Key points
1 Prepare samples.	• Select duplicate sets of six milled kernels without cracks and put in plastic boxes
2 Dissolve samples	• Add 10 ml of 1.7% KOH.
3 Arrange samples.	• Provide enough space between kernels to allow for spreading.
4 Cover boxes. Let stand for 23 hours	• Maintain constant temperature at 30°C or use ambient temperature to ensure better reproducibility.
5 Visually rate appearance and disintegration of endosperm	• A rating for spreading of 1-3 is classified as high, 4-5 as intermediate, and 6-7 as low gelatinization temperature. Clearing values are usually 1 unit lower than spreading values.

Table 3 gives the scale for scoring gelatinization temperature. Brown rice does not react satisfactorily to alkali; separating the high and intermediate classes with brown rice is particularly difficult and samples must be milled.

Homemade mills must be used because adequate mills for small samples are not commercially available. Such mills operate on the principle of shaking a mixture of brown rice and an abrasive in test tubes. The major

Table 3. Numerical scale for scoring gelatinization temperature of rice.

Score	Spreading	Clearing
1	Kernel not affected	Kernel chalky
2	Kernel swollen	Kernel chalky; collar powdery
3	Kernel swollen; collar complete or narrow	Kernel chalky; collar cottony or cloudy
4	Kernel swollen; collar complete and wide	Center cottony; collar cloudy
5	Kernel split or segregated; collar complete and wide	Center cottony; collar clearing
6	Kernel dispersed merging with collar	Center cloudy; collar clear
7	Kernel completely dispersed and intermingled	Center and collar clear

draw back of some test-tube mills is that they require prolonged shaking to mill to the necessary degree.

At CIAT, a satisfactory mill was built from a discarded one-cylinder engine. A hard piece of wood was shaped to fit precisely into the cylinder and was bolted to the top of the piston, leaving a few centimeters clearance above the cylinder when the piston was completely depressed. A wooden block, with holes bored for 27 test tubes, was attached to the top. The engine was connected with a belt to an electric motor.

To mill, place from 1 to 2 grams of dehulled grains of single plant selections in the test tubes with about an equal volume of 60-mesh fused aluminum oxide. Close the tubes with stoppers and attach a cover to hold them steady within the wooden block. Run the electric motor for 60 seconds to thoroughly mill the grain. Remove the test tubes and screen off the abrasive, leaving the milled rice.

If facilities are available, a laboratory routine can easily be established for determination of amylose content, gel consistency, gelatinization temperature, and evaluation of size, shape, and appearance.

Until alternate screening techniques are available, programs subject to financial constraints might limit more complex analysis to fixed lines as they enter observation trials. This would involve only a few hundred analyses a year. This alternative is obviously inferior to the evaluation of thousands of plant selections per year beginning with F_2 or F_3 grain, but such mass evaluation is beyond the financial capability of many programs.

Rice is classified into broad groups of cooking quality by the complementan evaluation of amylose content, gel consistency, and gelatinization temperature. However, varieties within each group differ somewhat in eating quality — a difference enough to be detectable to consumers. This variability within groups is still not well understood. Conse-

quently, breeders should always cook and test both hot and cold cooked rice of their most promising material before releasing them as varieties. Field laborers are particularly useful on the taste panel because their quality preferences often differ from those of persons of higher income. Samples of milled rice along with a simple questionnaire may also be distributed to families in the area for evaluation of cooking quality. Rough rice should be stored at least 4 months after harvest before taste panel evaluation. Aging increases water absorption and volume expansion during cooking, resulting in a more flaky cooked rice than can be obtained with freshly harvested grain.

PROTEIN CONTENT

Rice is nutritionally superior to many other foods that are rich in carbohydrates. The protein content of the grain, although subject to extreme varietal and environmental variability, averages about 7% in milled rice and 8% in brown rice. The amino acid balance of rice protein is exceptionally good. Lysine content, for example, averages about 3.8 to 4.0% of the protein.

One important and well-documented fact is that, when supplied with little or no nitrogen fertilizer, the grain of the new high yielding varieties contains as much protein as that of the traditional varieties. But both grain yield and protein content of the new varieties increase when abundant nitrogen is used and cultural practices are improved. Agronomically induced increases of one to two percentage units in protein content at yield levels of 6 to 9 t/ha are common. This shows that the new high yielding varieties increase human consumption of protein.

Despite those positive aspects of the nutritional quality of rice, it may be important to further increase the inherent protein content of the grain, particularly for areas of Asia where rice consumption accounts for as much as 80% of the caloric intake and major substitution of other protein sources for rice is difficult. In such areas a genetic increase from 7 to 9 or 10% average protein content could be an enormous contribution.

In other developing areas rice consumption is less than 50 kg/person per year and the lower economic classes consume large amounts of cassava, plantain, potato, maize, unrefined sugar, and other foods that are inferior to rice in either protein content or amino acid balance, or both. The local market price of rice is often similar to or less expensive than that of the substitutes on a unit dry weight basis. Yet paradoxically, housewives in the Americas often discriminate against rice because of a widespread but erroneous belief that its nutritional value is inferior.

The quality of rice protein is basically a function of the protein content of the grain. As the protein level is increased, either agronomically or genetically, the degree of protein loss in milling is reduced, indicating that most of the additional protein is not in the bran. Furthermore, the

amino acid composition remains relatively stable. Some essential amino acids, including lysine, tryptophan, and threonine, do decrease modestly as protein increases. But the proportion of these amino acids does not decrease nearly as rapidly as protein increases. This was verified by observation of a better nitrogen balance in subjects fed high-protein milled rice that contained higher total levels of essential amino acids. Thus, high-protein rice appears to be nutritionally superior to rice of normal protein content.

Some breeding programs are focusing attention on total protein content as the principal nutritional limitation of rice. A basic difference between high-protein and normal varieties is that high-protein rices translocate more leaf nitrogen to the developing grain. Also, high-protein varieties have a higher level of free amino acids in the developing grain and protein is synthesized faster. IRRI has evaluated much of the world germplasm collection in the search for high-protein varieties. During one preliminary study, 7,419 samples harvested during the wet and dry seasons from fertile soils at IRRI averaged 10.5% protein. Of these, 101 samples, including several glutinous varieties, contained more than 13.5% in each season, and a few exceeded 15%. These high values exemplify one of the problems of protein evaluation. Protein analysis figures from experimental plots are routinely higher than those from farmers' fields because nitrogen use is greater and water and weed control are better in experimental plots.

The IRRI experience indicates that it may be possible to combine somewhat higher protein content and normal amino acid balance with the high yields of the better dwarf plant types. But breeding for increased protein content involves many problems. It is doubtful that farmers, processors, or consumers will pay a premium for high-protein grain, and superior nutritional value in itself will not sell a new variety. Improved protein content, therefore, will have to be incorporated into lines that are at least equal or superior in yield to existing varieties. In this sense breeding for higher protein content is more difficult than breeding for improved milling or eating quality, which by themselves can determine acceptance or rejection of a variety. Until further knowledge is gained, breeding for improved protein content should not be an objective of most national and local rice improvement programs.

The inheritance of protein content appears to be complex. No single genes for increased levels of individual amino acids, analogous to the opaque-2 gene for increased lysine content in maize, have been identified. The extreme variation in protein content caused by environment makes it difficult to identify lines in which high protein content is genetically determined. Only about 25 to 50% of the protein variability is estimated to be genetically controlled. The major environmental influences are disease or insect damage, weather, uniformity of rates of applied fer-

tilizer, and water control. Because there is considerable variability among and within the panicles of individual plants, the entire plant should be harvested to assure a uniform sample.

Protein content is not related to any visible character of the grain, so analytical analysis is essential. Brown rice is probably superior to milled rice for analysis because it is difficult to standardize the degree of milling for all samples. Samples of high protein content are more resistant to abrasive milling, yield less bran and polish, have higher head rice yields, and may be somewhat darker than lower-protein samples. Milled rice of high protein content requires more water and longer cooking time but has the same eating quality as normal rice.

Cereal chemists at IRRI have modified the standard protein determination to increase its efficiency and accuracy. From 200 to 300 samples per day are analyzed with an autoanalyzer system by the colorimetric assay of ammonia from the micro-Kjeldahl digestion. Nevertheless, because of the cost of the necessary laboratory equipment and the complexity of analysis, few breeding programs in developing countries can or should attempt to breed for increased protein content at present. Too many important and more easily solved problems are of higher priority.

AROMA

Scented or aromatic grain, a relatively minor quality character of limited importance, is preferred in some areas of Asia and draws a premium price in certain specialty markets. Pakistan and Thailand are the best sources for strongly aromatic varieties such as Basmati 370, Leuang Hawn, and Khao Dawk Mali. At IRRI, the scented character has recently been transferred to improved plant types of both common and glutinous endosperms.

Breeders working in areas where scented rice is undesirable must be aware of the character when introducing improved lines or established varieties from countries where aroma is prized. For example, several advanced lines of IR841 were initially promising in Latin America and one was multiplied for release in Costa Rica until blast susceptibility eliminated its consideration. When cooked, lines from this cross had a trace of aroma that would have been objectionable to consumers in some countries.

The inheritance of aroma depends on from one to three complementary factors. Little is known about the breeding behavior of aroma or the influence of environment on its intensity.

A simple laboratory test to evaluate aroma was developed at IRRI. Place from 20 to 30 freshly harvested milled grains in a test tube with 20 ml of distilled water. Then stopper the tube and place it in boiling water for 10 minutes (brown rice requires 20 minutes of cooking). Remove the test tube and cool it. Rate the aroma as strong, intermediate, slight, or absent. Include a strongly scented variety in each test to give a basis for comparison.

CHAPTER 7

Breeding for pest resistance

THE CHALLENGE OF INCORPORATING stable resistance to major diseases and insects into modem tropical varieties rivals any past contributions of rice breeding. Several factors make pest resistance an important rice improvement objective.

- Rice is widely grown in the warm, humid tropics where pests are more prevalent than in the temperate regions because pathogens do not overwinter in the tropics and insects do not go into diapause.
- The widespread adoption of the new dwarf rices has produced conditions that are highly favorable for some pests. Heavy nitrogen applications, close spacing, and continuous cropping have commonly increased the severity of blast, bacterial blight, sheath blight, and brown planthoppers.
- The cost of agricultural pesticides is rising and the public is increasingly recognizing the deleterious effects of such chemicals on the environment. The alternate approach is to increase reliance on host resistance to minimize production costs and reduce field losses.
- The spread of a handful of new, modern varieties over millions of hectares threatens hundreds of local varieties with genetic suffocation. This increase in genetic and phenotypic uniformity has removed an important natural barrier to widespread epidemics. Although the number of new varieties is steadily increasing and will continue to expand, the amount of genetic variability will never approach its former level.

Fortunately, the wide genetic variability in rice provides useful resistance to most of the major pests. But this resistance has just begun to be properly exploited.

Breeding for disease resistance in tropical rice has been successful to varying degrees in the past. The resistance of the dwarf varieties to blast, for example, has not been adequate for the endemic areas in Latin America, but has generally been broader than the resistance of many indigenous varieties in the delta regions of monsoon Asia. Resistance has been highly effective in reducing losses to bacterial blight and the tungro, grassy stunt, and hoja blanca viruses in several countries. On the other hand, varieties with resistance to sheath blight and brown spot have not yet been developed. Although some varieties are resistant to narrow

brown leaf spot and leaf scald the development of varieties resistant to these diseases has not been emphasized in breeding programs.

But breeding for insect resistance in rice has been spectacularly successful in some cases, and illustrates the importance of not automatically accepting prevalent professional opinion. Before 1962 most scientists considered insect resistance an unrewarding area of research But IRRI entomologists persistently evaluated thousands of rice varieties for resistance to important local species of stem borers and planthoppers. Once large differences in varietal reaction were found, insect resistance was accepted as a major breeding objective. Tests for resistance were rapidly developed and resistant donors were identified. Major insects that can now be satisfactorily controlled through plant resistance include four planthoppers and leafhoppers, gall midge, and, to a lesser extent, several species of stem borers.

Resistance has occasionally been found in varieties in which it was not suspected. For example the Sogatodes planthopper, a severe rice insect in tropical Latin America, is unknown in Asia. But when the new dwarfs were introduced into Latin America, they were found to have superior resistance to the pest. Similarly, many japonica varieties from Asia are resistant to hoja blanca virus, which is limited to the western hemisphere. A wild rice from India, *O. nivara,* remains the best source of grassy stunt resistance; no strong resistance to it has been found in the more than 12,000 *O. sativa* entries screened.

Mutation breeding has not contributed significantly to pest resistance in rice, despite the substantial expenditures of time and money. A few selected programs should attempt to use mutation breeding procedures to develop resistant varieties against some pests where no resistance sources have yet been found. Major emphasis of all programs, however, should be to exploit by conventional breeding means the existing genetic variability in cultivated rice.

Much remains to be done in the effort to develop many rices with diverse but stable pest resistance for broad areas of production. Pest-resistant improved varieties are probably grown on less than half of the world's irrigated rice land. Most of these varieties are resistant to only one or two pests, but breeders now have the potential to develop new varieties with combined resistance to most major diseases and insects.

INTERDISCIPLINARY APPROACH TO PEST RESISTANCE

Although lip service is often paid to the fundamental tenet of interdisciplinary cooperation in pest resistance work, insufficient effort is being made to attack serious pest problems through a unified approach. One all-too-common breeding practice that must be discarded is that of breeders narrowly selecting for agronomic characters in the early generations, then requesting pathologists and entomologists to determine which

of the relatively few advanced lines are resistant. It is surprising that any useful resistance has been identified and utilized at all through this practice. Breeders must change their attitudes and invite other specialists into their programs — and share with them both responsibilities for failure and recognition for accomplishments.

On the other hand, too many pathologists and entomologists feel that their main mission is to exhaustively investigate pathogen and host peculiarities, mostly to enhance their publication records and with little concern for the successful farm use of varietal resistance. The first challenge for rice scientists, therefore, is to realize that their paramount responsibility is to improve and protect the crop's yielding ability, and that they must meld their specialized talents to achieve this goal.

Pathologists and entomologists encounter many challenges through day-to-day association with plant breeders, such as placing major emphasis on the continued improvement of screening methods and on the identification and utilization of donors with stable resistance to different pest races and biotypes. The epidemiology of the host pathogens as well as the ecology of the various insects must be studied more thoroughly to better understand the factors that influence pathogen and predator variability and lead to disease and insect outbreaks.

STABLE RESISTANCE

The major objective of all resistance breeding programs is to identify and effectively use stable resistance to the major pests. A source of broad, stable resistance to a pest should maintain a satisfactory long-term level of resistance against diverse races, strains or biotypes in many regions.

Host plants generally display one of two types of resistance to plant diseases:

- vertical or specific resistance, by restricting the infection process, or
- horizontal or nonspecific resistance, by restricting the colonization, growth, and dispersal of the parasite before infection. The specific type of resistance has generally been rather short-lived while nonspecific resistance has lasted longer.

The number of genes that directly control resistance conditions the ease and effectiveness with which that resistance can be exploited. Specific resistance, which is usually controlled by one or two genes, is relatively easy to exploit because reactions among segregating populations are discrete and easy to recognize. On the other hand, nonspecific resistance, which is under multigenic control, is much more difficult to evaluate and manipulate. Transferring quantitative traits into plants of improved type is a formidable task. Variability of major rice pathogens and insects is shown in Tables 1 and 2.

Single vertical resistance genes have been used individually in many crops. Such resistance has been long lasting against pathogens that have

Table 1. Variability of major rice pathogens and sources of resistance.

Disease	Pathogen or vector	Pathogen variability	Apparent type or resistance	Resistance genes	Some donor varieties
Blast	*Pyricularia oryzae*	very high	vertical; horizontal suspected to exist	12 or more	Many but Tetep, Carreon and Tadukan have proven quite stable.
Sheath blight	*Rhizoctonia solani*	low	unknown, but probably horizontal	not defined	Ta-poo-cho-z
Bacterial blight	*Xanthomonas oryzae*	intermediate	vertical with modifying genes	*Xa 1*	
				Xa 2	
				Xa 3	
				Xa 4	TKM 6, Sigadis, IR22, MTU 15, Pelita I/1
				xa 5	BJ 1, DZ 192, Kele, Chinsurah Boro II, Dular, Hashikalmi
				Xa 6	Zenith
				Xa 7	DV 85
Tungro virus	*Nephotettix virescens*	intermediate to low	vertical	not defined	Many but Peta, Gam Pai, and Sigadis have been widely used.
Grassy stunt virus	*Nilaparvata lugens*	low	vertical	*GS*	*O. nivaro*

Table 2. Variability of major insects and sources of resistance.

Insect	Scientific name	Variability	Type of resistance	Genes for resistance	Donor varieties
Brown planthopper	*Nilaparvata lugens*	high	antibiosis	*Bph 1*	Mudgo, TKM 6
				bph 2	ASD 7, PTB 18
				Bph 3	Rathu Heenati
				bph 4	Babawee
Green leafhopper	*Nephotettix virescens*	low	antibiosis	*Glh 1*	Pankhari 203
				Glh 2	ASD 9
				Glh 3	IR8
				glh 4	PTB 8
				Glh 5	ASD 8
Rice planthopper	*Sogatodes oryzicola*	low	antibiosis		IR8, CICA 4
Whitebacked plant-hopper	*Sogatella furcifera*	low	antibiosis		N22
Gall midge	*Orseolia oryzeae*	intermediate	antibiosis		PTB 18, PTB 21
Stem borer		low	nonpreference and antibiosis		
striped	*Chilo suppressalis*				TKM 6
yellow	*Typoryza incertulas*				IR1820–52

little genetic variability but vertical resistance has been unstable against pathogens that are genetically variable. Several breeding strategies have been suggested to prevent pathogen populations from shifting and therefore to extend the length of effective resistance (Table 3). A few strategies

Table 3. Relative effectiveness of several breeding strategies in developing stable resistance to diseases.

Breeding strategy	Stability of resistance when pathogen variability is		
	Low	Intermediate	High
Vertical resistance:			
Genes used individually	long	intermediate	short
Gene deployment	long	long	intermediate to long
Multilines	[a]	[a]	long
Horizontal resistance[b]	[a]	long	long

[a]Not relevant. [b]Mechanisms that help slow disease epidemics in horizontal resistance are reduced sites and areas of infection, lengthened incubation periods before pathogen reproduces, restricted amounts of colonized tissue from each infection site, and reduced levels and duration of inoculum production and dispersal from each infection site.

have been tried on a limited scale, but all need considerable study. Three of these breeding strategies are outlined below.

- *Gene deployment* is the selective growing of varieties with several individual genes for vertical resistance in different geographical regions where a crop is widely grown. If three genes are deployed over a wide area, for example, yield losses to new pathogenic races may be severe in one area, but not in the two other areas. This method has little relevance for most rice-growing areas because the distribution of farmer varieties cannot be easily manipulated.
- *Pyramiding genes* is the incorporation of several major genes for vertical resistance into a single variety. Genes for vertical resistance that function collectively in a single genetic background may contribute to horizontal resistance. Pyramiding genes may be a promising way to provide stable resistance to several rice diseases, although selection processes have not yet been developed. Some scientists are concerned that pyramiding genes into single varieties may expend resistance genes too rapidly.
- *Multilines* are mixtures of several component lines, each with similar phenotypic traits but with different genes for vertical resistance. Multilines have some traits of both vertical and horizontal resistance because they reduce the amount of initial disease as well as the rate of disease buildup. But multilines are complex to develop and maintain. This limits their possible use to only those diseases with high pathogenic variability such as blast, for which stable resistance cannot be provided by simpler methods.

Most of the resistance identified and used for the major rice diseases so far apparently is vertical. Vertical resistance has been used primarily because of the simplicity and speed with which donors can be screened

and identified, and resistance genes incorporated into improved varieties. Duration of vertical resistance has been long for tungro and grassy stunt virus, intermediate for bacterial blight, and short for blast.

Resistance to insects is classified into three broad categories:

- nonpreference because of plant factors that render it unattractive for the oviposition, feeding, or shelter of insects;
- antibiosis, which adversely affects the feeding and multiplication of the insect on the plant; and
- tolerance, whereby plants support large insect populations but suffer little damage.

Nonpreference and antibiosis are the most effective types of resistance for control of most insects because they reduce insect populations. Tolerance, on the other hand, does not inhibit insect multiplication and may lead to higher population buildup.

Simply inherited resistance has been long lasting in the cases of the green leafhopper and *Sogatodes oryzicola.* But brown planthopper resistance has been short-lived. The effect of multigenic resistance to stem borer has been hard to measure because levels of resistance have generally been low and because the major stem borer species have generally been relatively low in numbers.

SCREENING PROCEDURES

Effective screening procedures are essential to a successful breeding program for resistance. Individual procedures must be worked out for each pest because host-pathogen interactions, like host-insect interactions, vary greatly. Simple screening procedures for vertical resistance are effective for some pests such as blast, bacterial blight, leafhoppers, and planthoppers. But other pests such as the vector-transmitted viruses and stem borers are more complex and require complicated procedures. Rapid progress can be made in resistance screening and breeding programs if screening techniques are simple and efficient and if their results correlate highly with field behavior of the pest. But progress is slow and valuable time and expense are wasted if procedures are too complicated and cumbersome, or do not relate well to pests' field behavior.

Pathologists and entomologists have recently made significant progress in the development of simplified and effective screening procedures for most rice diseases and insects. The procedures now used to screen for various pests (Table 4) are modifications of tests conducted under two basic conditions:

- field screening under natural or partially modified conditions, and
- seedling screening under partially modified conditions in the field or greenhouse or screenhouse.

All screening procedures must be adapted to fit local environmental conditions and to most efficiently and effectively use available resources

Table 4. Screening procedures used to evaluate rice varieties for pest resistance.

Screening procedure	Pests[a]
Field screening	
Natural infection or infestation:	
Year-round in endemic areas, or seasonal with favorable environmental and cultural conditions	many
Natural infection or infestation with cultural and environmental manipulation:	
Time of planting	many
Relay planting	RTV, GSV, BPH
Close spacing	BB
Plant nutrition (nitrogen)	B, BB, SHB
Weather factors (temperature, humidity, and leaf wetness)	B, BB, SHB, GM
Artificial lights	GM
Selected insecticide application	BPH
Artificial inoculation and infestation:	
Single plant inoculation	BB, SHB
Bulk inoculation	B, BLS, SHB
Seedling screening	
Natural infection with manipulation:	
Tune of planting	B
Relay planting	B
Close spacing	B
Plant nutrition (nitrogen)	B
Humidity and leaf wetness modification	B
Greenhouse and screenhouse:	
Artificial inoculation or infestation in greenhouse	BB, RTV, GSV, BPH, GLH, SPH, WBPH
Artificial inoculation or infestation with manipulation in greenhouse or screenhouse	
Time of planting	SB
Humidity and leaf wetness modification	GM

[a]B = blast, SHB = sheath blight, BB = bacterial blight, BLS = bacterial leaf streak, RTV = rice tungro virus, GSV = grassy stunt virus, BPH = brown planthopper, GM = gall midge, GLH = green leathopper, SPH = Sogatodes planthopper, SB = stem borer, WPH = whitebacked planthopper.

and manpower. Natural field screening should generally receive top priority if pest pressures are adequate to give consistent results. By manipulation of the host, pest, and environment, pressures may be maintained at consistently higher levels over longer periods of time to enable several screenings each year.

Seedling screening can be highly efficient if the results agree with those at the adult stage. Unfortunately, results of seedling and adult screening

may not completely agree for several of the rice pests. Furthermore, there is considerable doubt that seedling tests are useful for the detection of horizontal resistance.

In areas where conditions cannot be manipulated to encourage disease or insect development, alternate testing sites must be found and used. For example, pest attacks are rare in the breeding plots at Lambayeque, on the arid Peruvian coast. Peruvian scientists solved this problem by testing in the interior jungle where blast disease and brown spot are epidemic. Although establishing alternate sites is costly and inconvenient, the alternative of not testing for resistance may result in disaster.

Each breeding program should take advantage of the screening nurseries in the International Rice Testing Program (IRTP). Selected entries from various programs can be screened naturally in "hot spots" around the world as well as under controlled conditions in those programs that have available resources. Thus, entries can be screened against diverse strains, races, and biotypes under many environmental conditions. The IRTP tests can provide helpful information on resistant donors and progeny for selection and use in local programs.

It is evident that major emphasis in the future must be placed on horizontal resistance. This will require much research on screening methodology and on the epidemiology and ecology of diseases and insects.

Regardless of screening methods used, it is of paramount importance that epiphytotics and insect infestations be encouraged to develop in all breeding plots. Breeders too often become alarmed by heavy disease attacks and attempt to eliminate or reduce them. Although the breeders argue that their plots look bad or that they will lose useful breeding material, the loss of such poor lines to pests is a "blessing in disguise" because they can then concentrate their resources on the fewer promising materials that survive.

INTEGRATION OF SCREENING AND BREEDING TECHNIQUES

To be effective, the various screening techniques and breeding procedures must be totally integrated into workable, productive resistance breeding programs. Each program requires a special blend of screening and breeding procedures to best meet local objectives.

The plant pathologist and the entomologist in each program should establish comprehensive screening programs to identify donors and evaluate progeny for resistance to individual stresses. The plant breeder must integrate the various individual screening programs into the total breeding effort.

Manpower and resources are limited in most rice-improvement programs. In such cases scientists should identify the major problems and concentrate their resistance work on them. It is better to solve a few `pest

problems than to work on too many and not solve any of them. Some of the criteria to use in the selection of priority pests and in the implementation of operational proedures follow:

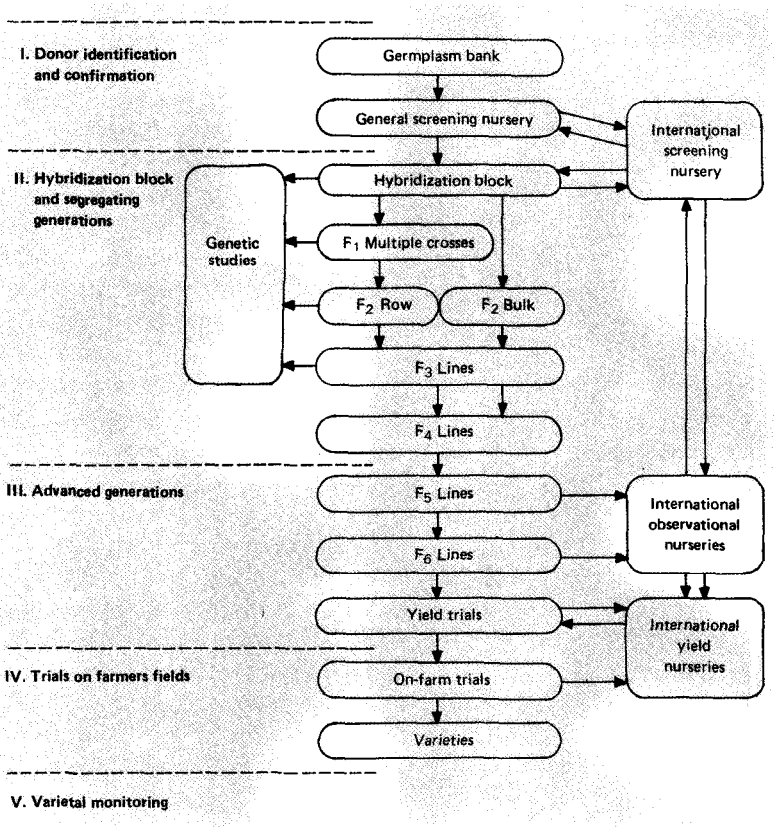
1. Give priority to the development of varieties resistant to those pests that annually cause the highest losses in farmers' fields.
2. Focus on those pests for which the prospects to identify and transfer stable resistance into breeding material are best. Use of material with simple modes of inheritance and use of simple screening procedures speed the development of resistant material, but stability of resistance is often short-lived. Therefore, efforts must be made to use multigenic resistance where possible.
3. Work on those problems in which available resources such as scientdic manpower, fields, greenhouses, screenhouses, and environmental conditions favorable for specific pests can best be used. If conditions are not presently available to screen for resistance against major problems, consider setting up new stations in epiphytotic areas, building new screenhouses, or having material cooperatively screened by other programs, or through the IRTP.

Comprehensive screening program

IRRI's comprehensive screening program for bacterial blight illustrates the importance of systematic evaluation (Fig. 1). The first step in evaluation is to identify and confirm resistant donors from the world germplasm bank and international screening nurseries. New sources become available to the program, and the stability of their resistance is evaluated and confirmed through continuous local testing in the hybridization block and in the general bacterial blight screening nursery, as well as through multilocation testing in the IRTP network. Because the amount of seed of germplasm bank entries is limited, the screening must be efficient. Seed of the resistant varieties should be simultaneously increased to provide seed for further tests. Screening results are often affected by the extreme variation in plant type, duration, and photoperiod sensitivity. They must therefore be carefully interpreted.

The importance of testing segregating populations cannot be overemphasized. Half of the plants can be discarded through tests of F_1 populations from three-way or multiple crosses in which one parent has a single dominant gene for resistance. For single crosses in which one parent has resistance to a disease, all plants are tested starting with the F_2 population and continuing through pedigree generations. For bacterial blight, this can usually be done quite early because the simple inoculation techique allows all plants to be screened in the breeder's plots. This screening phase also includes genetic and allelic studies of the resistant donors.

Because most advanced lines are fixed for resistance, only a few plants must be inoculated for each progeny line or yield trial plot. Those prog-



1. The comprehensive screening program for bacterial blight at IRRI.

eny lines that are segregating for resistance are purified in headrows. Despite rigorous selection pressures in preceding generations, a few lines may not become homozygous for resistance to bacterial blight even by the F_6 or F_7. Therefore, it is not surprising that varieties are released without homozygosity for many traits in programs where selection pressures are less than rigorous.

Multilocational screening by natural infection and artificial inoculation in farmers' fields of entries that have been promoted to national and regional varietal trials is important. It shows how entries react under farm conditions and against possible distinct strains of bacteria. Furthermore, it confirms or rejects the reliability of experiment station screening.

The fifth and final component of the bacterial blight evaluation program is continuous monitoring of varieties in farmers' fields and at experiment stations around the country, and selectively in other countries.

Such monitoring provides information on the stability of resistant varieties when grown in wide areas and indicates the types of resistance to be used in future varieties.

Screening is often less comprehensive in smaller rice improvement programs than in larger ones, but all programs should provide for rigid selection pressures on as much material as possible.

Coordination of screening and breeding

Although IRRI's comprehensive screening and breeding program for disease and insect resistance is larger than most, it can be used to illustrate the importance of effective coordination.

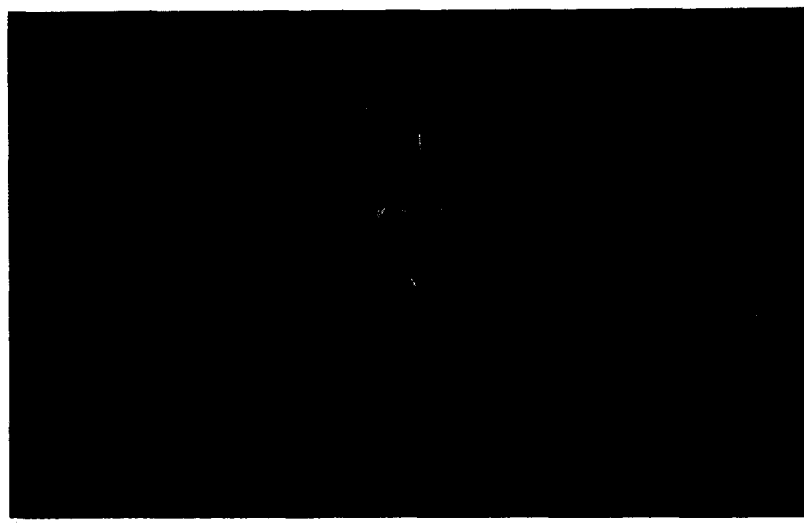
IRRI is systematically screening the 35,000 entries in the world germplasm bank for resistance to five diseases, five insects, and several problem soils. More than 20,000 entries have already been tested for reaction to diseases such as bacterial blight and blast. Far fewer have been screened for diseases such as sheath blight that require complex procedures.

The important link between screening for donors and varietal development is the quick and efficient transfer of new sources of resistance into the breeding material. As soon as a new source of resistance is identified, numerous crosses are made to incorporate the genes into improved breeding lines with diverse genetic backgrounds. The progeny are then screened against an array of diseases and insects.

The screening for various stresses starts at different generations, depending on the screening procedures. Screening starts in the F_1 populations of many multiple crosses for bacterial blight, brown planthoppers, and grassy stunt virus. For tungro virus, screening begins in the F_2, and for blast and green leafhoppers, in the F_3. Figure 2 shows F_2 plants segregating for resistance to bacterial blight and tungro virus. Most pedigree materials are grown without protection beginning in the F_2, so that they are often exposed to natural disease pressures such as narrow leaf brown spot, bacterial leaf streak, and to outbreaks of insects such as whorl maggot, leaf roller, and stem borer. All highly susceptible lines are discarded.

Some F_2 populations, as well as the elite lines, are distributed internationally so that other rice improvement programs can use the resistant materials either in segregating populations or as fixed lines. Resistance that has been transferred into plants of improved type is more easily used than that of the original unimproved donors as a source of new parents.

Intense disease pressure continuously applied over several generations can result in unexpected, if not inexplicable, gains in the expression of resistance. Two clear examples of this occurred in the Colombian national program between 1958 and 1967 when resistance to hoja blanca virus was a major objective. A few moderately resistant introductions



2. F_2 plants being simultaneously screened for reaction to bacterial blight and tungro virus.

were crossed with highly susceptible material. Every generation of the segregating populations was exposed to violent epiphytotics of the virus, so selection pressure for the least diseased segregates was strong. Although no single cross included more than one moderately resistant parent, several fixed lines were selected within a few years that were considerably more resistant than any of the original parents.

While this work was in progress, the breeding plots were also affected by an unknown soil problem (diagnosed some years later as zinc deficiency) that damaged most plantings to a moderate degree. The least affected plants were selected each season and several were combined in continuing crosses. The final selections were highly resistant to hoja blanca virus and to zinc deficiency. The remarkable aspect is that the progeny lines, which were highly resistant to zinc deficiency, were developed from moderately to highly susceptible parents. Apparently, repeated intercrossing of the better progeny and intense selection pressure resulted in the rapid accumulation of many genes, each of which conferred small increments of tolerance.

It is important for each program to screen local and national germplasm collections. Resistant donors from such collections often have locally desirable characters such as specific grain quality or tolerance for soil problems. Local germplasm also often serves as good sources of resistance to local strains, races, or biotypes of pests. But it may be desirable for smaller programs that cannot make many complex crosses to introduce some resistant sources from segregating populations of exotic materials available from larger programs.

In summary, it is of vital importance that scientists in each program

focus on the major diseases and pests and that the pathologists and entomologists develop comprehensive programs for each stress. The plant breeder must integrate these elements into effective programs to produce the diverse varieties needed by the world's rice farmers.

BLAST

Blast is the most widespread rice disease and its causal organism *Pyricularia oryzae* is the most variable pathogen. International cooperation is needed to successfully control blast.

The uniform blast nursery method of screening used in the International Rice Blast Nursery (IRBN) is highly efficient for identifying vertically resistant parents and breeding lines. Through the IRBN, plants can be quickly and continuously screened to determine the stability of resistance against the many races of blast around the world.

Because neck blast causes the most serious yield losses and resistance at the two stages may differ for some varieties, breeding lines and varieties should be periodically screened at both the seedling and neck stages.

Several varieties that have been strongly resistant in repeated IRBN tests at IRRI and many locations around the world are Tetep, Tadukan, Carreon, Dissi Hatif, C46-15, and Colombia 1. These rices have been extensively crossed with commercial dwarf varieties. Some progeny lines that have shown broad-spectrum resistance are being extensively used as donor parents in several breeding programs. These progeny lines combine well and have other favorable attributes, although not all may carry the full complement of resistance genes from the donors.

The genetics of blast resistance has been studied in several countries. Scientists have identified more than a dozen resistance genes, but the relevance of the information is questionable because the fungus is so variable.

Wherever blast is a major problem all breeding programs, regardless of size, should have a uniform blast nursery to continuously screen donors and progeny beginning with the segregating generations. The following three breeding approaches may be used to incorporate blast resistance into future varieties.

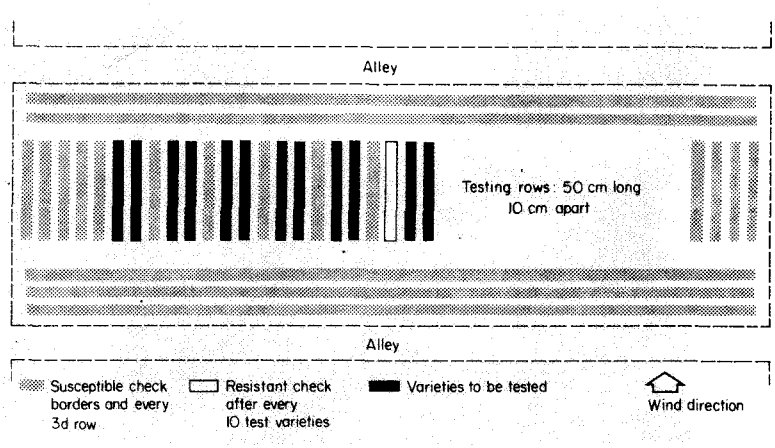
1. *Diverse single-source resistance.* Individual donors of broad-spectrum resistance such as Tetep can be crossed with outstanding varieties and breeding lines in single and in multiple hybridizations. Through continuous and rigid selection pressure, varieties with adequate resistance may be identified for areas such as the Asian river deltas where blast pressure is not too high.
2. *Pyramiding resistance.* International institutes and larger national programs can intercross various blast resistant varieties selectively to combine the F_1's with each other and with other dwarf progeny from

blast resistant donors. Rigorous screening of early generation progeny will readily identify the resistant segregates. An important limitation is the absence of a technique to indicate whether the resistant lines carry genes from one, two, or more donors. Elite progeny can be shared with rice scientists around the world through the IRBN or on a regional collaborative basis. Worldwide screening should identify progeny that have broad-spectrum resistance in combination with regional and local adaptability.

3. *Modified multilines.* There may be a need for large breeding programs to work cooperatively on the development of multilines. Breeders should cross broadly adapted improved varieties with many sources of broad resistance. They should backcross the F_1 once or twice to the broadly adapted varieties and carry the resistant progeny through the segregating generations while selecting for the phenotypes of the recurrent parents. Phenotypically similar lines with distinct genes for resistance can be tested internationally by national programs. Similar lines best adapted to local growing conditions can be bulked for varietal trials.

Figure 3 shows the layout of the uniform blast nursery test. The required materials and procedures used are:

- upland plot with good soil
- fertilizer (NPK)
- an irrigation system (overhead preferred)
- garden hoe, rake, or other tools to prepare soil
- stakes (split bamboo or sticks of 2 sizes; 1 m and 30 cm long)
- insecticides (carbofuran or BHC granules if available)
- rat baits, and
- test varieties and susceptible and resistant checks.



3. Layout of the uniform blast nursery.

Auxiliary items

- planting board to mark the rows, and
- polyethylene cover and frame to use when weather is dry.

Screening procedures for blast resistance.

Steps	Key points
1 Select area.	• The land should be uniformly fertile, with some protection from direct sunlight during part of the day and a good windbreak
2 Choose seeding date.	• The fungus develops best in cool temperatures (20-24°C night temperatures) and long hours (more than 11) of leaf wetness. For many sites. the best time is in the wet season, about 1 month after the beginning of the normal rice-growing season • Tests conducted during hot, dry seasons require modification of the relative humidity and length of dew period to induce infection. Also bombardment (spreader) plots should be planted 2-3 weeks in advance of the nursery seedling date to increase the inoculum. Polyethylene sheets and overhead water sprinklers are needed to maintain long periods of leaf wetness.
3 Prepare land.	• Lay out and prepare seedbeds. 1.2 m wide and of a convenient length Leave narrow alleys between the beds.
4 Apply fertilizer.	• Apply abundant nitrogen (60 kg N/ha or more) and other nutrients as needed before seeding. • Fifteen days after seeding, topdress 60 kg N/ha.

(continued on next page)

Screening procedure for blast resistance continued

Steps	Key points
5 Prepare for seeding.	• On the upwind side prepare 3 border rows parallel to the long dimensions of the bed (10 cm apart) and 2 rows on the downwind side for the susceptible bombardment variety (Fig. 3). • Prepare 50-cm rows perpendicular to the border rows for the test materials.
6 Seed the nursery	• Dibble 5 g of seed of each entry into the rows according to the layout shown in Figure 3. • Seed the border rows densely and uniformly. • Cover the seed with fine soil and apply water.
7 Manage nursery.	• Keep weed free. • Apply insecticide and rat bait as needed. • Water the plot two or three times dally if there is no rainfall. Watering in the late afternoon is important to maintain high humidity and long dew periods at night.
8 Aid spore production	• This may be necessary only during dry, windy seasons or during periods of very heavy rains. • Plant a susceptible variety 2-3 weeks prior to the regular nursery to build up Inoculum. • Collect and chop blast-infested leaves into pieces (3-5 cm) and broadcast over the test plots. • Cover the plots with polyethylene sheets at sunset each day. Support the sheets with bamboo stakes and leave plots covered until 0900 the next day.

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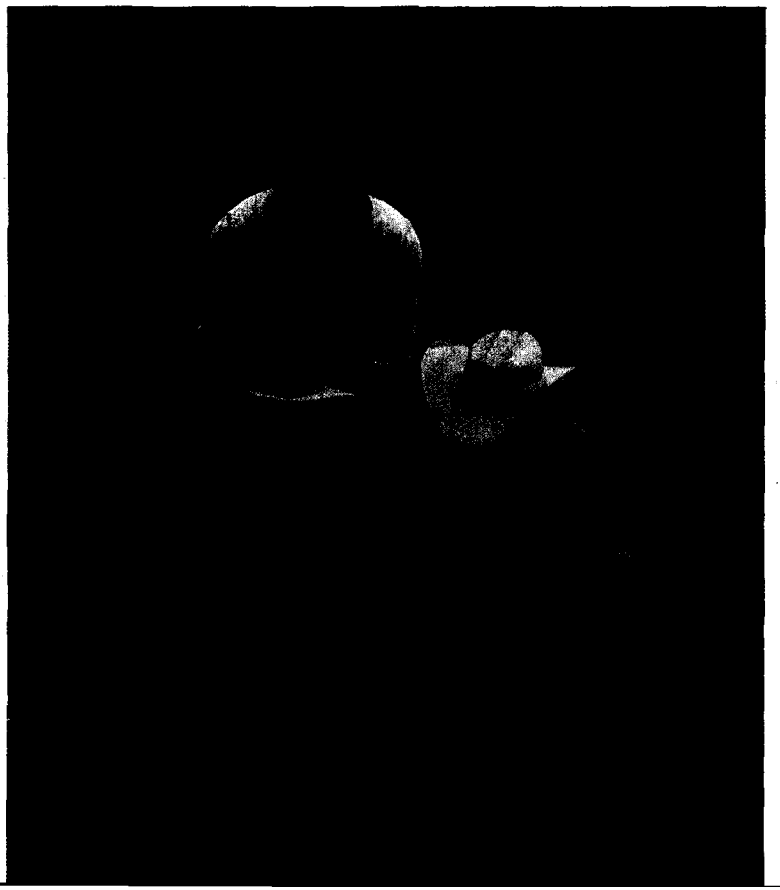
Screening procedure for blast resistance continued

Steps	Key points
9 Score nursery.	• The infection on the susceptible check must be severe before readings are taken (Fig. 4). The best time to score is usually 25 to 35 days after sowing but the scoring should be delayed if the susceptible checks are not completely infected. • Use the 1-9 scale in the standard evaluation system.
10 Score neck infection.	• If water is available and the nursery is planted at the appropriate season, thin out the plants and add fertilizer. Water as needed so that the plants will mature and neck infection can be assessed.



4. Scoring breeding lines in the uniform blast nursery.

SHEATH BLIGHT

The sheath blight causal organism *Rhizoctonia solani* is the imperfect stage of *Thanatephorus cucumeris,* which has a wide host range. The lack of strong rice resistance to sheath blight may be explained by the general principle governing disease relationships — that strong varietal resistance to pathogens with wide host ranges is unusual.

Several procedures have been developed for testing varietal reactions to sheath blight. The most common method in Asia is to grow the fungus on rice hulls and either place the sclerotia in the leaf whorl or tape it to the stem. Varietal response is measured by the length of the lesion at a fixed time after inoculation. Some resistance has been found but it has not been strong. Lesion length and subsequent spread to the leaves are greatly influenced by plant type, relative humidity, and level of nitrogen application.

A field screening method developed in Louisiana, USA, has been reported promising. Many sclerotia are placed on the soil surface. The disease then develops naturally. Such natural inoculation has identified some tolerant lines.

Although a few Asian varieties have moderate sheath blight resistance, it has not been transferred to dwarf varieties. Several intermediate statured varieties, however, have some resistance.

To better exploit such moderate levels of resistance, pathologists and breeders might

1. improve the screening method to more efficiently and effectively identify varieties with intermediate resistance;
2. intensify thesearch for new and better resistant varieties in IRRI's and in national germplasm banks; and
3. use multiple crosses to combine and pyramid the sources of resistance.

The material needed to screen for sheath blight resistance is sclerotia of *Rhizoctonia solani.*

Screening procedure for sheath blight.

Steps	Key points
1 Prepare inoculum.	• Culture the most virulent isolate for 1-2 weeks on either autoclaved unhulled rice grains or 10-cm-long pieces of rice straw.

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Screening procedure for sheath blight continued

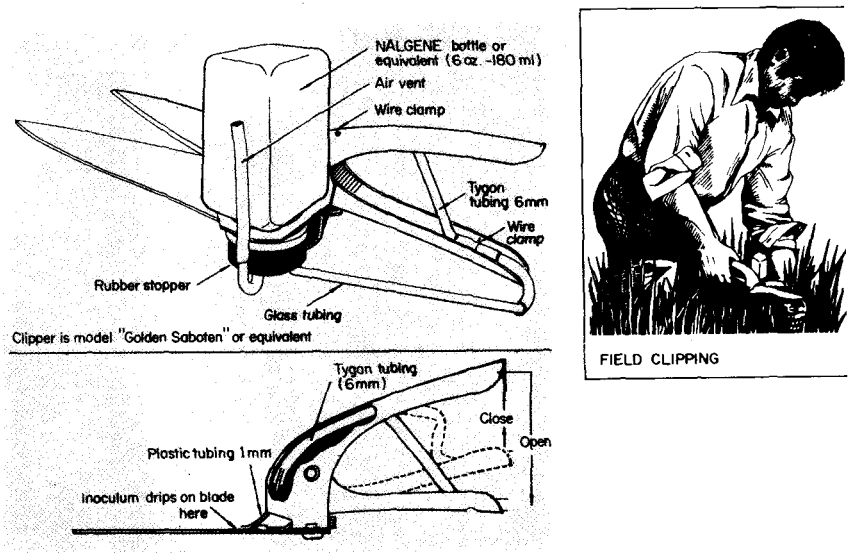
Steps	Key points
2 Manage plots	• Plant the test varieties in rows or small plots. Small plots are more convenient to measure spread of secondary disease. • Add high rates of nitrogenm, potassium, and phosphorus to stimulate luxuriant plant growth.
3 Inoculate	• Inoculate each variety 1 month before flowering. • Drop the grain culture inoculum at the center of each hill or insert three pieces of rice straw between the tillers in each hill.
4 Score	• The lesion length and size should be evaluated based on the standard evaluation system for rice. • If secondary spread results, record the amount.

BACTERIAL BLIGHT

The improved practices of rice culture used in recent years, such as high nitrogen rates, dense planting, and continuous cropping, have contributed to the increased incidence of bacterial blight in both temperate and tropical Asia. Because chemical control measures are not practical, resistant varieties must be used to minimize disease losses.

The development of the clipping method of inoculation has helped scientists identify resistant donors and evaluate progeny lines. In most countries the method has clearly demarcated varieties that are resistant to the pathogen. Results of artificial inoculation correlate closely with the field resistance of the varieties with major resistance genes.

But the demarcation has been less clear in several South Asian countries, where the virulence of *Xanthomonas oryzae* is highest. Rigorous artificial screening makes most varieties appear moderately susceptible, even though they may be quite resistant in the field. Appropriate isolates must be used for screening in these locations. Also, the clipping method does not easily identify varieties with intermediate levels of resistance. Natural field screening is necessary to identify such types of resistance.



5. Bacterial blight inoculation clipper.

The virulence of the bacterial blight pathogen varies considerably in Asia. Isolates from South Asia are most aggressive; those from East Asia are less aggressive. Three strains have been identified in the Philippines but the common strain makes up most of the natural population. Genetic resistance in the improved dwarf varieties has been quite effective against the pathogen in the Philippines and in other Southeast Asian countries.

Three separate single genes for resistance — *Xa 1, Xa 2,* and *Xa* 3 — were identified in the 1950's in Japan and used in breeding programs. But new virulent strains of the bacterium appeared within a few years after the resistant varieties were introduced and the varieties became susceptible.

In the Philippines, single genes at three different loci (*Xa 4, xa 5,* and *Xa 6*) were found to convey resistance. The single dominant Xu 4 has been widely used. Varieties with the *Xa 4* gene have been grown on from 30 to 50% of the rice land in the Philippines for the past 5 years, drastically reducing bacterial blight incidence. But several isolates of *X. oryzae* that are virulent on varieties with the *Xa 4* gene have recently been identified. As a result, the *xa 5* gene is now often used but up to now (1978) it has not appeared in any released varieties. The *Xa 6* gene has not been extensively used.

Through comprehensive screening of the IRRI germplasm bank many varieties have been identified with varying levels of resistance to *X. oryzae.* Allelic studies have shown that most of the varieties have either *Xa 4* or the recessive *xa 5* gene. But recently, DV85 was found resistant

to all available isolates of the bacterium. DV85 appears to have the *xa 5* gene plus one dominant gene other than *Xa 4*.

The following is an effective strategy to genetically control bacterial blight:

1. Continue the systematic screening of germplasm bank entries for new resistant varieties and genetically analyze and classify the new sources.
2. Initiate comprehensive screening and crossing programs to rapidly incorporate the resistance into breeding material of all Asian programs. In areas where strong single-gene resistance is available, it should be incorporated into a broad array of varieties.
3. Improve screening methodology to identify and utilize intermediate levels of resistance.
4. Pyramid the single-gene resistances into an array of varieties to provide broad-based resistance to many strains of the pathogen.

The clipping method is widely used for screening for bacterial blight resistance. Figure 5 is a description of inoculation clippers; Figure 6 shows the clipping method. The materials are outlined below:

- inoculum from pure culture
  agar media (Wakimoto or peptone sucrose)
  3- to 4-day-old *X.* oryzae cultures
- inoculum from leaf extract
  a bucket
  leaves with fresh bacterial blight lesions from a nearby area
  tap water
- a pair of scissors or inoculation clippers for inoculation.

Screening procedure for bacterial blight resistance.

Steps	Key points
1 Prepare Inoculum from pure culture on Wakimoto's or peptone-sucrose medium	*From agar plates* • Streak 2 loops of 3- to 4-day-old pure cultures evenly on agar plates. • Incubate Inverted plates for 3-4 days at 28°C • Pour 10 ml of water on each uncontaminated plate and scrape the bacterial growth with the end of a glass slide Suspend the bacteria from each plate in about 100 ml of water to give a population of about 10^8 cells/ml.

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Screening procedure for bacterial blight resistance continued

Steps	Key points
	From 2-liter bottles with 10 ml solidified medium • Pour 10 ml of sterile water into a slant of 3- to 4-day-old cultures. • Scrape the bacterial mass with a sterile wire loop and homogenize the suspension by shaking. • Pour the bacterial suspension into the bottle and distribute the inoculum evenly on the agar surface. • After 3-4 days incubation at 28°C, pour 1 liter of water into the bottle and shake thoroughly to remove the bacterial mass from the agar surface. The resulting suspension will give about 10^8 to 10^9 cells/ml. For some locations liquid culture may be more convenient than solid media. If so, follow standard procedures.
2 Prepare Inoculum from Infected leaves (Fig. 7) Note: Leaf extract inoculum gives only moderately good infection, whereas pure culture gives more uniform infection and more rapid disease development. Therefore, leaf extract should generally be used only where facilities are not available to make pure culture inoculum.	• Select infected leaves with young, light-green lesions. Discard the area with old brown lesions. • Cut the diseased leaf into small pieces of 3 mm or shorter. • Place the cut leaves into a beaker and pour just enough water to submerge them. • After 20 minutes of soaking, remove the leaves. The resultant suspension is ready for use. The inoculum should be used within 2 hours after preparation as *X. oryzae* quickly loses its viability.
3 Inoculate.	*With inoculation clippers (Fig. 5).* • Place 150 ml of inoculum in the inoculation-clipper bottle. • With one hand, grasp most of the leaves of a hill and clip off the top 5 cm of the leaves.

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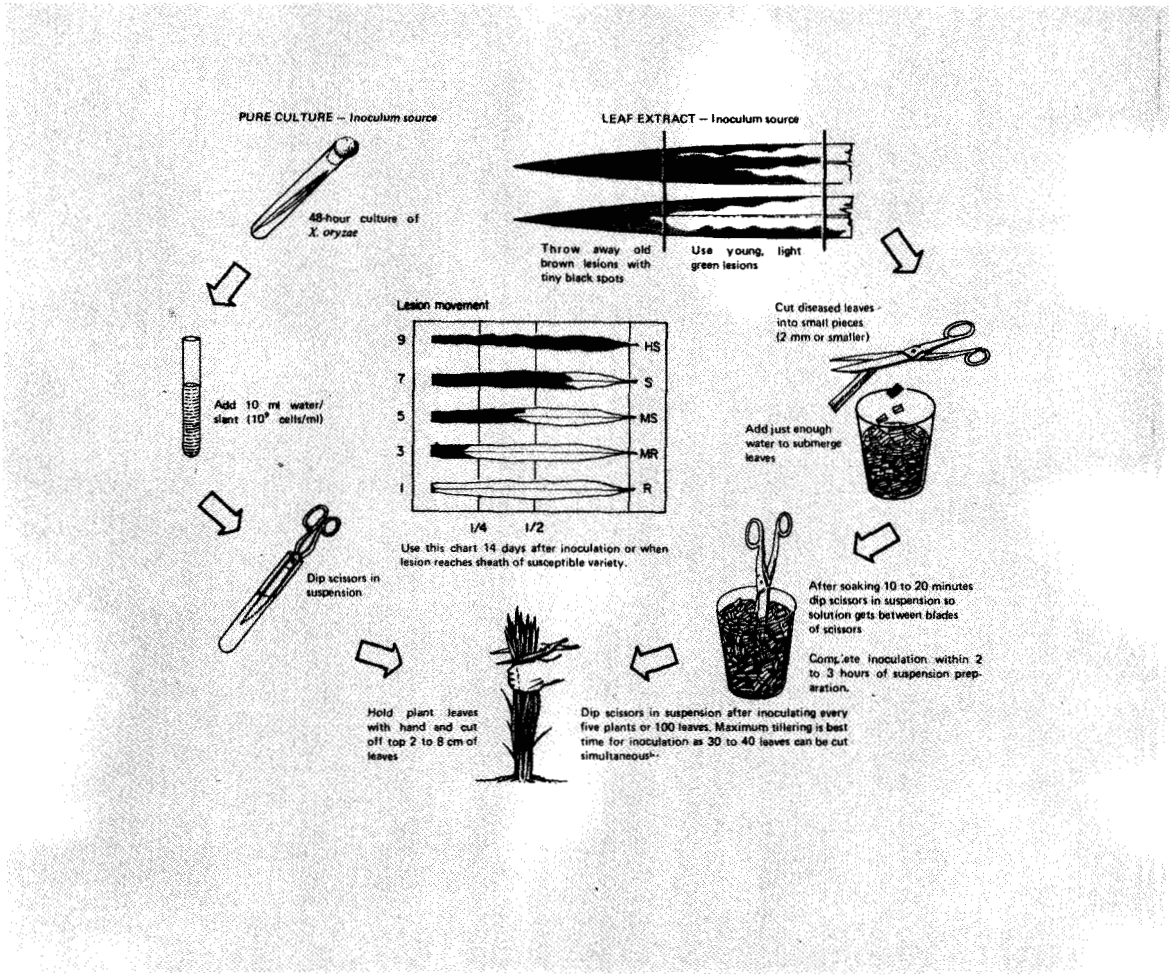
Screening procedure for bacterial blight resistance continued

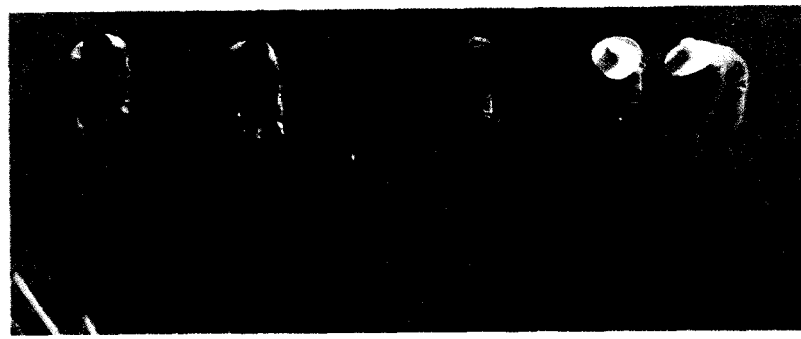
Steps	Key points
	• Bacterial suspension should be dripping on the clipper blades when the clipper is in an open position. To avoid loss of inoculum. dripping should stop when the clipper is closed. Adjust the dripping mechanism as necessary to ensure proper flow. • In the field, plants at maximum tillering stage are generally best to inoculate (Fig 8). Inoculate at least 5 hills per entry. *With scissors* • Dip the scissors into the inoculum and clip off the leaf tips of one plant. • Dip the scissors back into the suspension before clipping the next plant.
4 Score.	• Rate most of the inoculated leaves of a hill 14 days after inoculation (Fig. 6). Disease reaction is based on the development of the lesions. A quick visual reading of the average length is usually adequate. • Carefully observe segregation among plants as it is easy to rate. • Use the descriptive scale in the standard evaluation system for rice.
5 Score secondary spread.	• During the wet season there is secondary spread of the disease from inoculated to neighboring plants (Fig. 9). The amount of disease and distance of secondary spread can be evaluated. Some varieties give a susceptible reaction when clip-inoculated, but have field resistance to secondary spread.



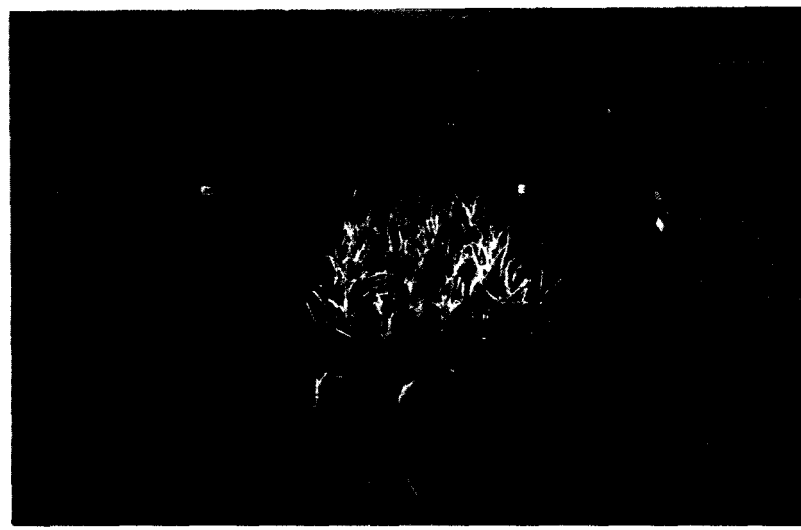
6. Clipping method for bacterial blight inoculation.

7. Preparation of leaf extract inoculum for bacterial blight inoculation.

a. Select diseased leaves.
b. Discard areas with old brown lesions and use those with young, light-green lesions.
c. Cut small sections of the leaves with the light-green lesions into a beaker.
d. Soak for 20 minutes, then use the suspension.



8. Field workers inoculating thousands of pedigree nursery lines.

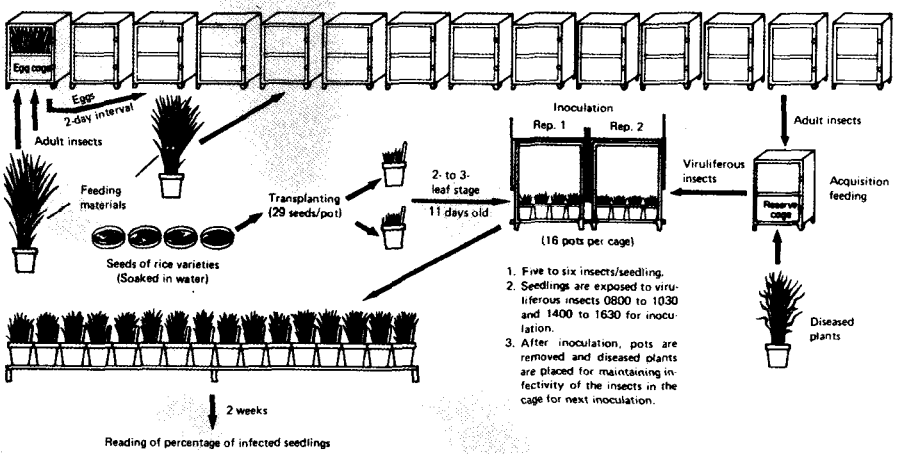


9. Variety in center shows high secondary spread of bacterial blight from border row that was artificially inoculated with *X. oryzae.*

TUNGRO VIRUS

Tungro virus disease has assumed major economic significance in tropical Asia since it was first identified less than 15 years ago. Epidemics on millions of hectares of rice have caused substantial production losses in Thailand, India, Indonesia, and the Philippines. Other countries will likely have tungro outbreaks in the future. Tungro matters are further complicated by the recent finding that strains in India and Southeast Asia differ significantly.

Tungro screening is complicated because the virus is transmitted by an insect — the green leafhopper *Nephotettix virescens.* Highly effective techniques for field screening are being used, however, in several Asian countries. Scientists in India and Indonesia take advantage of high seasonal buildups of the vector to encourage epidemics by adjusting the

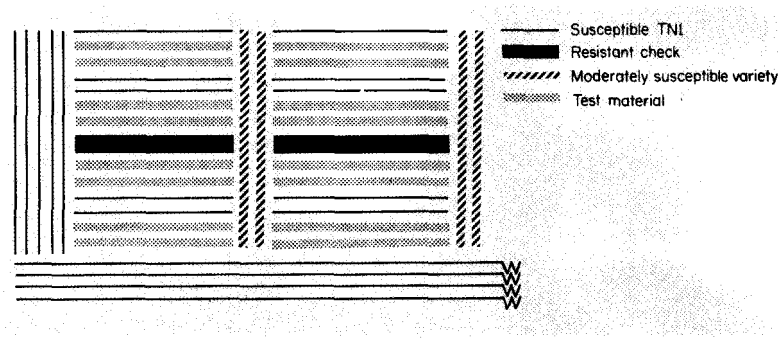


10. Improved mass-screening method for testing varietal resistance to tungro disease.

planting time, introducing the virus, and maintaining enough susceptible plants. At IRRI, both susceptible host plants and inoculum are kept growing continuously in the field through relay planting and interplanting. Vector populations are usually adequate to transmit the virus, but sometimes grassy stunt or the new ragged stunt virus predominates and the tungro readings become unreliable.

Precise screening measures have been developed for testing varieties in the greenhouse (Fig. 10). Although the screening of seedlings is rigorous, it has several weaknesses. Not all epidemiologic factors that contribute to total disease incidence in the field are measured at the seedling stage. For example, the seedling reaction often differs from the adult plant reaction because greenhouse screening measures neither the plant's ability to recover from the disease nor its reaction to repeated reinoculation from viruliferous insects.

Although many tungro-resistant varieties have been identified, the genetic inheritance of their resistance has not been determined. Evidence from the IRRI breeding program indicates that the inheritance is relatively simple, but studies in India indicate that it is rather complicated. It has been clearly demonstrated that resistance to the green leafhopper alone does not protect plants from virus infection. But insect-resistant varieties do help reduce leafhopper populations, which in turn reduces the chance for large outbreaks of tungro.



11. Layout for seasonal field screening for tungro virus resistance used in several countries.

An effective breeding program for tungro resistance calls for the following:

- Clarification of the differences in strains between Southeast Asia and India.
- Determination of the gene action of resistance to the two important strains in Southeast Asia and India through genetic studies.
- Utilization of the different resistance sources by all breeding programs.

Three methods to follow in screening for tungro resistance are seasonal field screening, continuous field screening, and greenhouse screening. Figure 11 shows the layout for seasonal field screening used in several countries.

The materials needed for tungro screening are viruliferous insects, virus inoculum, and cages and other items necessary to rear the leafhoppers.

Screening procedures for tungro virus resistance.

Steps	Key points
Field screening	
	Single-season screening
1 Build up inoculum.	• Inoculate seedlings of a highly susceptible variety such as TN1 about 2-4 weeks before planting the nursery and transplant them around the nursery site. • Inoculate a moderately susceptible variety such as IR8 by the mass screening method just before planting the nursery.

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Screening procedures for tungro virus resistance continued

Steps	Key points
	Continuous screening • Plant a susceptible variety monthly in the nursery area in the middle of the field. • Make seedbeds in the center of the virus-infected plots and transplant seedlings at 25-30 days after seeding (Fig. 12).
2 Screen.	• Plant test entries in two rows of at least 2 m each. • Plant two rows of a moderately susceptible variety perpendicular to the test entries. Moderately susceptible varieties will carry inoculum for long periods of time without being killed. • Plant two rows of a susceptible variety alternately with two rows of each test entry (Fig. 13). • Plant resistant checks after every 10 test entries. • Apply moderate levels of fertilizer but do not use insecticides.
3 Score.	• Use the scoring system outlined in the standard evaluation system. • Compare the score of the test entries with that of the resistant checks.
Greenhouse screening	
1 Prepare viruliferous insects.	• Rear and multiply the green leafhopper. • Confine nymphs on diseased plants for acquisition feeding about 11 days before inoculation.
2 Prepare test seedlings.	• Soak rice seeds in water. • Transplant or direct seed in pots or boxes.

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Screening procedures for tungro virus resistance continued

Steps	Key points
3 Inoculate.	• Place the test seedlings in cages with viruliferous green leafhoppers. • Shake seedlings, if necessary, to induce an even distribution of the insects.
4 Read reaction.	• After inoculation, keep the test seedlings in the greenhouse for symptom development. • About 3 weeks after inoculation, count infected and noninfected seedlings. • Calculate the percentage of infected seedlings to determine the reaction.

12. Seedbeds are made in the center of diseased plots so that viruliferous insects will transmit tungro virus to the seedlings.

13. A tungro-resistant variety flanked by two rows of susceptible check varieties.

GRASSY STUNT

Grassy stunt disease has become a serious threat to rice production in tropical Asia because of

- the widespread distribution of its vector, the brown planthopper,
- the high yield losses in diseased plants, and
- the potential danger in reliance on only one resistance source.

The single source of resistance to grassy stunt is *O. nivara,* a wild rice from India. This single gene has been incorporated into most breeding material and is being used in many countries. The resistant varieties are almost immune in all countries. The causal organism appears to be a virus although the particle shape has not been defined. There is no evidence of different strains of the virus.

Several varieties have low levels of resistance in the field under epidemic conditions. Those rices are being evaluated to see if intermediate resistance can be combined in them and effectively used.

Seedling screening in the greenhouse is highly effective in identifying resistant varieties with the *O. nivara* gene (Fig. 14). Correlation between seedling and adult plant resistance is good. Field screening is also highly effective during epidemics, but epidemic conditions are difficult to maintain over a long period of time.

A strategy to effectively control grassy stunt must include the following factors:

1. The *O. nivara* resistance must be used in combination with the various sources of brown planthopper resistance.
2. The search for alternate sources of resistance must be intensified, especially for rices with intermediate levels of resistance.
3. There must be continued monitoring for the appearance of new strains of the causal organism:

Materials required for grassy stunt virus screening are grassy stunt viruliferous insects of *Nilaparvata lugens,* test seedlings, and facilities for rearing insects such as cages and pots.

Screening procedure for grassy stunt virus resistance,

Steps	Key points
1 Prepare viruliferous insects	• Rear and multiply the brown planthopper. • Confine nymphs on diseased plants for acquisition feeding about 11 days prior to inoculation.
2 Prepare test seedlings	• Soak rice seeds in water. • Transplant or direct seed in pots.

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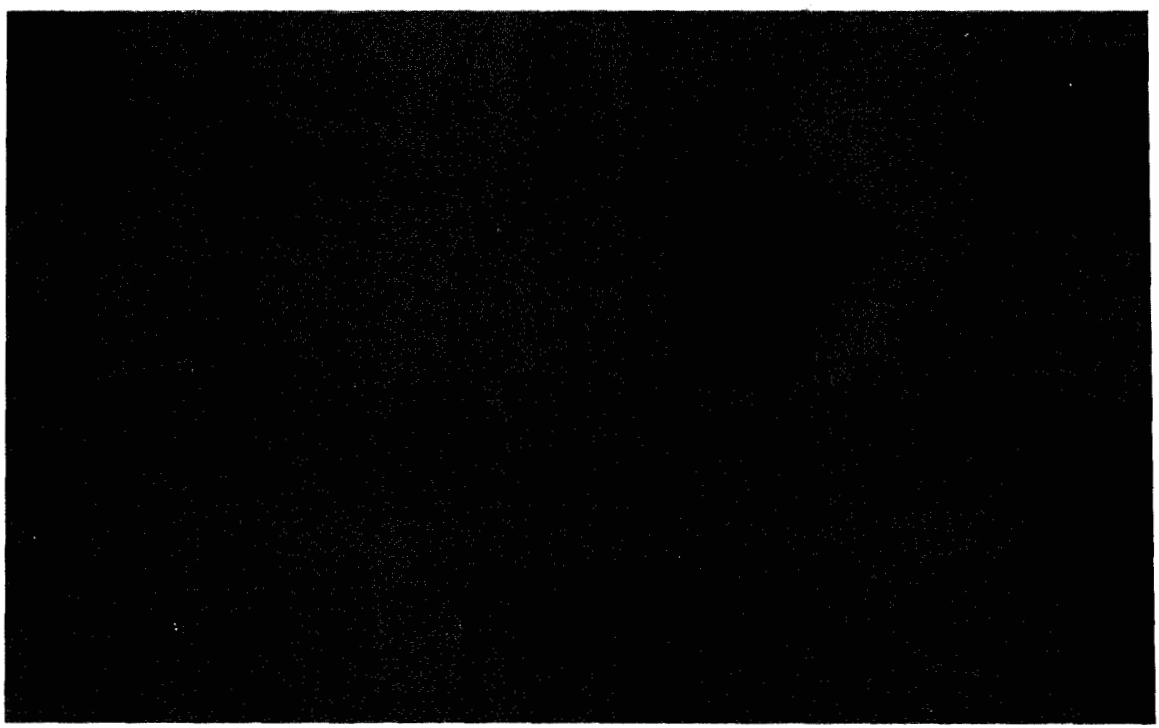
Screening procedure for grassy stunt virus resistance continued

Steps	Key points
3 Inoculate.	• Place the test seedlings in cages with viriuliferous brown plant-hoppers • Distribute the Insects evenly on test seedlings.
4 Read reaction	• After Inoculation, keep the test seedlings in the greenhouse for symptom development. • About 3 weeks after inoculation, count the infected and noninfected seedlings. • Calculate the percentage of infected seedlings to indicate the score.

14. Screening procedure for grassy stunt resistance.



OTHER DISEASES

Besides the rice diseases that cause moderate to severe losses across wide-, spread areas, other potentially serious diseases cause either low yield losses or heavy yield losses that are restricted to a few locations (Table 5). It is important to monitor and control these so-called "minor diseases" through effective breeding programs to prevent them from spreading or becoming major diseases in the future.

Some of these diseases cause little yield loss either because the pathogens lack epidemiological fitness or because existing rice varieties have strong, stable resistance. Others have the potential to become widespread and serious if

- changes are made in cultural practices,
- widespread contiguous areas are planted to susceptible varieties, or
- virulent races or strains of the pathogens develop.

Several recent examples demonstrate this phenomenon. Bacterial blight was a minor disease in Japan before World War II but became a major disease primarily because of the increased use of nitrogen fertilizer. Bacterial blight also became serious in tropical Asia during the mid- and late 1960's because susceptible first-generation dwarf varieties were grown and nitrogen use was increased. Losses in the tropics were usually greater than in Japan.

In the early 1970's *Cercospora oryzae,* generally considered a weak pathogen, made narrow brown leaf spot a major disease in many countries. The disease first became severe on experimental stations and then spread to farmers' fields where susceptible varieties such as IR20 were grown.

To monitor the occurrence of these diseases, breeding materials should always be grown unprotected. Breeding material that is extremely susceptible to many of these diseases usually shows up during the wet season even if incidence is low. Breeders should automatically discard such material. If disease incidence begins to increase because certain germplasm is widely used, regular screening procedures should be developed and new resistant material selected.

SCREENING FOR LEAFHOPPER AND PLANTHOPPER RESISTANCE

Four species of leafhoppers and planthoppers cause major damage to rice. Three species transmit virus diseases as well as cause damage to the plants by direct feeding: the green leafhopper *Nephotettix* sp., the brown planthopper *Nilaparvata lugens,* and the planthopper *Sogatodes oryzicola.* The whitebacked planthopper *Sogatella furcifera* does not transmit a virus but damages plants by direct feeding. *Sogatodes oryzicola* is limited to the Americas, while the others are primarily found in Asia.

The correlation between the seedling and the adult reaction to the four insects is good.

Table 5. Other diseases of rice that should be controlled genetically.

Disease	Causal organism	Distribution	Resistance		Pathogen variability	Comments
			Sources	Type		
Leaf diseases						
Brown spot	*Helminthosporium oryzae*	Worldwide	Several moderately resistant sources but they have not been utilized	Probably horizontal	Little	Pronounced environmental and nutritional influences on the disease. Causes heavy losses in upland rice.
Narrow brown leaf spot	*Cercospora oryzae*	Worldwide	Many	Vertical	Moderate	Dynamically influenced by host resistance.
Leaf scald	*Rhynchosporium oryzae*	Worldwide	Many	Unknown	Unknown	Common in upland rice; strongly influenced by environment
Bacterial leaf streak	*Xanthomonas translucens* f. sp. *oryzicola*	Tropical Asia	Many	Appears vertical	Moderate	Very severe after tropical storms.
Stem and sheath diseases						
Stem rot	*Helminthosporium sigmoideum* & *H. sigmoidem* var. *irregulare*	Worldwide	Several	Unknown	Moderate	
Sheath rot	*Acrocylindrium oryzae*	Asia	Several	Unknown	unknown	
Sheath net blotch	*Cylindrocladium scoparim*	Worldwide	Several	Unknown	unknown	
Bakane disease & foot rot	*Gibberella fujikuroi*	Principally Asia	Several	Unknown	unknown	
Systemi diseases						
Yellow dwarf	Transmitted by *N. virescens* *N. nigropictus* *N. cincriceps*	Asia	Several	Unknown	Little	Long incubation period in vector and host makes it epidemiologically inefficient.
Hoja blanca	*Sogatodes oryzicola*	Americas	Many	Resistance is dominant	None	Virus is controlled effectively by insect resistance to the vector.
Transitory yellowing	*N. virescens* & *N. cincticeps*	Taiwan	Several	Unknown	Little to none	
Panicle diseases						
False smut	*Ustilaginoidea virens*	Worldwide	Many	Not studied	Unknown	
Kernel smut	*Tilletia barclayona*	Worldwide	Many	Not studied	Unknown	
Udbatta	*Ephelis oryzae*	India & China	Many	Unknown	Unknown	Causes severe losses when it occurs.
Grain discoloration	Many organisms	Worldwide	Many	Unknown	Unknown	
Nematodes						
White tip	*Aphelenhoides oryzae*	Worldwide	Many	Unknown	Little	

The materials needed for screening are:

- insects
- cages placed in a screenhouse that is protected from the rain and maintained at a favorable temperature. The roof and one side of the cages should be glass and the other sides, nylon cloth.
- boxes or pots with fertile soil to grow healthy seedlings (Fig. 15)
- galvanized iron trays.

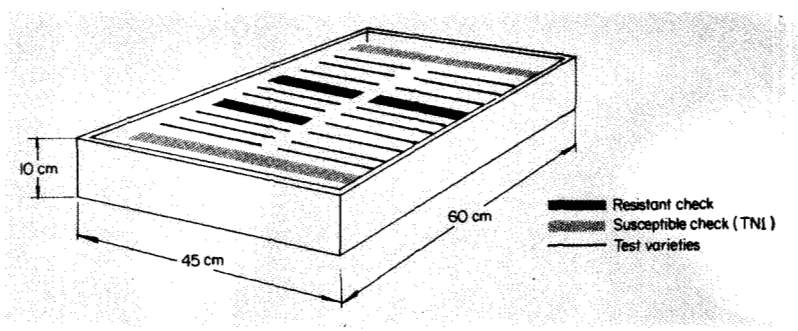
Screening procedure for planthopper and leafhopper resistance in greenhouses or screenhouses.

Steps	Key points
1 Rear insects.	• Rear original colony of the virus-free insects on 50-day-old plants of a susceptible variety. • Transfer insects to 50-day-old potted plots in cages and change the plants as needed. • Produce eggs of about the same age by placing the plants overnight in a cage of adult insects.
2 Lay out and plant.	• Sow test plants in pots or 60 × 45 × 10-cm seedboxes filled with good soil. Rows 20 cm long of the test varieties are spaced 5 cm apart. • Plant susceptible plants around the outer edge of the box and plant resistant checks in three individual rows spaced randomly around the box (Fig. 15).
3 Infest and screen.	• Seven to fourteen days after seeding, thin the plants to 20 to 30 seedlings per row. • Place the pots or boxes of plants into galvanized iron trays on a table inside a fine mesh screen cage with 5 cm of water in the tray. • Infest the plants by gently tapping the pots with the insect colonies to uniformly scatter a large number of insects on the test plants. An average of 5 seconds is optimum to transfer enough insects to kill the susceptible plants in 7-1 0 days.

(continued on next page)

Screening procedure for planthopper and leafhopper resistance in greenhouses or screenhouses continued

Steps	Key points
4 Score.	• Score when the susceptible variety is dead. • Base the score on that in the standard evaluation system for rice. • Calculate the percentage of dead seedlings.



15. Boxes for screening seedlings for leafhopper and planthopper resistance.

Screening procedure for planthopper and leafhopper resistance in the field

Steps	Key points
1 For year-round screening in some locations (Note: Continuous high populations of leafhoppers and planthoppers can be maintained in the field under favorable conditions.)	• Plant susceptible varieties monthly in the center of the field to maintain the insect population. • Release insects into the field to start the infestation, if necessary. • Plant some moderately susceptible varieties to maintain the insect population without killing the host plants. • Plant the seedbed of the test entries in the center of the infected plots so the insects will go to the new seedlings. Cut the old plants periodically so the insects will migrate to the test plants.

(continued on opposite page)

Screening procedure for planthopper and leafhopper resistance in the field continued

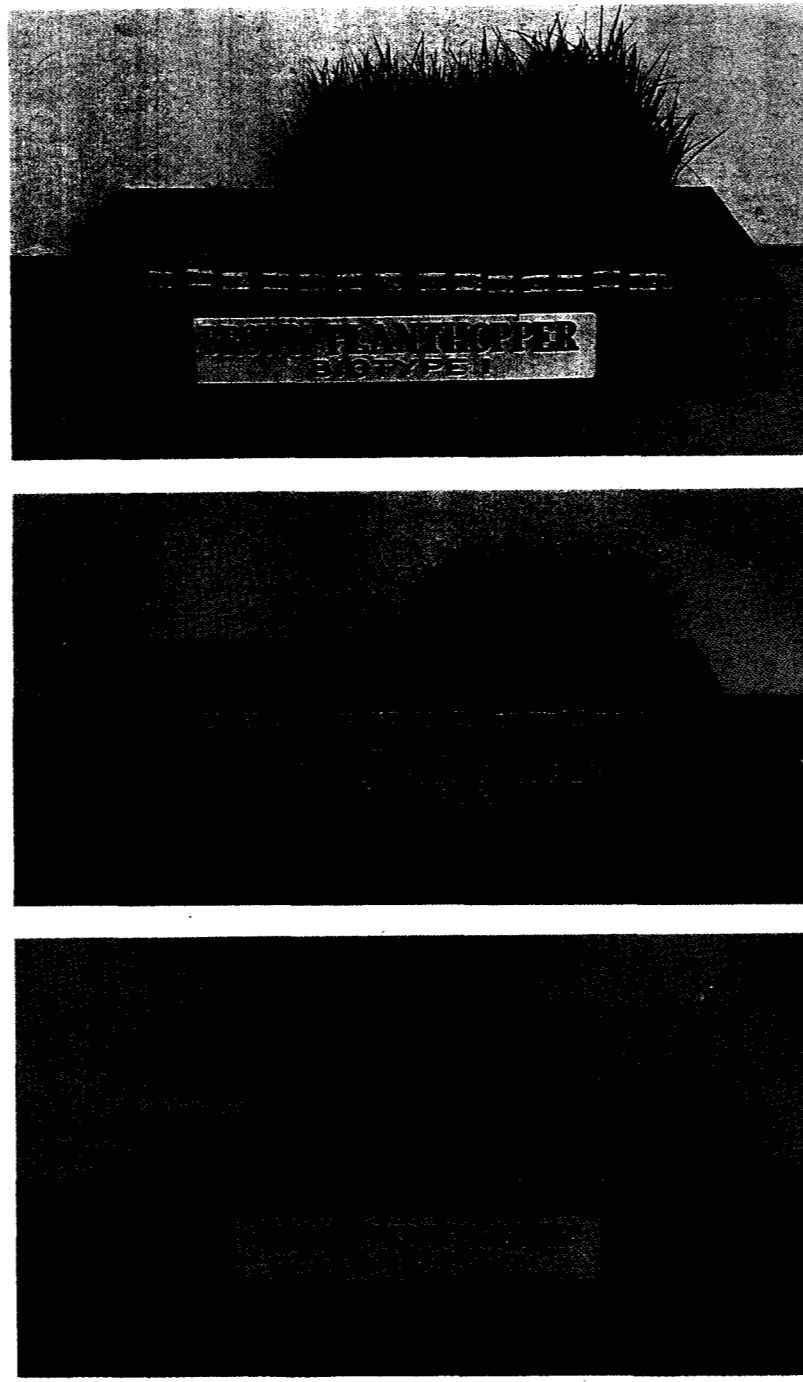
Steps	Key points
2 For seasonal screening (Note: Rice can be screened effectively for resistance to some leafhoppers and planthoppers by planting the nursery to coincide with high natural population buildups.)	• Plant test varieties, surrounded by susceptible varieties, 6-8 weeks after the beginning of the main season crop. • If necessary, release insects either reared in the greenhouse or collected in other fields. • The use of certain insecticides kills predators and may result in buildup of some planthoppers.
3 Score.	• Score the entries by the standard evaluation system for rice. • Count the planthoppers on four hills selected at random at peak periods of infestation.

BROWN PLANTHOPPER

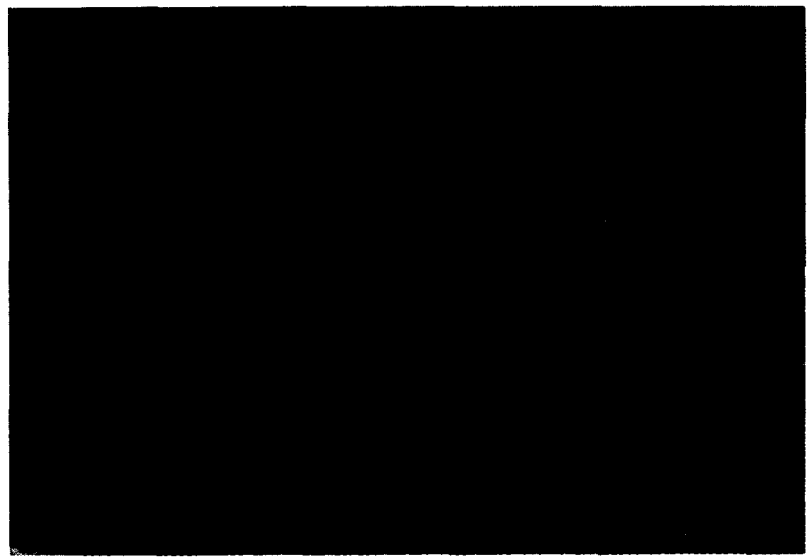
The widespread growing of dwarf varieties in Asia has increased field populations of the brown planthopper more markedly than that of any other insect. Brown planthopper outbreaks have caused serious economic losses in the Philippines, Indonesia, and India and localized outbreaks have occurred in other countries. The discovery of the existence of different biotypes, each of which differs in the ability to attack resistant varieties, greatly complicates the use of monogenic resistance to effectively control *Nilaparvata lugens* (Fig. 16).

The procedures for screening seedlings have effectively identified single gene resistance to the various biotypes. Many programs are now screening breeding material for resistance by this method and some screen for several biotypes in the greenhouse. Methods for easily idenufying moderate or field resistance, however, have not yet been developed (Fig. 17).

Research on insect variability indicates that at least five biotypes exist (Table 6). Although biotype I appears to predominate in East and Southeast Asia, biotype II has recently become widespread in the Philippines



16. Reaction of IR varieties in the Philippines to three biotypes of brown planthopper.



17. Three types of reaction to the brown planthopper in the field resistant (green entry on left), moderately resistant (second and fourth entries from left), susceptible (between and to right of moderately resistant entries).

and Indonesia, where varieties resistant to biotype I have been grown for several years. The biotype picture in South Asia is not completely clear but a different biotype, still unnamed in 1977, predominates.

Recently in the Philippines varieties with monogenic resistance to biotype I, such as IR26 and IR1561, were grown continuously in areas with year-round irrigation, for 2 to 3 years before a new biotype overcame this resistance. But in other locations, the number of insect generations would be expected to vary depending on the existing variants in the population, the mutation rate of the insect, the population size, and the host varieties.

Table 6. Biotypes of the brown planthopper and major resistance donors for each biotype.

Biotype	Areas where predominant	Major resistance donors	Gene for resistance
I	East and Southeast Asia	Mudgo	*Bph 1*
II	Philippines at Indonesia	ASD 7 PTB 18	*bph 2*
III	?	Rathu Heenati	*Bph* 3
IV	?	Babawee	*bph 4*
Unnamed	South India & Sri Lanka	PTB 19 PTB 20 ARC 6650	

The lack of stability in brown planthopper resistance is of great concern. New and better breeding strategies to improve the stability of resistance as well as improved cultural methods of control must be developed.

Stable resistance may already exist in certain improved varieties and breeding lines. Some rices that are found susceptible in seedling tests in the greenhouses have been relatively resistant in the field. Presently, the phenomenon is not well understood but monogenic, vertical resistance is clearly not a satisfactory solution. Few local programs have the resources to keep pace with the rapidly shifting planthopper populations, and vertical gene resistance developed through large national and international programs will not be useful for most areas. But such resistance is a valuable first step and an essential tool with which to identify a more stable form of resistance.

GREEN LEAFHOPPER

Severe outbreaks of the green leafhopper have recently occurred in tropical Asia. Most notable were the outbreaks in India in 1968 and 1969 and in the Philippines in 1971. The most serious consequence was the epidemics of tungro virus disease (transmitted by the green leafhopper) that followed in the wake of the attacks. In some localized areas, however, the green leafhopper damages rice seedlings by direct feeding.

Several species of *Nephotettix* are found throughout the world. *N. virescens* is the dominant species on rice in most areas, although *N. nigropictus* dominates in some areas at times.

Four dominant single genes and one recessive gene for resistance to *N. virescens* have been identified and given the names *Glh 1, Glh 2, Glh 3, glh 4,* and *Glh 5.*

Fortunately, several of the native varieties first used in the IRRI breeding program such as Peta and Sigadis were resistant to *N. virescens.* Because of their frequent use as parents, a high proportion of the breeding materials from IRRI and in many national programs is resistant to the green leafhopper.

The most appropriate strategy to genetically control the green leafhopper is to incorporate the five single genes individually into diverse varieties. Green leafhopper populations should be continuously monitored for the appearance of biotypes. To prepare for the day when new biotypes appear, the single resistance genes should be pyramided into varieties of diverse genetic background.

WHITEBACKED PLANTHOPPER

The whitebacked planthopper *Sogatella furcifera* is distributed widely throughout Asia and is a serious local pest in several areas. For example, the whitebacked planthopper population builds up annually after the onset of the monsoon in central India.

The whitebacked planthoppers transmit no viruses but they cause damage by direct feeding. The seedbeds or the young transplanted crop are generally most severely damaged.

Entomologists have found some sources of resistance in the germplasm bank during recent years. Because several moderately resistant donors were used early in IRRI's breeding program, several modern varieties and many of their progeny carry some resistance. IRRI continues to screen the germplasm bank for additional donors and all advanced breeding lines.

SOGATODES PLANTHOPPER

The Sogatodes planthopper *Sogatodes oryzicola* is limited to the Americas where it transmits the hoja blanca virus. Highly resistant indica varieties from Southeast Asia have been identified by seedling screening in Colombia. When caged on resistant varieties, the insects suffer high mortality, grow slower, lay fewer eggs, and suffer reduced longevity.

Sogatodes planthopper resistance is highly heritable and is easily combined with other favorable agronomic traits. Although Sogatodes resistance is independent of hoja blanca virus resistance, varieties that are resistant to Sogatodes planthopper fully protect varieties that are genetically susceptible to hoja blanca on farms. All varieties released in Colombia have maintained their resistance after being grown for several years from Mexico to southern Brazil, indicating that no new biotypes have developed.

STEM BORER

The stem borers have generally been considered the major insect pest in the rice-growing world. Four species are widespread in Asia and are of major significance: the striped borer *Chilo suppressalis,* the yellow borer *Trypoyza incertulas,* the white borer *T. innotata,* and the pink borer *Sesamia inferens.* Of these four, only *C. suppressalis* and *T. incertulas* have been widely studied. Other species are found in Latin America and Africa. They cause significant damage in localized areas and warrant the discarding of obviously susceptible segregants in breeding plots.

Scientists in several countries have screened varieties by adjusting planting to coincide with high natural populations. Sometimes plants are heavily infested, but insect populations frequently are sporadic under field conditions. Therefore, at IRRI a large cage is effectively used to screen for *C. suppressalis* and *T. incertulas.* Although expensive to construct, the cage is justified by the consistency of screening results from the heavy population of insects in the cage (Fig. 18). Moderate levels of multigenic resistance have been found. Screening of individual plants of resistant varieties is also done by caging the stem borer larvae.

The general breeding strategy calls for a continued search for varieties

18. Evaluating entries for resistance to *C. suppressalis* in the large screenhouse at IRRI.

with higher levels of resistance. A diallel selective mating program at IRRI to concentrate several resistance genes into one genotype shows some promise. Promising material is screened in selected "hot spots" through the IRTP network.

Screening procedures for stem borer resistance.

Steps	Key points
Field screening	
1 Lay out.	• The time of planting should coincide with the peak insect population. • Plant the test varieties in two rows up to 5 m long. • Resistant and susceptible checks should be spaced randomly around the plot.
2 Score.	• Although entomologists have developed accurate scoring techniques based on counts, these are not satisfactory for large numbers of breeding lines. • The only practical method is to visually score lines in comparison to the nearest resistant check at both the deadheart and the whitehead stages.

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Screening procedures for stem borer resistance continued

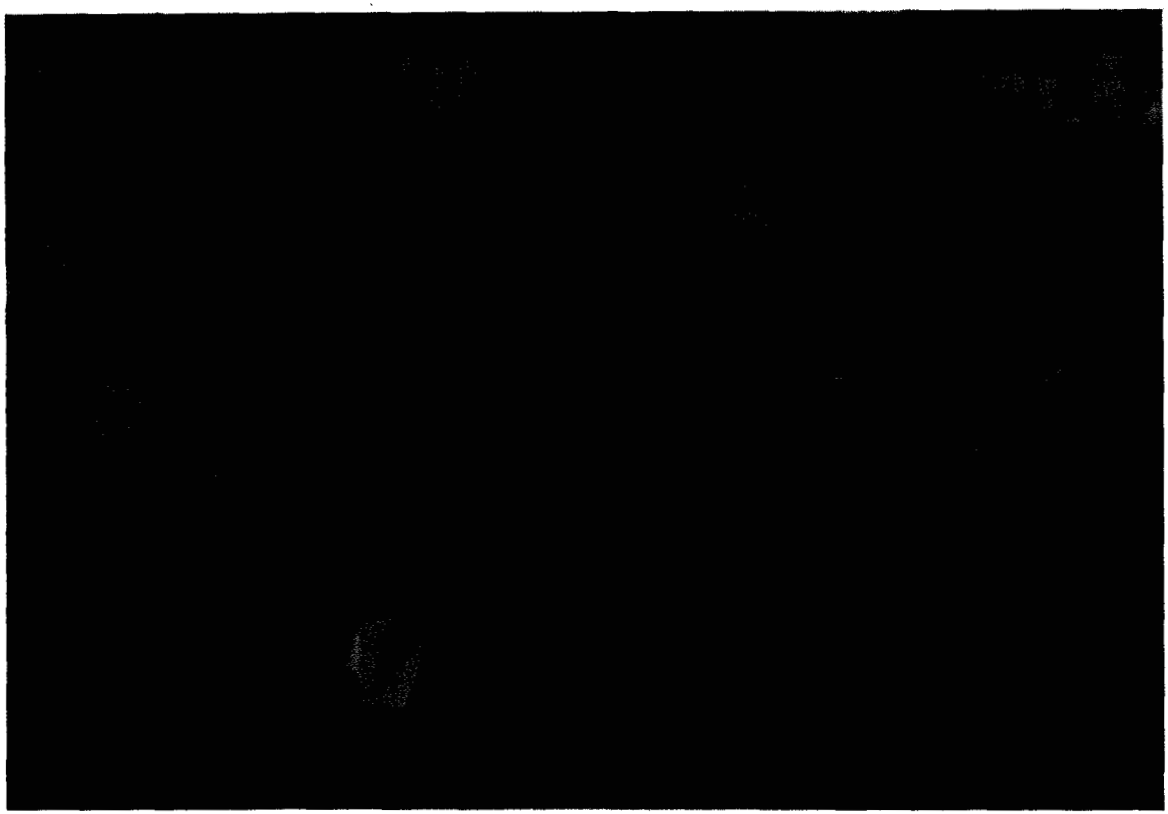
Steps	Key points
Insectary screening	
1 Plant and infest.	• Plant in 27-cm diameter pots (4 single plants/pot) with 3 replications per variety. • Infest each hill with 10 first-instar larvae of the borer (the larvae are hatched from egg masses placed on a moist filter paper in a petri dish). Pick up the larvae with a soft brush and place them near the auricle of the top leaf. • Space the pots and clip off the longer leaves to prevent the migration of the larvae. Place the pots in shallow trays filled with water to prevent the larvae from leaving.
2 Score.	• At 5-day intervals, record the discoloration of the leaf sheaths and the formation of deadhearts and whiteheads. • At 20-25 days cut the plants at the base and dissect the individual tillers to count the number of surviving larvae. • Weigh the larvae and the pupae separately for each variety.

GALL MIDGE

The rice gall midge *Orseolia oryzeae* has long been a serious pest during the monsoon season in India, Sri Lanka, Thailand, and Indonesia. In recent years the gall midge population in these areas has increased and infested areas have expanded.

Tests indicate that biotypes of gall midge vary within India as well as among India, Indonesia, and Thailand. Although the extent of variation is not yet clearly known, indications are that each local breeding program must screen and select its own resistant varieties. Since no gall midge-resistant varieties have been widely grown, it is not yet known if new insect biotypes will develop in response to resistance or if biotypes that heady exist in the populations will simply increase in frequency.

Highly effective procedures for greenhouse screening have been developed in Sri Lanka, Thailand, Indonesia, and India (Fig. 19). Field



19. Gall midge screening in the glasshouse by Dr. M. B. Kalode, entomologist, All India Coordinated Rice Improvement Project, Hyderabad, India.

screening by planting the test materials to coincide with high pest populations has also been highly successful. Proper plant spacing and the use of lights for several hours at night increase insect populations.

The inheritance of gall midge resistance is not clearly understood but studies at three locations indicate differing modes of inheritance. On the other hand, the ease of transferring resistance to dwarf varieties suggests that the resistance is simply inherited.

Several countries have released varieties with gall midge resistance. Although the resistance has effectively reduced gall midge infestation, these varieties are not widely grown because they lack some other desirable traits.

An effective breeding strategy should be to incorporate the known resistance into a wider array of genetically diverse varieties. The degree of variation and distribution of biotypes must be further studied and monitored. Pyramiding the resistance genes of several donors may provide stability in new resistant varieties.

Screening procedures for gall midge resistance.

Steps	Key points
Greenhouse screening	
1 Rear insects	• Seed susceptible plants closely (1 × 1 cm) in flats or pots • When plants are 10-14 days old, place them in cages and infest them with freshly emerged adult females. The gall midge adults lay eggs on the leaves the first night (1 adult/ 15 plants). • On the third morning after introduction of adults, place the plants in a mist chamber at 95% relative humidity so that eggs can hatch and first-instar larvae can move into plants. • Remove plants after 3 days in the moist chamber. The duration of each growth stage is about. egg 3–4 days first instar 3–4 days second instar 3–4 days third instar 6–7 days pupa 3–4 days adults (female) 3 days (male) 1/2 day
2 Screen	• Plant test varieties in flats or pots at spacing of 3 cm between rows and 1 cm within rows. • Infest with 1 adult midge/5 plants when plants are 10–14 days old. • On the third morning move the plants into the moist chamber maintained at 95–100% at relative humidity. • Remove plants after 3 days and keep in the greenhouse.
3 Score.	• One month after midge infestation, calculate the percentage of total plants with visible galls.

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Screening procedures for gall midge resistance continued

Steps	Key points
Field screening	
1 Plant nursery.	• Make planting coincide with maximum population development. • Plant 2 plications of two 10-hill rows at a spacing of 15 x 20 cm. Plant 1 seeding/hill. • Add sufficient fertilizer to give good vegetative growth.
2 Infest the plants.	• Put lights over the field for several hours at night to attract the adult insects. • If infestation is low, clip the plants to induce more tillering for late infestation.
3 Score.	• About 30 to 40 days after transplanting, visually score all lines for number of galls in comparison with the adjacent resistant checks. A visual scale of 1–9 should differentiate among resistant, moderately resistant, and susceptible reactions.

OTHER INSECTS

Many other insects cause damage in rice areas around the world. Some like whorl maggot *(Hydrellia philippina)* are widespread and annually cause some reduction in yield. Others like the leaf folder *(Cnaphalocrosis medinalis)* or leaf roller *(Susumia exigula)* occur sporadically, but are devastating when they do occur. Some varietal variations have been found in reaction to the whorl maggot. On the other hand, all varieties appear susceptible to the leaf folder and leaf roller as well as to many other chewing insects. An integrated chemical and cultural control program appears most practical for controlling these and other similar insects.

CHAPTER 8

Adverse soils tolerance

THE DEMAND FOR RICE is high but available arable land is limited in densely populated South and Southeast Asia. But about 100 million ha of land that is physiographically and climatically suited for rice lies idle in the Asian humid tropics, especially in the river basins. Large areas of these regions have adverse soils that can be brought into cultivation with a combination of flooding, proper soil management, and the use of adapted varieties (Table 1). Rice is the only crop logically suited to these areas because it thrives in submerged soils. Although the application of expensive chemicals such as gypsum and lime can amend some types of problem soils, it must be used in conjunction with tolerant varieties to bring large areas of land into production in the developing countries.

Rice varieties vary greatly in genetic tolerance for several types of adverse soils. Rice varieties with some tolerance for salinity, alkalinity, iron toxicity, strong acidity, zinc deficiency, phosphorus deficiency, and organic soils have evolved or been selected over the centuries. Most of these varieties, however, yield poorly and lack resistance to major diseases and insects.

Soil chemists have developed screening procedures to identify varieties that are tolerant of most types of adverse soils (Table 2). But interactions between the rice plant and the many soil factors are so complex that procedures are still being refined and improved. The prevalent problem soils are also being further characterized. Major progress has recently been made in modifying greenhouse and field soils to expand the areas where screening can be conducted. The capacity for screening, however, is still low for most tests. Plant breeders have recently begun to transfer tolerance for adverse soils into a wide array of high yielding varieties; prospects now look good for developing new rices with stable tolerance for the major soil problems. This genetic tolerance, supplemented with cultural practices, can help bring new areas into rice production.

Figure 1 shows the flow of genetic material through IRRI's GEU program to develop varieties adapted to adverse soils. Soil chemists are identifying many sources of tolerance from the germplasm bank. The tolerance of such sources is quickly being incorporated into diverse genetic backgrounds through a high-volume crossing program. Progeny are

Table 1. Some characteristics of major soil problems.

Soil problem	Estimated affected area in tropics (million ha)	Soils			Chemical and cultural amendments	Comments
		Types	Range of pH	Organic matter (%)		
Toxicities						
Salinity	South and Southeast Asia, 55[a]	irrigated arid and coastal	4.0–8.5	1 to 50%	Flooding and leaching	Fe toxicity on low pH soils
Alkalinity	South & Southeast Asia, 2 Africa, 26 S. America, 3	arid (irrigated)	8.5–10.0	low	Gypsum, leaching, and flooding	
Iron toxicity	[b]	acid Ultisols acid Histosols acid sulfate	5.0	—	Water management and lime	
Acid sulfate	South & Southeast Asia, 10	acid sulfate	1.0–4.5	—	Flooding, lime, MnO_2, leaching & fertilizers	In reclamation there is excess aluminum followed by excess iron.
Histosols	South & Southeast Asia, 30	strongly acid to neutral	2.0–7.0 —	—	Applying fertilizers and micronutrients	These soils are also low in NPK, zinc, copper and molybdenum
Deficiencies						
Zinc	widespread	alkali, calcareous and neutral all continuously wet soils	5.4–8.7	1.7–37	Zinc	
Phosphorus	widespread	Ultisols, Oxisols, Vertisols, acid sulfate soils, calcareous and sodic	4.0 to 7.5	—	Flooding	Also fixes part of applied P fertilizer (occurs also in flooded calcareous and sodic soils low in organic matter).

[a] Includes 30 million ha of arid land and 25 million ha of coastal land. [b] Not known.

screened in adjusted soils in the IRRI greenhouses and fields and in selected areas of the Philippines. Donors and advanced materials are tested collaboratively with national scientists and through nurseries of the IRTP.

SALINITY AND ALKALINITY

Excess salt is the most widespread soil problem. Toxic levels of salt prevent or limit rice cultivation on more than 50 million ha of arid land or coastal plains of South and Southeast Asia — often near densely popu-

Table 2. Screening procedures for major soil problem.

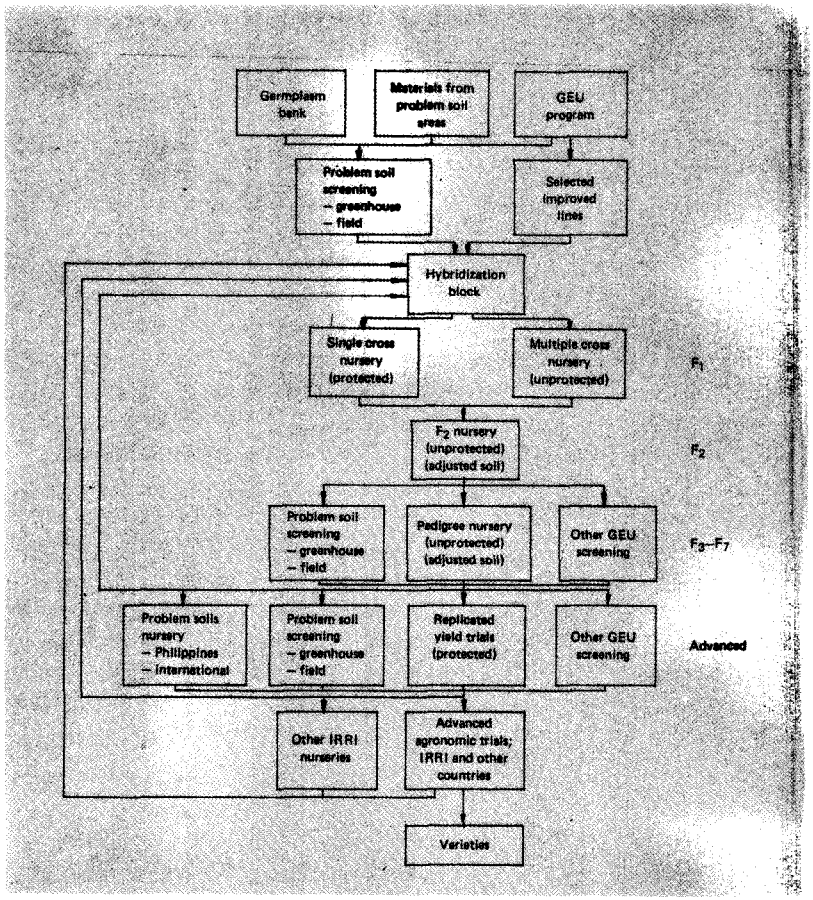
Sad problem	Screening			Level or availability of chemical	Plant age at scoring	Check varieties or lines	
	Greenhouse	Field amended with chemical	Natural			Resistant or tolerant	Susceptible
Toxicities							
Salinity	x	x [a]	x	EC[b] of 8-l0 mho/cm	4 wk after transplanting	IR2153–26–3 Pokkali	IR28, M1-48 IR4630–22–2
Alkalinity	x	x [c]	x	pH of 8.5	3 wk after transplanting	Pokkali	IR2153–26-3
Iron toxicity	x		x	400 ppm Fe^{2+}	8 wk after transplanting	Mat Chanda BW 78 Devarredi Gissi 27	IR26
Acid sulfate			x			Bahagia Khao Dawk Mali 105	Many
Histosol			x			IR34	E425
Deficiencies							
Zinc	x		x	0.2–0.4 ppm Zn	4 wk after seeding	IR34	E425
Phosphorus	x		x	0.5 ppm P	4 wk after seeding (gh) transplanting (field)	IR1514-E666 Khao Dawk Mali 105	Many
Iron			x	0.0 ppm Fe	10 wk after seeding	IR36	Peta

[a] 0.5% table salt; problems with seepage and runoff. [b] EC = electrical conductivity. [c] 1.4% Na_2CO_3; must add zinc to prevent zinc deficiency.

lated urban areas. Large tropical and subtropical regions in Africa and South America also have saline soils. Much of about 25 million ha of the coastal saline soils in South and Southeast Asia can be brought under rice production without heavy capital inputs if salt-tolerant, high yielding varieties are available.

Alkalinity is common in the arid regions of the Indo-Gangetic plain of India and Pakistan. Although underground water is often available, much of the alkaline land lies idle. Millions of hectares of alkaline soils are also present in Australia and Africa but water is a limiting factor in bringing these areas under crop production.

Salinity in rice fields of both arid and coastal regions varies widely during a cropping season. Salinity is highest in the dry season of arid regions but it may not be a major problem in the rainy season. Salinity in coastal



1. The flow of genetic materials through IRRI's Genetic Evaluation and Utilization (GEU) program to develop varieties that are adapted to adverse soils.

regions fluctuates, depending on the incoming tides and the rainfall. Because salinity is always distributed nonuniformly, uniform screening is difficult. Rice plants are most susceptible at the seedling stage and become progressively more tolerant with age. Salt concentrations giving a specific conductance of 8-10 mmho/cm at 25°C clearly differentiate between tolerant and susceptible rices. Moderate to warm temperatures are needed to screen properly.

Alkaline soils can be reclaimed by applying gypsum or by leaching the soil. Rice with tolerance for alkalinity is the best crop to grow during and after reclamation in those areas where soil alkalinity is high. Moderately alkaline soils can be reclaimed by the application of gypsum, proper water management, and the growing of tolerant rice varieties.

Effective greenhouse procedures to screen for salinity and alkalinity tolerance have been developed at IRRI. Field screening procedures have been developed jointly with scientists from several countries. But, the screening procedures are continually being improved as additional experience is gained.

The following items are needed for salinity and alkalinity screening in the greenhouse:

- air-dried crushed soil
- ammonium sulfate, superphosphate, and potash
- ground rice straw
- ground dried *Glyricidia sepium*
- plastic trays (35 × 27 × 11 cm)
- common salt (Na_2CO_3 instead of common salt is needed for alkalinity tests)
- resistant and susceptible check varieties.

Screening procedures for sallnity and alkalinity tolerance.

Steps	Key points
Greenhouse screening	
1 Prepare soil and ingredients.	• Air-dry and crush soil. • Grind rice straw. • Dry and grind *Glyricidia sepium.*
2 Mix soil.	• Mix 5 kg of crushed soil with: – 1.6 g ammonium sulfate – 0.75 g concentrated super-phosphate – 0.25 muriate of potash – 3.8 g ground straw – 0.75 g *Glyricidia sepium* • Place soil in plastic trays. The wet soil in the trays can be used continuously if adjusted with sodium chloride after every third test. • Add 4 liters of a 0.5% solution of common salt (Na_2CO_3 for alkalinity) and thoroughly mix the soil. This level of salt solution gives an EC of 8–10 mmho/cm at 25°C.
3 Prepare seedlings.	• Prepare culture solution: – 40 ppm each of nitrogen, potassium, calcium, and magnesium. – 10 ppm of phosphorus – 0.5 ppm of manganese – 0.05 ppm of molybdenum – 0.2 ppm boron

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Screening procedures for salinity and alkalinity tolerance continued

Steps	Key points
	— 0.01 ppm each of zinc and copper — 5 ppm of iron as Fe EDTA — adjust to pH of 6.0 • Two weeks before transplanting soak 20 seeds of each variety in 1/10th strength cultural solution. • Three days later replace with 1/4 strength solution. • Six days later replace with full strength solution.
4 Transplant and maintain.	• Select 6 healthy seedlings and transplant in tray 2 days after the trays are prepared. • Use one tray of resistant check (Pokkali) and one of susceptible check (T26) for every 20 trays.
5 Evaluate	• At 4 weeks after transplanting (3 weeks for alkalinity), score the plants according to the Standard Evaluation System for Rice. The 4-week score correlates highly with that of plants grown to maturity.
Field screening	
1 Prepare field.	• Plow, puddle, fertilize, and thoroughly level the field. Add some zinc to prevent zinc deficiency in the alkaline screening plots. • pH meter, and • electrical conductivity (EC) meter.
2 Prepare seedlings.	• Sow pregerminated seed in the seedbed in best available soil. • Add optimum amount of fertilizer to get good growth.

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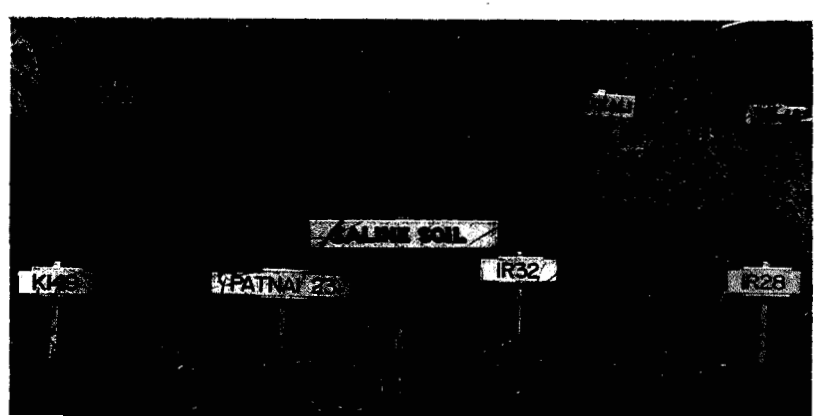
Screening procedures for salinity and alkalinity tolerance continued

Steps	Key points
3 Transplant.	• Select uniform seedlings at 3 weeks for inland areas and 4–6 weeks for coastal saline areas. • Transplant 1 seedling/hill at 25 × 25 cm. • Because of the spotty occurrence of salinity and alkalinity in fields, replications are advisable.
4 Manage nursery.	• Separate experimental lots from water inlets with border strips of 3–4 rows at right angles to the water flow. • Maintain several centimeters of water on the plots at all times.
5 Score.	• Score only those plots where the susceptible check indicates the presence of salt (Fig. 2, 3). • At scoring time measure the electrical conductivity (EC) of the soil and super-natant water of a convenient number of saline spots as indicated by plant stress. • At scoring time take soil samples at a convenient number of saline spots and measure pH of the dried soil. Also take EC of the saturation extract if not done in the field. • Score rest of plants and resistant and susceptible check by the Standard Evaluation System for Rice scoring system.



2. Varietal differences to salinity in the field.

3. Varietal differences to alkalinity in the field.

IRON TOXICITY

Iron toxicity is a nutritional disorder of rice that occurs widely on strongly acid Ultisols and Histosols and on acid sulfate soils. The damage ranges from death of the plants to poor grain yields despite good vegetative growth. Several factors influence the damage: soil type, rice varieties, age of crop, general nutritional situation of the plants, and weather.

Growing varieties that are tolerant of iron toxicity can partially alleviate the need for adding lime as a chemical amendment if water management is proper.

Most screening is done in areas where iron toxicity occurs naturally. It is difficult to maintain the proper level of iron in adjusted soil in the greenhouse or the field. Good screening results have been obtained in Sri Lanka and other countries.

ACID SULFATE SOILS

Almost 10 million ha of the more than 15 million ha of the world's land that suffers from acid sulfate problems are in the tropical and subtropical areas of South and Southeast Asia. Most are climatically and physiographically suited to the growing of rice.

When submerged, such land becomes almost neutral in reaction, but when dried it becomes extensively acid and lethal to plants. Because rice can grow in submerged soils, tolerant varieties could be used to bring the

less strongly acid soils under production without the recurring expenses for lime application.

Acid sulfate soils vary widely in chemical and hydrological properties. Therefore, screening is best done in areas where the problem occurs. Varieties also need tolerance for iron toxicity, salinity, and phosphorus deficiency to grow effectively in acid sulfate soils. Excess aluminum occurs at the beginning of reclamation but excess iron builds up after the soil is reduced.

Screening on acid sulfate soils has been initiated in Thailand. There are distinct varietal differences in tolerance for acid sulfate soils.

ZINC DEFICIENCY

Zinc deficiency is found in many kinds of soils: in alkali, calcareous, and neutral soils as well as on Histosols and continuously wet soils regardless of pH. Because of its widespread occurrence, zinc deficiency may be the third most important nutritional problem limiting yields of wetland rice. Even more important, the incidence of zinc deficiency is likely to increase in severity in areas because of

- the removal of large amounts of zinc by growing the high yielding varieties,
- the replacement of the acid fertilizer ammonium sulfate by urea,
- the increased use of phosphate fertilizer, and
- double- and triple-cropping of wetland rice.

Therefore, varieties with some tolerance for zinc deficiency should reduce the amount of zinc needed to correct the problems.

Effective tests have been conducted in soil with zinc content of as low as 0.04 ppm, but only a few rices survived. Soil with available zinc content of 0.5 ppm seems adequate for most screening. Both greenhouse and field screening can be effective.

PHOSPHORUS DEFICIENCY

Many types of soil in the tropics are deficient in phosphorus and fix large amounts of phosphate fertilizer. Rice varieties that extract soil phosphorus and use it efficiently would be helpful to small farmers.

Rice can be screened for phosphorus deficiency both in the greenhouse and the field.

In the greenhouse, a culture solution should be prepared consisting of the following:

N, 40 ppm; K, 40 ppm; Ca, 40 ppm; Mg, 4.0 ppm; Fe, 5.0 ppm; Mn, 0.5 ppm; Mo, 0.05 ppm; Zn, 0.01 ppm; B, 0.02 ppm; and Cu, 0.01 ppm.

Screening procedures for tolerance for phosphorus deficiency.

Steps	Key points
Greenhouse screening	
1 Prepare culture solution.	• 0.5 ppm of phosphorus 10 ppm of phosphorus
2 Seed.	• Pregerminate seeds. • Arrange 4 seeds in a square of 7.5 cm on nylon net floats placed in the cultural solutions in 4-liter pots.
3 Maintain.	• Check and maintain pH of cultural solutions daily. • Change culture solutions weekly.
4 Score.	• After 4 weeks count the tillers of each variety at the two concentrations of P and express tolerance as a relationship of tillers present.
Field screening	
1 Field preparation.	• Plant in phosphorus-deficient field.
2 Management.	• For a check, add 25 kg of phosphorus and compare the yields under both conditions.

CHAPTER 9

Upland adaptability

THIS BOOK IS DIRECTED to the improvement of lowland rice. But it would be incomplete without reference to the special problems of upland rice breeding. After decades of almost total neglect, rice scientists are beginning to study upland rice. Within a generation the improvement of upland rice will probably be the subject of a book in itself.

Despite the importance of upland rice, particularly in Asia and Latin America, and also in parts of Africa, the crop has consistently received low governmental research priority and few concerted efforts have been made to improve upland varieties or cultural practices. Some argue that in Asia the increased yields of irrigated rice, coupled with progressive improvement in rainfed rice and extension of irrigation systems, will reduce the importance of upland rice and that much of the actual upland rice area should be devoted to other crops. But this is not the case in Brazil, for example, where increases in the yield and area of irrigated rice are not likely to replace the predominant upland culture for many years.

The upland problem is complicated by the range of soil types and rainfall situations in which the crop is grown. One relatively favored type of area is that found in much of Central America and extensive areas of western South America, and in Asia where soils are relatively fertile, rainfall is abundant, and the water table is often high. When rainfall is well distributed in these areas, some of the new dwarf lowland varieties such as IR5, CR1113, IR8, and CICA 4 can yield from 3 to 5 t/ha on farms. Critical research areas for this favored type of upland rice culture are blast and leaf scald resistance and weed control to protect existing yielding ability. Work in Peru and elsewhere suggests that high yielding varieties for this upland situation will also yield well when irrigated. However, the reverse is not true because some highly productive lowland varieties and lines are not satisfactory under favorable upland moisture and soil conditions, indicating basic varietal differences in growth on upland soils that are essentially free of drought.

The great bulk of upland rice in Latin America, however, is grown on relatively infertile, acid soils where rainfall is unpredictable, as in eastern Colombia, Venezuela, and much of Brazil. The absence of a high water table, the extreme soil permeability, and an irregularity of rainfall indicate that drought is the major factor limiting yield, particularly in Brazil.

Although rice farming in Brazil is highly mechanized, regional yields average only about 1 t/ha and the highest yields on experiment station plots rarely reach 3 t/ha. For such upland culture, where rice is subject to periodic drought stress, increased farm yields is more than a question of providing a good dwarf variety, weed control, better agronomic practices, or disease protection. This exceedingly difficult problem is the subject of the rest of our discussion of upland rice.

Upland rice has competed reasonably well with irrigated rice for decades because its lower yield per hectare was largely offset by lower production costs. But the adoption of the high yielding varieties by lowland growers has grossly disturbed that balance and threatens to force those upland rice farmers who cannot switch to the new technology out of rice growing. This would be tragic in areas where increased irrigated yields would not compensate for the loss in upland production.

Partially in recognition of this, research on upland rice appears to be receiving increased priority in some countries. But there is a lack of accumulated knowledge to draw upon that is comparable to the one that existed when the IRRI began its work on tropical lowland rice.

Present upland varieties are moderately tall and have intermediate tillering ability. The leaves are long and broad. Because of their droopy character, the upper leaves are often sun-scalded during periods of water stress.

In Brazil upland rice is planted in rows spaced about 60 cm. At this wide spacing the plant type is reasonably good, blast is usually not severe, and the vegetative growth appears to be in an excellent physiological condition. But the foliage never covers the ground between the rows, the leaf area index remains low, much of the solar radiation is lost, and yields would remain low even if moisture stress of the plant were eliminated.

Sufficient research has been done to show that close spacing does not increase — and may even decrease — the yield of traditional upland varieties. A major reason appears to be that spacing closer than 30 cm between rows results in a deterioration of plant type because the plants grow taller and leafier. Obviously, this causes mutual shading, which adversely affects yielding ability. Probably more important, the increase in plant size and leaf area index in relation to a constant root development intensifies plant moisture stress. Another major reason that density and yield are negatively correlated in traditional upland varieties is that blast disease increases at closer spacing. But high yielding dwarfs at close spacing can not simply be substituted for the locally adapted tall upland varieties because the dwarfs lack drought resistance.

The logical starting point for a breeding program, therefore, is a search for the best levels of drought resistance among the thousands of indica varieties in the world collection. The best material identified so far is

from Brazil. Such varieties should be shortened somewhat with the objective of developing a plant about 1 meter tall that can be planted at a relatively high density and that can withstand drought. Short, erect leaves should be sought to reduce evaporation and sun scalding. Moderately high tillering ability probably would not be a disadvantage under drought stress because the tiller number would automatically decrease during early stress. But with favorable moisture conditions, plants with high tillering ability and seedling vigor would cover the ground quickly, thereby reducing soil moisture evaporation and competing better with weeds.

Some Brazilian upland varieties have two important characters not found in other upland rices. They appear to be resistant to brown leaf spot, an important disease on acid, infertile soils. They also have high grain weight and quality. The milled grain has clear endosperm and intermediate amylose content.

Several modifications should be made in existing breeding procedures. In Brazil, a 60-cm row spacing is used in breeding programs. This should be reduced to 30 cm to increase efficiency of nitrogen use and to apply greater selection pressure for drought resistance in segregating populations. Upland soils are easy to work and a breeder could easily space 1 plant every 10 cm within the rows to facilitate plant selection and to avoid the problems of two or more plants growing together.

Many single crosses between the improved varieties of intermediate height and drought-resistant upland varieties should be made. These should be followed by backcrosses and three-way crosses to short-statured parents to produce 200 to 400 F_1 seeds for each backcross. The tall backcross plants would be eliminated and the F_2 seed of the fertile intermediate-height plants with good grain appearance would be bulked.

Replicates of bulk hybrid populations should be spread over several stations to increase the likelihood of encountering drought at different growth stages. As the bulks would be homogeneous for moderate stature, little adverse interplant competition for light would be expected. Modified bulk selection should start in the F_2 for drought resistance, brown spot and leaf scald resistance, intermediate height, desired maturity period, and grain traits. Bulk selection should be continued for four or five cycles of breeding. Selected intercrossing of the better drought-resistant short lines would favor the recombination of these characters with disease resistance, seedling vigor, high tillering, and thick culms for lodging resistance.

Upland rice improvement will require well-organized teams of scientists of several disciplines. If productive varieties can be produced for planting at closer spacing, agronomists will need to improve existing cultural practices for seed density, fertilizer rates and timing, and weed control. Pathologists will have to work closely with the breeders in varietal

development, especially in the breeding for resistance to brown spot, leaf scald, and blast. No upland variety from Latin America is resistant to blast, which indicates that improved plant and grain types having stable blast resistance will have to be incorporated into the most drought-resistant, intermediate-statured lines developed through bulking. Mineral nutrition work should be directed toward the evaluation of plant differences in tolerance for such typical upland problems as aluminum and manganese toxicity, and iron and phosphorus deficiency. Basic studies on varietal differences in root development in relation to moisture stress and on alternative ways to measure drought resistance in large segregating populations would be helpful to breeders.

DROUGHT RESISTANCE

RESEARCH EFFORTS AT IRRI and elsewhere only recently have emphasized drought resistance in rice. This has been due mainly to the complexity of the problem rather than to a lack of recognition of its importance. Productivity in upland, rainfed lowland, deep-water, and even irrigated rice has long been known to be limited by inadequate water at certain phases of growth. IRRI scientists concerned with drought resistance estimate that upland rice comprises 10% (8.1 million ha) of the rice hectarage in South and Southeast Asia, almost 80% (4.5 million ha) of the rice area in Brazil, and 75% of Africa's rice hectarage. Rainfed lowland rice is thought to account for about 50% (40 million ha) of the rice hectarage in tropical Asia. Another 10% is floating or deep-water rice, sown in dry soil and grown under upland conditions where there is a risk of drought for several weeks before flood water rises. Water deficiency also occurs in many, if not most, of the irrigation systems serving rice. Thus as much as 90% of the world's rice-growing area is estimated to suffer from drought at some critical growth stage.

Varieties clearly differ in their ability to survive and yield in moisture-deficit situations. The phenomenon, however, is highly complex and may involve several mechanisms. IRRI scientists have found that drought-resistance mechanisms in relation to climatic, edaphic, and cultural conditions are inherently different and location specific. They seek mechanisms that will function over a broad spectrum of environments.

The IRRI drought program has three major objectives:

- to better understand the physiologic basis of drought escape, avoidance, tolerance, and recovery in relation to varietal differences in these component traits;
- to devise and refine techniques to enable researchers to quickly identify the different components of drought resistance, each of which may operate at a particular stage of plant growth; and
- to use the appropriate techniques to screen breeding lines and

accessions in the germplasm bank for adaptability to different water regimes.

DROUGHT SCREENING TECHNIQUES

A number of techniques of varying sophistication may be used to evaluate drought resistance. Presently, the most practical method is to simply plant in fields for a simulated upland or rainfed lowland crop in the dry season. The plants may be established by watering with sprinklers or gravitational irrigation. Water is withheld to impose stress at the appropriate growth stage, which can be determined by examining the climatic data of the target region for the varieties under development. In many soils, it takes at least 2 weeks of rainless days before any marked differences appear in susceptibility to drought during the vegetative stage, and at least 1 week during the reproductive stage. At the appropriate time the test entries are scored for stress symptoms and ability to recover after water is applied. The scale in the standard evaluation system for rice is used.

The results of such dry-season tests should be verfied during the rainy season under natural drought conditions. IRRI scientists have found a good correlation, but that might not be true at all locations.

DROUGHT-RESISTANT GERMPLASM

Accessions from the germplasm bank as well as improved breeding lines with some degree of drought resistance are available directly from IRRI and through the International Rice Testing Program (IRTP), especially the International Upland Rice Observational Nursery (IURON). Workers in areas where drought is a pronounced problem should make a special effort to stay abreast of efforts at IRRI and elsewhere.

CHAPTER 10

Temperature tolerance

LOW TEMPERATURE

SCIENTISTS IN TEMPERATE RICE PROGRAMS have selected for resistance to low temperature for decades. Their varieties are recognized today as being strongly low temperature tolerant. Many workers in the tropics now appreciate the desirability of incorporating some degree of low temperature tolerance into varieties. Such tolerance is required at high elevations within the tropics and also for successful commercial use of tropical varieties in subtropical areas. Thus, cold tolerance is considered an important breeding objective by both IRRI, which cooperates with workers in Korea and Pakistan, and CIAT, which works with national programs in coastal Peru, southern Brazil, and Argentina.

Many sources of tolerance for low temperature are available. Japonica varieties from northern Japan, Korea, Hungary, Italy, and the western USA have good resistance. Many indica rices from high altitudes in Nepal, India, and the Philippines are cold tolerant and some southern USA varieties have moderate tolerance. A few tropical rices have enough tolerance to permit successful cultivation in latitudes extending to 25 or 30°. A tropical line, IR12-178, was crossed with the highly cold-susceptible IR8 to develop the variety CICA 4, which has adequate tolerance in several subtemperate areas. When only moderate tolerance is required for indica production areas, tolerant indica sources such as CICA 4 are more useful than resistant japonicas because of the problems involved in most wide crosses of indicas and japonicas.

The inheritance of low-temperature tolerance must be exceedingly complex, although it appears to be independent of all important culm and leaf characters, and it is obviously affected greatly by environment. Repeated cycles of natural selection under appropriately low temperature appear to result in a progressive and cumulative advance toward tolerance. One example of this may be the variety Caloro, selected in California in 1913 from a Japanese introduction, Early Wataribune. Natural selection for 60 years seems to have steadily increased Calor's tolerance without appreciably changing other varietal characters; Caloro now has excellent cold water tolerance and seedling hardiness.

Tolerance for damage at one growth stage does not necessarily relate to tolerance at other stages. Although Caloro is highly cold tolerant in the seedling stage and at early vegetative growth, it is susceptible to floret

sterility, presumably induced by low temperatures. Other materials withstand low temperature during flowering and ripening but are susceptible during germination and seedling development.

Susceptibility is expressed in many ways at different growth stages, indicating that evaluation of material at only one stage is insufficient. Vegetative growth is stunted by low temperature. Seedlings and lower older leaves often turn yellowish orange. Panicles are poorly exserted and partially sterile. The upper spikelets often degenerate and branch into white frail structures. Air temperature of 15 to 19°C during meiosis in the microsporocytes causes high spikelet sterility. The maturity period in susceptible material is prolonged and irregular. Different combinations of night and day temperatures probably damage different stages of vegetative and grain development.

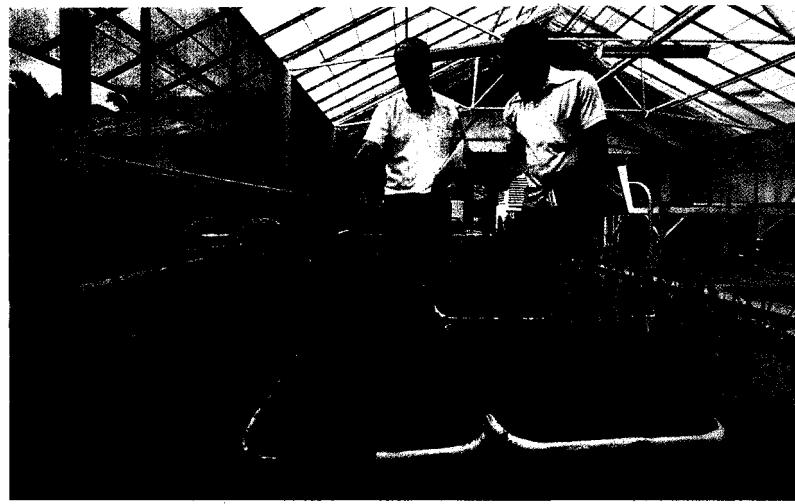
Selection for cold tolerance depends on the timing of the cold period during crop development. In some areas low temperature and damage occur only during vegetative growth, while in others only the inflorescence is affected. In the high valleys of Colombia, where night temperatures are moderately low throughout the year, useful guides for selection are slow seedling development, stunting, sterile and degenerated florets, incomplete panicle exsertion, and delayed maturity.

Strong selection must be practiced whenever possible from the F_2 through yield trials as symptoms are not usually expressed clearly in all seasons at any one site. Some symptoms such as stunting, partial sterility, and delayed maturity are not sufficiently diagnostic to evaluate individual F_2 plants. In such cases, begin selection in the F_3 by evaluating material on a line basis. The degeneration of terminal panicle spikelets into frail white structures, when it occurs, is clearly visible and is a reliable indicator of susceptibility.

Breeding materials are evaluated more consistently and reliably in Japan and other temperate areas by irrigating fields with cold water at night. In the tropics, this would be practical only at high elevations. Resistance can be determined accurately by regulation of air temperature in cold chambers but the number of plants is restricted. In California seedling development is measured by exposing duplicate breeding nurseries to cold water in tanks.

In many tropical countries, altitude varies enough to permit breeding stations located in hot areas to conduct off-station evaluation trials. Progeny testing of all selections each generation may be impractical, but evaluation of all fixed lines entered into observation plots would yield much useful information.

Evaluation techniques for low-temperature tolerance depend greatly on local situations. IRRI has developed an artificial technique in screening for cold water tolerance whereby flats of 7-day-old seedlings are



1. B. S. Vergara, IRRI plant physiologist (left), and Alioune Coly from Senegal, evaluate seedling tolerance for cold water.

placed in tanks for 10 days with the water held continuously at 13°C (Fig. 1).

Field screening is more sensible for programs in areas where tolerance for cold water is required. But maintaining uniform water temperature throughout the nursery is impossible if the planting is of any appreciable size. But it is relatively easy to establish a uniform gradient in temperature, correcting the results through the use of appropriate standard check varieties at frequent intervals.

Screening for low air temperature is much more difficult because it is unpredictable, and uncontrollable except with expensive controlled-environment equipment. However, air temperature is uniform and can be monitored, so materials can easily be tested for tolerance for cold air with the use of appropriate check varieties. The planting dates may need to be adjusted to local farm practices to assure effective screening temperatures at the appropriate growth stage or stages.

Temperature regimes vary from low-high-low in the temperate and subtemperate areas to high-low-high in subtropical or boro areas during the winter season. In the high-elevation tropics, temperature is relatively low and constant. Local climatic and edaphic factors, combined with prevailing situations create many unusual situations for rice cultivation. Screening techniques must be modified accordingly.

Scoring for tolerance is perhaps the most crucial aspect of testing. A general rating of overall phenotypic acceptability at maturity is essential. Materials are usually scored on a scale of from 1 to 9. Ratings of 1 to 3 indicate varietal potential under local conditions while 7 to 9 indicate that

the material is completely unacceptable. Other data such as degree of sterility and panicle exsertion, plant height, and tillering capacity are useful but not essential.

HIGH TEMPERATURE

A few rice workers have recently focused attention on high temperature tolerance. It is increasingly important in areas where modem cropping patterns have shifted traditional planting dates so that temperatures are excessively high at critical growth stages.

IRRI scientists have determined that blooming, or anthesis, is the only stage of growth at which rice is sensitive to high temperature. The precise mechanism has not been determined but desiccation of the pollen is probably the most important factor. Varieties differ dramatically in their ability to withstand high temperatures at this critical stage. At IRRI, varieties are evaluated by placing plants at the booting stage of growth in a glasshouse or phytotron under a regime of 38°/30°C day/night temperature.

Varieties such as Hoveyzeh from southern Iran are fertile at temperatures higher than 45°C, while others become completely sterile. The inheritance of tolerance for high temperature has not yet been investigated.