Rainfed lowland rice improvement

D.J. Mackill
W.R. Coffman
D.P. Garrity

IRRI
INTERNATIONAL RICE RESEARCH INSTITUTE

Rainfed lowland rice improvement

D.J. Mackill
W.R. Coffman
D.P. Garrity

1996
IRRI
INTERNATIONAL RICE RESEARCH INSTITLIE
P.O. Box 933, 1099 Manila, Philippines

The International Rice Research Institute (IRRI) was established in 1960 by the Ford and Rockefeller Foundations with the help and approval of the Government of the Philippines. Today IRRI is one of 16 nonprofit international research centers supported by the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is sponsored by the Food and Agriculture Organization of the United Nations (FAO), the International Bank for Reconstruction and Development (World Bank), and the United Nations Development Programme (UNDP). Its membership comprises donor countries, international and regional organizations, and private foundations.

As listed in its most recent Corporate Report, IRRI receives support, through the CGIAR, from anumber of donors including UNDP, World Bank, European Union, Asian Development Bank, Rockefeller Foundation and Ford Foundation, and the international aid agencies of the following governments: Australia, Belgium, Canada, People's Republic of China, Denmark, France, Germany, India, Indonesia, Islamic Republic of Iran, Italy, Japan, Republic of Korea, The Netherlands, Norway, Philippines, Spain, Sweden, Switzerland, United Kingdom, and United States.

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

The designations employed in the presentation of the material in this publication do not imply the expression of any opinion whatsoever on the part of IRRI concerning the legal status of any country, territory, city, or area, or of its authorities, or the delimitation of its frontiers or boundaries.

Los Baños, Philippines
Mailing address: P.O. Box 933, Manila 1099, Philippines
Phone: (63-2) 818-1926,812-7686
Fax: (63-2) 891-1292
Email: Postmaster@IRRI.CGNET.COM
Telex: (In) 40890 Rice PM; (CWI) 14519 IRILB PS;
(RCA) 22456 IN PH; (CWI) 14861 IRI PS

Suggested citation:

Mackill DJ, Coffman WR, Garrity DP (1996) Rainfed lowland rice improvement. International Rice Research Intitute, P.O. Box 933, Manila, Philppines. 242 p.

CREDITS

Editor: **Denise Bryant**
Assistant editor: **Tess Rola**
Editorial assistant: **Uza Gellsan**
Cover and graphics design: **Ana Mae A. Wenceslao**
Cover photo: **Eugene Hettel**
Artwork: **Juan Lazaro IV**

ISBN 971-22-0071-X

Contents

Foreword

Despite its importance, rainfed lowland rice has only recently received the attention it deserves from the rice research community. Rice is grown on some 37 million ha of rainfed lowlands worldwide, about one-fourth of the total rice area. These lowlands are heterogeneous in any single location, diverse across locations, and unpredictable everywhere—perhapsthese facts account, in part, for the historical neglect of rice grown in this ecosystem.

This book covers all aspects of a rice improvement program, in the tradition of the classic manual, *Rice improvement,* by P.R. Jennings, W.R. Coffman, and H.E. Kauffmann, published by IRRI more than 16 years ago, but it focuses on the details and peculiarities of dealing with rainfed lowland rice.

Fourteen comprehensive chapters bring a wealth of information to rice researchers by describing the components of rainfed lowland environments, explaining typical and appropriate objectives for rainfed lowland breeding programs, and examining breeding procedures from selection of parents to release of varieties.

It has been a decade since IRRI published anything substantive on rainfed lowland rice. This monograph is the second of two IRRI books to focus on the topic. In 1995, IRRI released *Rainfed lowland rice-agricultural research for high-risk environments,* edited by K.T. Ingram. In 1996, Narendra Deva University of Agriculture and Technology (NDUAT) and IRRI will release *Rainfed lowland rice: physiology ofstress tolerance* edited by R.K. Singh, B.B. Singh, V.P. Singh, and R.S. Zeigler.

Additional information on the complex topic of rainfed lowland rice is available in papers contained in *Fragile lives in fragile ecosystems,* the proceedings of the 1995 International Rice Research Conference.

George Rothschild

Director General

Preface

Rainfed lowland rice is difficult to define precisely; in fact, the very ambiguity of the definition of rainfed lowland rice may account, in part, for its historic lack of attention from rice researchers.

Rice breeders working in predominantly rainfed areas, such as eastern India and Thailand, made some effort to develop improved rainfed lowland rices before the 1950s. The major focus in the 1950s and 1960s, however, when rice breeding intensified internationally, was on developing high-yielding, modern varieties for irrigated and favorable rainfed lowlands.

These programs' initial success with semidwarf rice varieties led many to believe that modern varieties would be appropriate for most of the tropical rice-growing areas. Researchers soon realized, however, that three out of four rice farmers had not benefited from the green revolution (IRRI 1976), and they began to look for ways to help these farmers.

As a result, increasing emphasis was placed on developing rice varieties for adverse environments. Upland and deepwater areas, which were recognized as distinctly different from irrigated areas, already were targeted by several breeding programs. To stimulate greater interest in rainfed lowlands, international conferences were held in 1977 in Bangladesh (BRRI 1980) and in 1978 at the International Rice Research Institute (IRRI 1979). In 1977, IRRI created a breeding program focused on rainfed lowland rice (IRRI 1978); and in 1978, the International Rice Testing Program introduced an international rainfed lowland observational nursery.

Rice researchers were becoming increasingly aware that, if they were to develop improved varieties for adverse environments, they needed a more detailed understanding of the rice-growing ecosystems (Buddenhagen 1978). So, in 1982, IRRI convened an international committee to address the need to classify rice-growing environments. The result was a system, now widely used, through which rainfed lowlands are classified into five cultural types (Khush 1984b).

During the decade that has passed since that system was developed, rice scientists have learned a great deal about rainfed lowland environments, the characteristics that plants must have to be productive in these environments, the objectives that are typical of and appropriate for rainfed lowland breeding programs, and the modifications that must be made to standard breeding procedures to support the development of improved rainfed lowland rices. This book is meant to consolidate and share that knowledge. We hope it also will encourage even greater interest and activity in breeding rainfed lowland rice.

The book is intended not only for plant breeders, but for readers of all backgrounds interested in improving productivity for the rainfed lowlands. Scientists of equally essential disciplines, such as plant pathology, entomology, and physiology, have important roles to play in rainfed lowland rice improvement for significant progress in developing improved cultivars for this complex ecosystem requires a strong interdisciplinary approach. The role of the agronomist is especially pertinent, as new cultivars must be accompanied by appropriate management practices, and must be integrated into more productive cropping systems. Agronomic and physiological studies must form the basis for a continuous refinement of breeding objectives.

Rainfed lowland rice improvement follows the pattern set by the classic *Rice improvement* (Jennings et al 1979); that is, we have tried to cover all aspects of a rice improvement program. We focus, however, on rainfed lowland rice, assuming that most of our readers are familiar with the terminology and techniques of plant breeding and with introductory genetics. If you are new to the field, you may find it helpful to review *Rice improvement.* For those who have a special interest in a particular aspect of rainfed lowland rice improvement, we have tried to provide ample references to pertinent literature.

This book is loosely organized into three parts. The first part describes the defining components of rainfed lowland environments: the ecosystems (Chapter 1) and the cultivars (Chapter 2).

The second part describes typical and appropriate objectives for rainfed lowland breeding programs, roughly in order of priority. Breeders usually are concerned first with agronomic or morphological traits (Chapter 3) and growth duration (Chapter 4)—primary considerations in determining whether a variety is adapted for the environments described in Chapter 1. Then, because water-related stresses are the predominant constraint in rainfed lowlands, breeders are likely to spend much of their time breeding for adaptation to drought (Chapter 5) or submergence (Chapter 6). Other problems—low temperatures (Chapter 7), adverse soils (Chapter 8), and diseases and insect pests (Chapter 9)—while common to all rice ecosystems, are somewhat different in rainfed lowlands than in irrigated or favorable areas. Grain quality (Chapter 10) is an important consideration for any rice breeding program.

The third part of this book focuses on breeding procedures: selecting parents and making crosses (Chapter 11), managing segregating generations (Chapter 12), evaluating advanced breeding lines (Chapter 13), and releasing varieties (Chapter 14). It is here that this book most closely follows *Rice improvement,* and for good reason: Regardless of their objectives, programs for breeding all types of rice—indeed, for breeding a wide range of self-pollinated crops—use similar procedures. We have suggested some modifications, however, that are particularly useful in dealing with rainfed lowland rice.

The publication of this book comes at a time of great change in the world of plant breeding. The application of molecular genetics to crop improvement has recently mushroomed. Molecular marker technology has made it possible to locate genes that control complex quantitative characters; and it is now possible to introduce genes from virtually any species into rice. The further development and use of such biotechnology will profoundly influence the direction of rice improvement. Though we have mentioned these techniques in the text, where appropriate, the field is developing too rapidly to be cataloged here. And, despite its importance, biotechnology does not invalidate the time-honored methods of crop improvement, which have been developed and refined over the past century. The new techniques must be supported by conventional breeding work if they are to realize their full potential. The commonly used rice improvement techniques will not be replaced in the foreseeable future.

IRRI's breeding program also is changing rapidly. Much of the breeding work is being moved from Los Baños to other sites. The national breeding programs of five Asian countries, which have joined with IRRI to form the Rainfed Lowland Rice Research Consortium, are beginning to pool their resources to address the challenges of improving rainfed lowland rice. Regional cooperation is increasing. Nevertheless, national programs must maintain their individual efforts to develop improved cultivars for their specific conditions: Cooperation is most powerful when it brings together agencies that already are strong.

David J. Mackill
W. Ronnie Coffman
Dennis P. Garrity

Abstract

This book, which consolidates and shares knowledge on rainfed lowland rice improvement gained by researchers over the past two decades, follows the pattern set by *Rice improvement,* a classic manual published by IRRI in 1979. While all aspects of a rice improvement program are considered, the main focus is on rainfed lowland rice. The 14 chapters cover three distinct areas: 1) the defining components of rainfed lowland environments, i.e., the ecosystems and the cultivars; 2) typical and appropriate objectives for rainfed lowland breeding programs, including agronomic or morphological traits, growth duration, drought resistance, submergence tolerance, low temperature tolerance, adverse soils tolerance, disease and insect resistance, and grain quality; and 3) breeding procedures: selecting parents and making crosses, managing segregating generations, evaluating advanced breeding lines, and releasing varieties. New techniques in biotechnology are briefly covered. These techniques will require the use of conventional rice breeding procedures covered to capture their impact.

Acknowledgments

We would like to thank staff from IRRI and national programs who read or reviewed parts of the manuscript including M. Akbar, J.M. Bonman, M. Dingkuhn, J.L. Dwivedi, S. Fujisaka, K.T. Ingram, A. Mazaredo, N.M. Miah, J.C. O'Toole, S. Pushpavesa, S. Sarkarung, R.C. Saxena, S. Senadhira, T.L. Setter, B.N. Singh, D.A. Vaughan, B.S. Vergara, and R.S. Zeigler.

Our technical staff at IRRI were instrumental in conducting the research that led to many of the concepts introduced in the book, especially M. Amante, A.M. Pamplona, P. Tenorio, C. Vejpas, P. Agustin, N. Edillo, and R. Pernito. S. Raymundo provided invaluable assistance in the writing process.

One of the most important sources of information for the book was the large number of coworkers in rainfed lowland rice breeding programs throughout Asia, who have worked closely with IRRI. Close interactions with our plant breeder colleagues at IRRI, particularly G.S. Khush, D. HilleRisLambers, S.S. Virmani, M. Arraudeau, D. Senadhira., and D.V. Seshu, were very influential. Also, we are grateful to Dr. Klaus Lampe for granting David Mackill a study leave to write most of the book.

This book has also passed through the hands of a number of editors, most notably Denise Felton Bryant in the United States who labored over it for many months, and T. Rola, R. MacIntyre, and G.P. Hettel at IRRI.

About the authors

David J. Mackill is a research geneticist with USDA-ARS at the Department of Agronomy and Range Science, University of California, Davis. He was a rice breeder at IRRI during 1982-91 in charge of the rainfed lowland rice breeding program.

W. Ronnie Coffman is associate dean for research at the College of Agriculture and Life Sciences and director of the Cornell Agricultural Experiment Station, Cornel1 University. He was a rice breeder at IRRI during 1971-80 and the first breeder in charge of the rainfed lowland program.

Dennis P. Garrity is systems agronomist and coordinator of the Southeast Asian Regional Research Program of the International Centre for Research in Agroforestry (ICRAF) and based in Bogor, Indonesia. He was rainfed agronomist at IRRI during 1982-92 and had most recently been head of the Agroecology Unit in the Agronomy, Physiology, and Agroecology Division.

What is rainfed lowland rice?

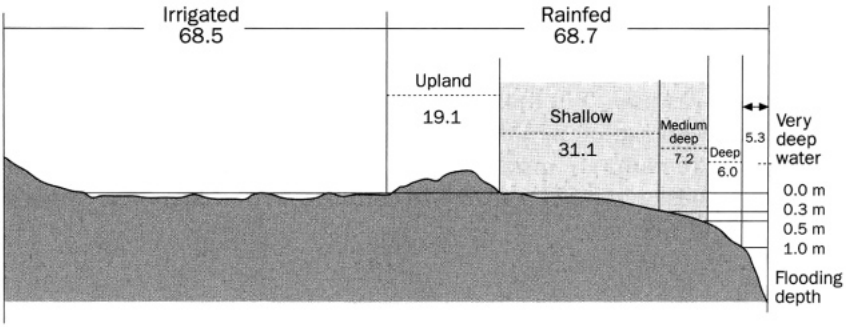
Rainfed lowland rice is difficult to define in precise scientific terms because it is central in the continuum of rice cultures. That is, the hydrology of rainfed lowland rice overlaps with those of irrigated, upland, deepwater, and tidal-wetland rices (Fig. 1).

In fact, rainfed lowland rice is most often defined by the characteristics that distinguish it from irrigated, upland, and deepwater rice (IRRI 1984):

- The crop is not irrigated.
- The soil surface is flooded for at least part of the crop cycle (thus it is not upland).
- The maximum sustained flooding depth is less than 50 cm (thus it is not deepwater).

Nevertheless, this definition is ambiguous because the terms involved are ambiguous.

- *Irrigated* implies complete water control. Many farmers try to accumulate water in their plots, though they cannot obtain complete control. Should a field that has a ditch for collecting water be considered irrigated or rainfed?
- *Upland* suggests that the rice is grown in dry fields that are not flooded. Immense areas are flooded only for short periods. Should a field that is flooded for nine days, as opposed to ten, be considered upland or rainfed lowland?



1. World rice area by water regime. Width is proportional to the extent of each class (values are in million ha) (Huke [1982b] and Herdt and Palacpac [1983]).

- *Deepwater* generally means rice grown in fields flooded to a sustained depth of at least 50 cm. *Sustained depth,* however, is difficult to determine. Water depth in naturally flooded fields varies continually within a season; it also varies from year to year. The length of time that the depth must be sustained is not clear. Should a field that is occasionally submerged by deep floods be classified as deepwater or rainfed lowland?

Further, the terms *upland* and *lowland* are inaccurate. They suggest relative differences in elevation or topography between the types of rice culture. In fact, lowland rice may or may not be lower in the landscape than upland rice. The distinction lies in surface hydrology, so terms such as *dryland* and *wetland* would be more appropriate. After so many years of use, however, the conventional terms are not likely to be replaced.

For most rainfed lowland rice—particularly that grown in the major river floodplains of South and Southeast Asia—the following working definition is sufficient: **It is rice, usually transplanted, that is grown in leveled, bunded fields that are shallowly flooded with rainwater.**

About one-half of the world's riceland is irrigated (Fig. 1). Of the half that is not, rainfed lowland rice occupies more area than all other cultural types combined—about 36 million hectares or 28% of the global rice area. The greatest concentration of rainfed lowland rice is in South and Southeast Asia, where it accounts for 41% of the total riceland.

Rainfed lowland rice is a dominant rice culture in countries that form a belt from India to Cambodia. In five of these countries (Bhutan, Thailand, Nepal, Bangladesh, and Myanmar), more than 50% of the area is rainfed lowland. In four others (eastern India, Cambodia, Laos, and the Philippines), it accounts for almost 40% of the riceland. Barker et al (1985) found that, in these countries, research in rainfed lowland rice would produce higher rates of return than research on irrigated rice.

At present, however, most research is directed to irrigated environments, even in countries where rainfed rice predominates. Barker et a1 (1985) found that research investment was lower in countries with a high proportion of rainfed rice compared to countries with predominantly irrigated rice.

When research workers and resources were scarce and the potential for increasing rice production was uncertain, it made sense to concentrate on irrigated rice. The full genetic potential of rice plants was more likely to be expressed in areas where water was easy to control than in areas where water control was poor. But the potential for productivity gains in rainfed areas has not been exploited. While sustaining and increasing yields in irrigated areas remains an important area of research, resources need to be shifted to emphasize rainfed research in countries with a significant area of rainfed lowland rice.

Chapter 1

The rainfed lowland ecosystem

The improvement of any crop depends on successfully combining the accumulated knowledge about a species with understanding about the environment in which the crop is grown. The objectives of a crop improvement program, and the approaches it uses to meet those objectives, are determined by variations in three elements—plant traits, environment, and consumers' preferences—and interactions between them.

Traditionally, breeding programs have focused on manipulating genetic material while keeping variability within the experimental environment to a minimum. As modern semidwarf varieties were developed, it became apparent that they were adaptable only to a limited range of environments. Scientists then began to question whether rice improvement objectives should be defined by plant characteristics or by the environments in which rice is produced (Herdt and Barker 1977).

Emphasis in rice breeding has shifted over the years from developing broadly adapted plants with certain characteristics (such as a desired height or resistance to a particular insect) to developing plants for target environments that have the combinations of traits needed for specific ecosystems. More and more scientists have realized that the diverse rice-growing situations must be understood before plants can be developed that will succeed in them (Buddenhagen 1978). To match an environment with the best adapted and most productive cultivar, the modern rice breeder must have a strong working knowledge of the agroecology of the crop.

The rice ecosystem includes

- type of rice culture,
- hydrology,
- climate (rainfall and temperature),
- soil constraints,
- biological constraints (weeds, diseases, and insect pests),
- socioeconomic factors.

This chapter discusses each of these in turn, focusing on how they impact on rice improvement programs. In addition, the characteristics of the major rainfed lowland geographic regions are described, and tools for understanding rainfed lowland environments are presented.

How rainfed lowlands are classified

Farmers tend to categorize rainfed rice culture according to the environment in which a cultivar will grow; that is, the categories are based on the ecological factors, such as water depth, that distinguish the adaptation zones of the cultivars. For example, farmers may speak of a "Mahsuri area" because this cultivar is particularly well adapted to the environmental conditions present in that area. Thus the complex array of environments that support rainfed rice culture have given rise to a multitude of descriptive terms. In fact, 23 distinct systems of terminology have been compiled from around the world (Garrity 1984).

To provide rice breeders with a simple, consistent means of communicating about rice culture, IRRI (1984c) developed a general terminology for rice-growing environments (Table 1.1). This system, geared to the needs of breeders, defines target areas according to their predominant constraints. Rainfed lowland rice comprises five environments, which are classified by their hydrologic conditions — the factor that most strongly influences farmers' choices of cultivars and management practices. The environments are

- shallow, favorable;
- shallow, drought-prone;
- shallow, drought- and submergence-prone;
- shallow, submergence-prone; and
- medium-deep, waterlogged.

Table 1.1 Terminology for rice-growing environments (IRRI 1984c).

Ecosystem	Subecosystem
Irrigated	Irrigated, with favorable temperature
	Irrigated, low-temperature, tropical zone
	Irrigated, low-temperature, temperate zone
Rainfed lowland	Rainfed shallow, favorable
	Rainfed shallow, drought-prone
	Rainfed shallow, drought- and submergence-prone
	Rainfed shallow, submergence-prone
	Rainfed medium-deep, waterlogged
Deepwater	Deep water
	Very deep water
Upland	Favorable upland with long growing season (LF)
	Favorable upland with short growing season (SF)
	Unfavorable upland with long growing season (LU)
	Unfavorable upland with short growing season (SU)
Tidal wetlands	Tidal wetlands with perennially fresh water
	Tidal wetlands with seasonally or perennially saline water
	Tidal wetlands with acid sulfate soils
	Tidal wetlands with peat soils

So far, breeders have made little progress in developing cultivars that excel traditional varieties in tolerating the adverse hydrological conditions that prevail in unfavorable rainfed lowlands. Where hydrology is favorable, rainfed lowland rices need to have short growth duration, fertilizer responsiveness, and a high grain-to-straw ratio. In areas where hydrology is unfavorable, however, these plant characteristics often are disadvantages.

Where the rainfed *shallow, favorable* environment is dominant, for example (as in the Philippines and Indonesia), rice yields have been steadily increasing. In other areas, such as eastern India and Nepal, rainfed rice yields have been stagnant at about 1.5 t/ha for decades. While these regions encompass a variety of rainfed subecosystems, unfavorable environments predominate.

The area of each subecosystem for tropical Asian rice-growing countries has been estimated (Table 1.2). The estimates, based on several assumptions about topography and hydrology, have been confirmed by local specialists; however, official statistics are not maintained by any country about areas planted or quantities of rice produced in rainfed subecosystems.

Shallow, favorable

The *shallow, favorable* rainfed subecosystem intergrades with irrigated rice. Field water cannot be completely controlled, but rainfall usually is adequate and well distributed or can be supplemented.

Most of the rainfed rice in Myanmar, Malaysia, Indonesia, and the Philippines falls within this category (Table 1.2). The total area considered *shallow, favorable* in Asia is about 7 million ha—about one-fifth of all rainfed lowland.

Modern semidwarf rice cultivars, usually the same cultivars found in irrigated areas, are commonly grown in this subecosystem. Their productivity is lower than in irrigated areas, however, because

- Crops are more likely to be subjected to short periods of drought stress or mild submergence.
- Farmers use less fertilizer, compensating for the reduced potential and increased risk in *shallow, favorable* areas.

In this subecosystem, rice usually is transplanted. The seedlings used tend to be older than those used in irrigated areas because the date of establishment is less predictable in *shallow, favorable* areas. Increasingly, however, farmers are shifting to dry or wet seeding so their crops can be established earlier, thereby advancing the crop cycle and making double cropping possible (IRRI 1991). Short-duration, photoperiod-insensitive varieties are preferred to keep the crop's field duration within the available rainy period and thus avoid drought stress at the end of the season.

There is no need for a special breeding program targeted to this transitional subecosystem. Varieties developed for irrigated and less favorable rainfed conditions can be used in *shallow, favorable* areas. The breeder needs only to conduct field trials with advanced lines (or varieties that already

Table 1.2. Estimated areas of the major rice environments in South and Southeast Asia (000 ha).

Country	Rainfed lowland (0-50 cm)									Irrigated		
		Shallow (0-25 cm)										
	Upland	Favorable	Drought-prone	Drought- and submergence-prone	Submergence-prone	Medium-deep (25-50 cm)	Total	Deep (50-100 cm)	Very deep (>100 cm)	Wet season	Dry season	Total of all cultural types
South Asia												
India	5,973	1,700	7,362	2,116	1,508	1,844	14,530	2,626	2,434	11,134	2,353	39,050
Pakistan	0	0	0	0	0	0	0	0	0	1,710	0	1,710
Bangladesh	858	847	837	1,001	1,608	1,035	5,328	1,552	1,117	170	987	10,012
Sri Lanka	52	89	32	0	89	13	223	9	0	294	182	760
Nepal	40	136	270	136	136	138	816	92	53	261	0	1,262
Bhutan	28	91	0	0	30	24	145	16	0	0	0	189
Total	6,951	2,863	8,501	3,253	3,371	3,054	21,042	4,295	3,604	13,569	3,522	52,983
Percentage of rainfed		14	40	15	16	15	100					
Percentage of total	13	5	16	6	6	6	40	8	7	26	7	100
Southeast Asia												
Thailand	250	513	3,166	1,437	723	200	6,039	802	400	866	320	8,677
Myanmar	793	1,224	283	0	784	699	2,990	466	173	780	115	5,317
Vietnam	407	663	332	0	554	195	1,744	782	420	1,326	894	5,573
Cambodia	499	71	214	428	0	34	747	136	435	214		2,031
Laos	342	92	92	92	0	0	277			67	9	695
Malaysia	91	113	0	0	34	7	154	4		266	220	735
Indonesia	1,134	811	141	0	132	320	1,404	214	258	3,274	1,920	8,204
Philippines	415	765	241	60	141	303	1,510	76	0	892	622	3,515
Total	3,931	4,252	4,469	2,017	2,368	1,758	14,865	2,480	1,686	7,685	4,100	34,746
Percentage of rainfed		29	30	13	16	12	100					
Percentage of total	11	12	13	6	7	5	43	7	5	22	12	100
South and Southeast Asia												
Total	10,882	7,115	12,970	5,270	5,739	4,812	35,907	6,775	5,290	21,254	7,622	87,729
Percentage	12	8	15	6	7	5	41	8	6	24	9	100

Source: Huke (1982) with revisions by Garrity and Agustin (unpubl.).

have been released) to identify the cultivars that are best adapted to the subecosystem.

Shallow, drought-prone

The dominant rainfed subecosystem, *shallow, drought-prone,* covers more than one-third of the Asian rainfed lowlands (Table 1.2). About 80% of the land in this category lies in India (7.4 million ha) and Thailand (3.2 million ha). Within the *shallow, drought-prone* category are two types of ricelands (Table 1.3).

Drought-prone I. One type of *shallow, drought-prone* land is constrained by a short rainy season. This type is typical, for example, in South Asia and particularly in eastern India, where the monsoon may last no more than 4-5 mo and rainfall may exceed 200 mm for only 3 mo or less (Huke 1982a). In well-drained landscapes, rice cultivars must have short growth duration if they are to avoid being damaged by drought; thus the best adapted plants are those that mature in 95-125 d.

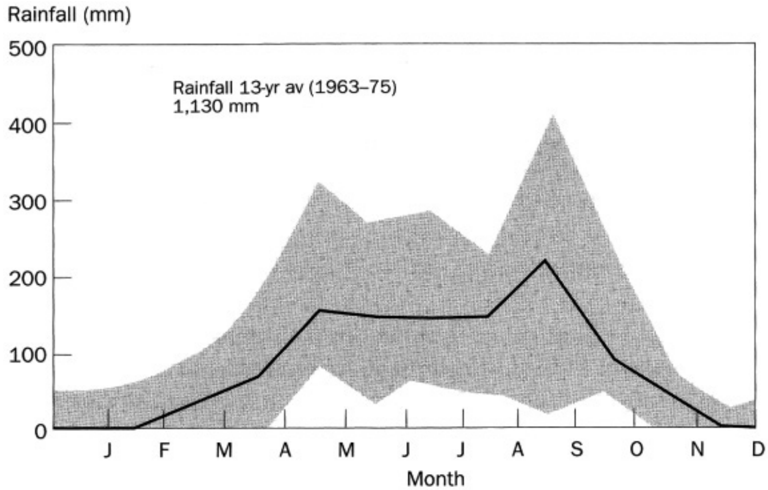
Much of the land is dry seeded before or at the beginning of the rains with photoperiod-sensitive varieties. Commonly, the field is plowed after the crop is established and the soil surface is naturally flooded, thus improving weed control and stand distribution (Fujisaka 1991). This practice, known as *beusani,* is typical in the plains of Madhya Pradesh, Bihar, Orissa, and Uttar Pradesh states of India.

In some countries, improved semidwarf varieties are grown in a small proportion of these lands where stresses are not severe and their short growth duration is an advantage. However, the area of drought-prone ricelands in which improved cultivars are used is modest.

In many rainfed lowlands, *drought-prone I* areas grade into upland areas. In the transitional areas between types, differences are blurred; for example, in the *aus* rice culture of eastern India and Bangladesh, short-duration cultivars are direct seeded on dry soil at the start of the rainy season. The fields are then flooded for brief or extended periods before harvest.

Table 1.3. Subclasses of drought-prone rainfed lowlands.

Characteristic	Drought-prone I	Drought-prone II
Rainy period	Short, monomodal	Long, erratic, bimodal
Agronomy	Direct seededTransplanted	
Variety	Photoperiod insensitive with early to very early maturity or photoperiod sensitive	Photoperiod sensitive with medium to late maturity
Distribution	Madhya Pradesh. India; western Nepal; central Myanmar	Northern and northeastern Thailand; Cagayan, Philippines



1.1. Rainfall distribution at Pimai shows a bimodal tendency, with a large peak in September and a smaller peak in May. The shaded area represents the range of rainfall amounts over years (Pushpavesa and Jackson 1979).

This lowland-upland transition also is typical in West Africa, where fields usually are not leveled or bunded. These transitional, hydromorphic areas may be similar to drought-prone rainfed lowlands in wet years (or at low positions in the landscape) and uplands in dry years (or high landscape positions).

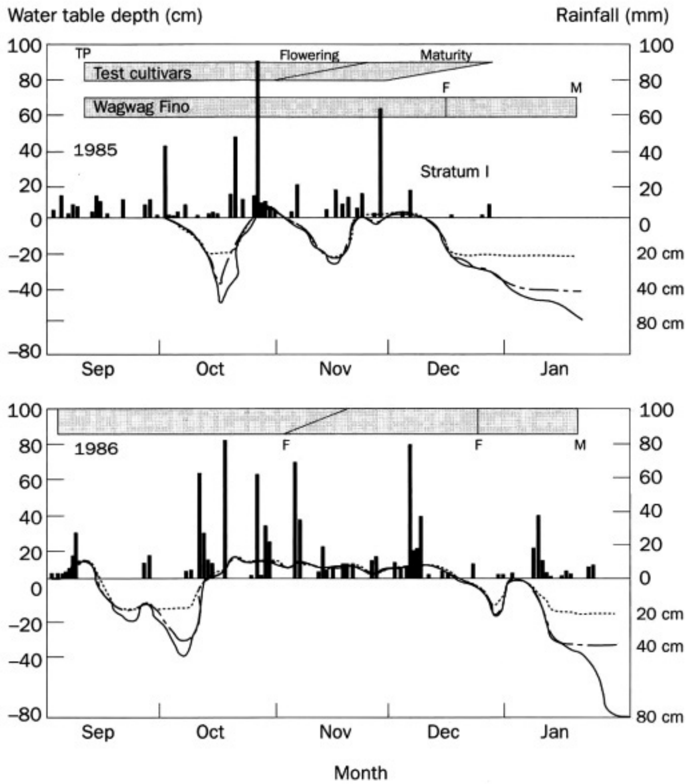
Drought-prone II. In the other type of *shallow, drought-prone* ricelands, the rainy season is longer but erratic, tending to be bimodal (Fig. 1.1). A drought frequently occurs at midseason, though the timing and duration of the drought varies. Typically, rice is transplanted after the rainfall has intensified and the fields are securely flooded.

Most of the cultivars used in these areas are photoperiod sensitive. The adaptive advantages of photoperiod sensitivity include (Pushpavesa and Jackson 1979)

- tolerance for late transplanting,
- a dependable maturity date after the rainy season ends.

The period of rainfall cutoff is dependable; therefore, photoperiod-sensitive cultivars, which have a constant maturity date, usually art harvested before conditions become too dry. By contrast, when photoperiod-insensitive cultivars are transplanted late, they also flower and ripen late, which increases the chance that the crop will fail due to drought.

The unpredictability of droughts is exemplified by the differences in the timing of drought in 1985 and 1986 at Solana, Cagayan, Philippines (Fig. 1.2). In 1985, serious drought occurred at panicle initiation and at flowering. In 1986, a single prolonged drought occurred just after transplanting. The cultivars most frequently grown at Solana are photoperiod sensitive and mature in January. Transplanting dates typically are delayed to late August or September due to the unpredictability of precipitation in the early rainy season (Fig. 1.3).



1.2. Daily rainfall pattern (bars) and surface hydrology (continuous lines) in 1985 and 1986 on an alluvial terrace (Stratum I), Solana, Cagayan, Philippines. The horizontal bars at the top show the transplanting, flowering (F), and maturity (M) dates for the test cultivars and the local check, Wagwag Fino.

1.3. A farmer in Solana, Cagayan, Philippines, pulls aged seedlings from a seedbed for transplanting to the field. Drought often delays transplanting at an optimal seedling age.

Shallow, drought- and submergence-prone

Shallow, drought- and submergence-prone ricelands often are contiguous to drought-prone areas, being the parts of the landscape that flood deeply when local precipitation is heavy or rivers overflow. Drought and submergence events may alternate within a growing season or may occur during different seasons. Lands in this category amount to about 5 million ha (Table 1.2).

This subecosystem is common in mainland Southeast Asia, particularly in Cambodia and northeastern Thailand. It is also important in eastern India and Bangladesh. Rainfall patterns are similar to those of *drought-prone II* areas. Rice usually is transplanted; but tall, aged seedlings often are used to mitigate damage from submergence. To adapt to growing conditions in *drought- and submergence-prone* areas, rice plants must tolerate drought and submergence, be sensitive to photoperiod, and have medium growth duration (120-140 d).

Shallow, submergence-prone

Shallow, submergence-prone lands are generally favorable for rice production except that they are subject to unpredictable, short-term submergence that may damage the crop, especially when it occurs soon after transplanting. The landscape favors prolonged, shallow surface flooding. The rainy season tends to be at least 5-6 mo long, and the crop usually is harvested after the rains end.

Tall, photoperiod-sensitive cultivars usually are grown in such areas (Fig. 1.4); and tall, aged seedlings are used because they are better able to withstand short-term submergence than shorter, less mature seedlings.

The *shallow, submergence-prone* ecosystem is found mostly in Vietnam, Myanmar, southern Thailand, Bangladesh, and eastern India.

Medium-deep, waterlogged

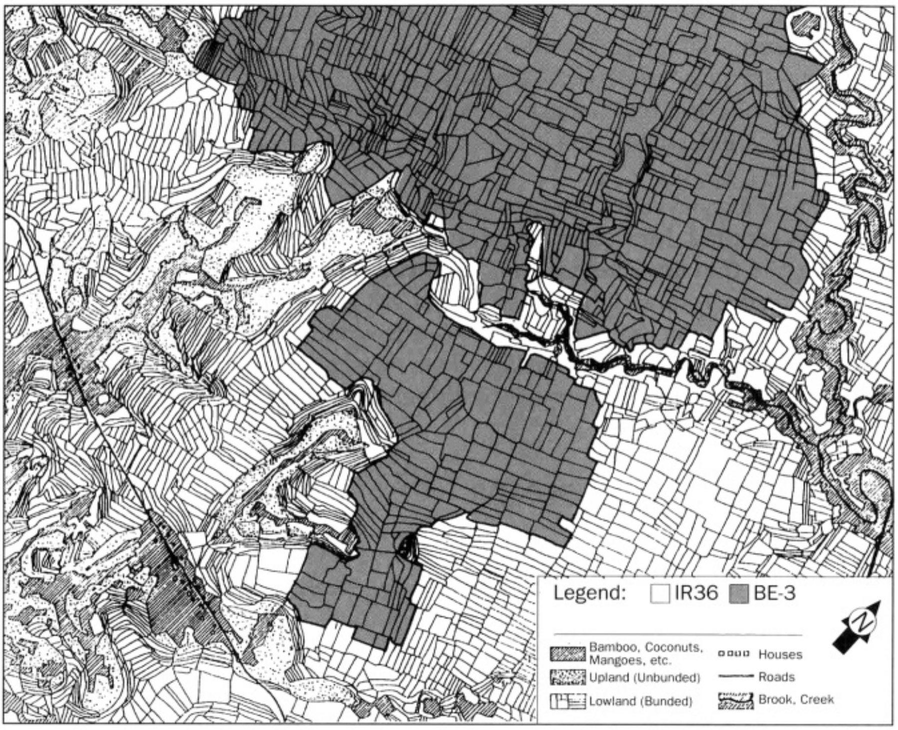
To be classified as *medium-deep, waterlogged,* ricelands must accumulate water to a depth of 25-50 cm for prolonged periods—2-5 mo—during the crop season. These lands also tend to experience frequent, short-term submergence, which is much more damaging to crops than the effects of standing medium-deep water.

This combination of factors results in three major stresses:

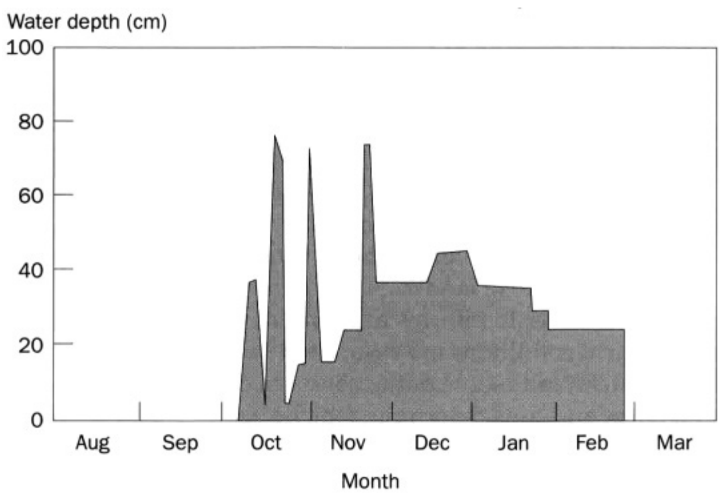
- Water levels are deeper than those to which rice is optimally adapted.
- The standing water stagnates, creating imbalances in oxygen and other chemicals.
- The crop is frequently submerged.

The hydrograph of Bay, Laguna, Philippines, during the 1986 wet season illustrates the complex of stresses affecting *medium-deep, waterlogged* rice (Fig. 1.5). Four submergence events were recorded in one growing season, exceeding a water depth of about 30 cm that was sustained for 2 mo.

Medium-deep, waterlogged ricelands occupy some 5 million ha in Asia (Table 1.2). In some areas (such as parts of Myanmar, Bangladesh, and eastern India), the fields are bunded and tall seedlings are transplanted. In other



1.4. Distribution of an improved cultivar (IR36) and a traditional cultivar (BE-3) in ricefields in a rainfed lowland area of Iloilo, Philippines. The two varieties are grown in contiguous areas. The distribution corresponds to water levels; the tall cultivar BE-3 is grown in the fields subjected to deeper flooding (medium-deep conditions).



1.5. Seasonal hydrology of a medium-deep rainfed lowland area, 1986 wet season, Bay, Laguna, Philippines.

areas, no bunds are used and the crop is dry seeded before the rains begin. Here the land must be prepared during the dry season, so tractors often are needed to dry plow the typically heavy clay soils. Some tidal wetlands, such as those of southern Bangladesh, are classified as *medium-deep, waterlogged* ricelands. Here rice culture is influenced by the diurnal fluctuations of the tides.

In this subecosystem, the rice crop usually is harvested after the surface water has receded. Most farmers adopt varieties that are tall and photoperiod sensitive and that have field durations exceeding 5-6 mo. Photoperiod-insensitive cultivars with intermediate height (120 cm) and long growth duration are suitable for some of the area; but photoperiod sensitivity is a great advantage under most *medium-deep, waterlogged* conditions. Any cultivar grown in this subecosystem must be able to tolerate stagnant water.

Hydrology and the landscape

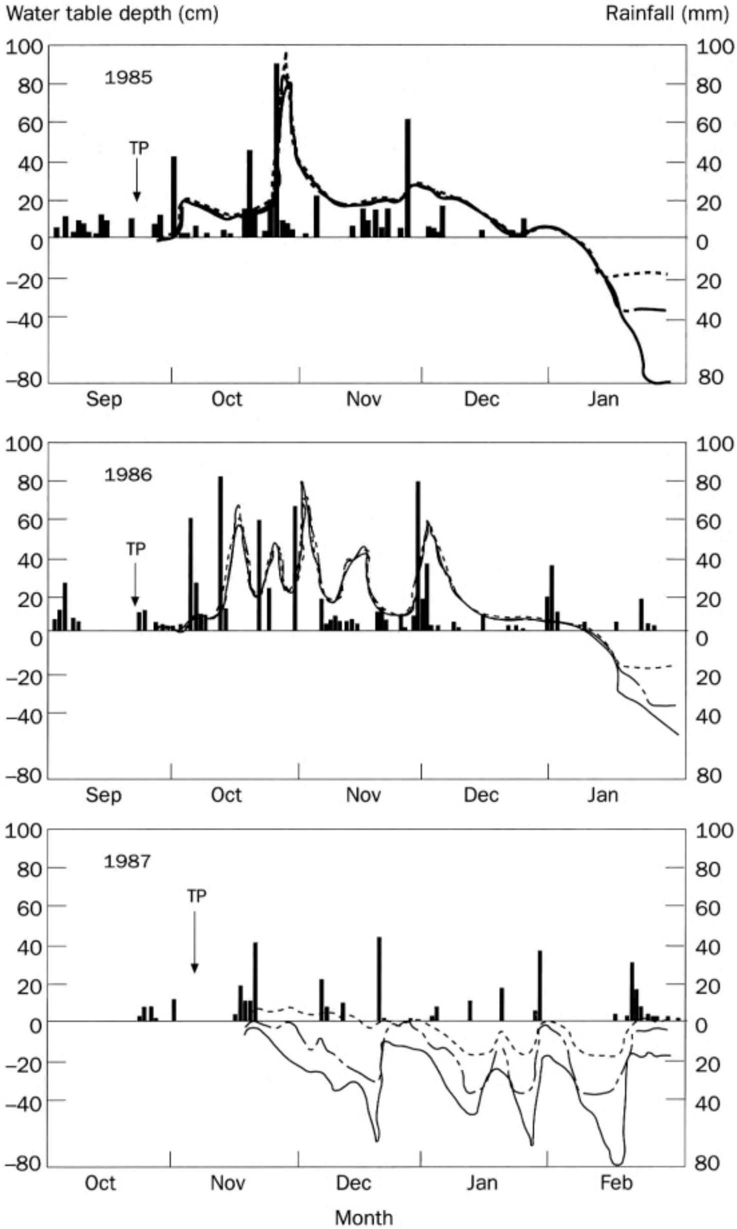
The classification boundaries between the five rainfed subecosystems are not discrete. The hydrological conditions of some ricelands place them on the borderline between classes. And the variability of weather may cause the conditions in a given field or region to change from year to year.

For example, at a site located in a poorly drained shallow depression in the backswamp of the Cagayan River, Philippines, the surface hydrology during 1985 was typical of the *medium-deep, waterlogged* subecosystem (Fig. 1.6). During 1986, surface flooding was shallow in general, but the rice crop was submerged five times. These conditions are typical of the submergence-prone subecosystem. During 1987, shallow flooding for a short period was followed by a devastating drought for most of the growing season—conditions typical of the *shallow, drought-prone* subecosystem. Thus the hydrology of this one site fit three different subecosystem classes in three successive years.

Such land must be classified by its modal hydrology—the water depth that occurs most often (that is, in 3 of 5 yr). In the example given above, experience at the site over a number of years revealed that its modal hydrology is *medium-deep, waterlogged.* In most cases, a researcher cannot directly observe a site over a number of years, but careful interviews of farmers can enable a site to be classified accurately. Tools for obtaining such data are discussed in the last section of this chapter.

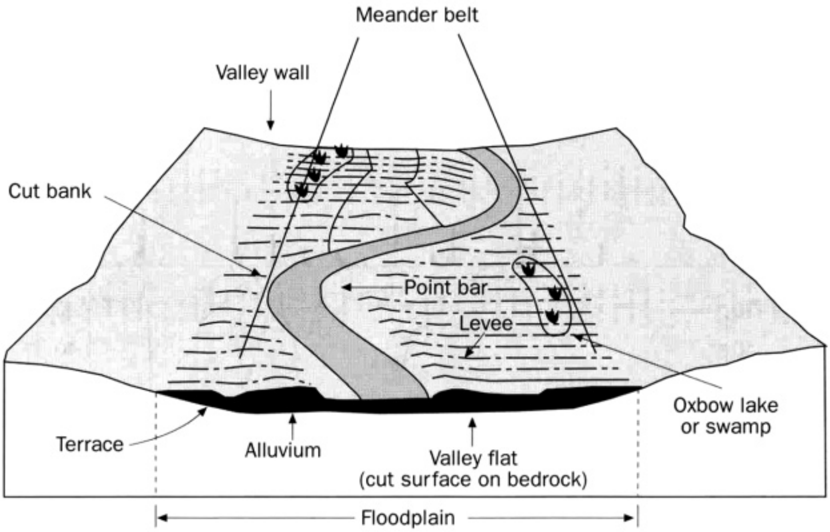
A small area may have several subecosystems that grade into one another (Fig. 1.7). Within the diverse landscapes of rice-growing lowlands, particularly in river floodplains, landforms are consistently repeated (Fig. 1.8), and typical hydrological conditions are associated with each of these landforms. Anyone who understands some of the concepts of geomorphology can detect their relationships and thus determine which subecosystem is predominant.

For example, most Asian countries that have predominantly rainfed lowland rice culture also have major river systems:



1.6. Daily rainfall pattern (bars) and surface hydrology (lines) in 1985, 1986, and 1987 at a site in Stratum III, Solana, Cagayan, Philippines. TP = date of transplanting.

1.7. In northern India, rainfed lowland and deepwater rice are grown in close proximity in low-lying areas. Water depth increases toward the center of the depression (away from the foreground of the photo).

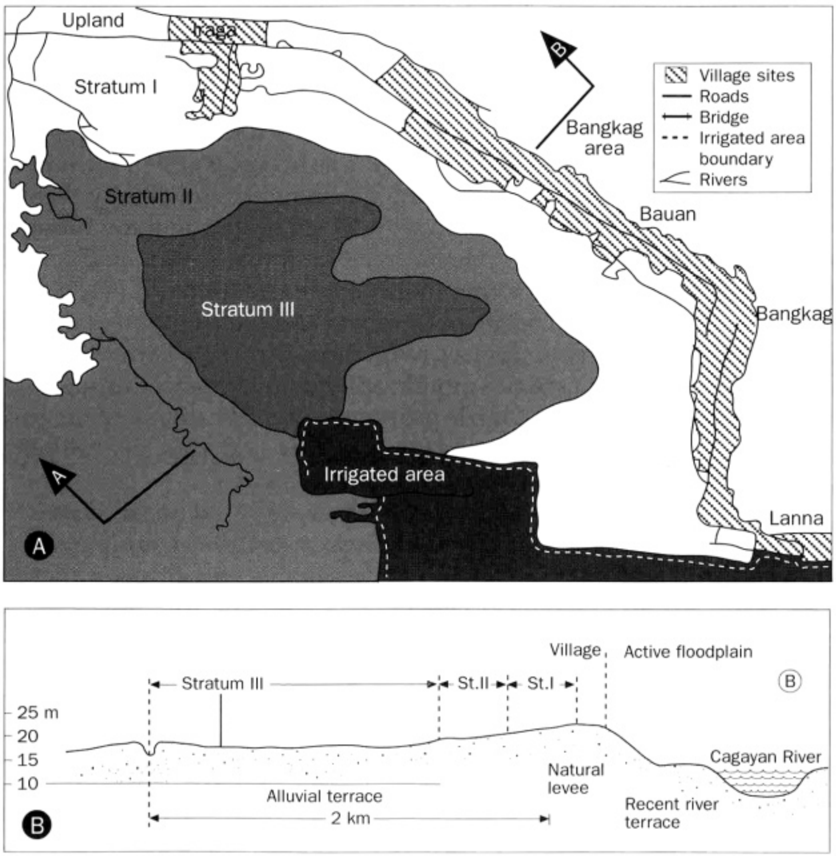


1.8. An idealized floodplain (Bloom 1969).

- the Ganges-Brahmaputra in Bangladesh and eastern India,
- the Irrawaddy in Myanmar,
- the Chao Phraya in Thailand,
- the Mekong in Vietnam.

More than one-third of the 37 million ha of unirrigated ricelands of this region lie in the floodplains and deltas of these river systems (Barker and Herdt 1979). Water control is limited at best in most of the delta areas. Short-term submergence and long-term flooding are the common hydrological stresses.

Rivers that are bordered by broad alluvial floodplains have a typical topographical pattern (Fig. 1.9). Shallow rainfed lowland rice (either *favorable* or *drought-prone*) tends to be located at the highest elevation—on or near the levee. Moving away from the levee, the elevation declines toward a



1.9. A) Distribution of rainfed lowland landforms in Solana, Cagayan, Philippines. Strata were defined based on flooding patterns: Stratum I is shallow drought-prone rainfed lowland rice, Stratum II is drought- and submergence-prone or submergence-prone, and Stratum III is medium deep. 6). The three strata are located at specific positions along the rice-growing toposequence. Stratum III is the lowest and is farthest from the river, corresponding to a backswamp.

backswamp; modal water depths increase gradually, and the land grades from the *shallow, submergence-prone* subecosystem (or *shallow, drought- and submergence prone*) to *medium-deep* and finally to the deepwater environment.

Landscape also affects hydrology outside river basins. Much of the shallowly flooded rainfed riceland in Asia is away from major rivers on gently to steeply sloping hillsides. Here the terraced ricefields are difficult to irrigate. The relative elevations of fields affect their surface hydrology and, thus, the cultivars and management practices used.

In the Korat Plateau of northeastern Thailand—the largest plateau in Southeast Asia where rice is grown extensively—about 3.5 million ha are planted with rice. The plateau accounts for about 40% of Thailand's total rice area. The soils are infertile, and only about 3% of the plateau's ricefields are irrigated; so average rice yields are only about 1.5 t/ ha.

In terraced environments, upper, middle, and lower fields tend to have distinct hydrological characteristics and soils that correlate with rainfed lowland subecosystems: upper fields tend to be drought-prone, middle fields *drought- and submergence-prone,* and lower fields *submergence-prone* or *medium-deep.*

Recognizing the hydrological conditions within a landscape requires some experience, but a knowledge of landforms makes it easier. Even people who have no special background in landforms can learn to identify them without great effort; and the precision with which researchers communicate about varietal fit and cropping systems greatly improves when that communication is based on landform terminology. Bruce and Morris (1981) observed a strong relationship between landform and the adoption of modern varieties. Farmers on alluvial terraces (with more favorable hydrology) tended to adopt modern varieties more readily than farmers of drought- or flood-prone lands. Bruce and Morris proposed a classification system, based on landform, that has now been used for more than a decade in evaluating the adaptation of cultivars developed for rainfed areas.

Some local systems of riceland classification are based on landforms. In eastern India, for example, rainfed ricelands are categorized as *highlands, mediumlands,* and *lowlands* (Table 1.4). Farmers in this area choose varieties and use cultural practices appropriate to the category of field; thus a farmer who has fields of all three categories who will use three different combinations of varieties and practices.

Latin America and Africa have immense land resources suitable for the development of rice production; but Latin America's rainfed lowlands total only 1.1 million ha, and Africa's total only 0.5 million ha. Thus only 22% of the total riceland in Latin America and only 6% of that in Africa are classified as rainfed lowland.

Brazil has the largest area of rainfed lowland rice in Latin America. Most is on the country's *varzeas* — the floodplains of the Amazon River and its tributaries.

In sub-Saharan Africa, most rainfed lowland rice is grown in narrow inland valleys in the extensive, undulating plateaus that cover most of the African landscape. The valleys, known regionally by different names, have

Table 1.4. Local system of riceland classification based on landforms, Orissa State, India.

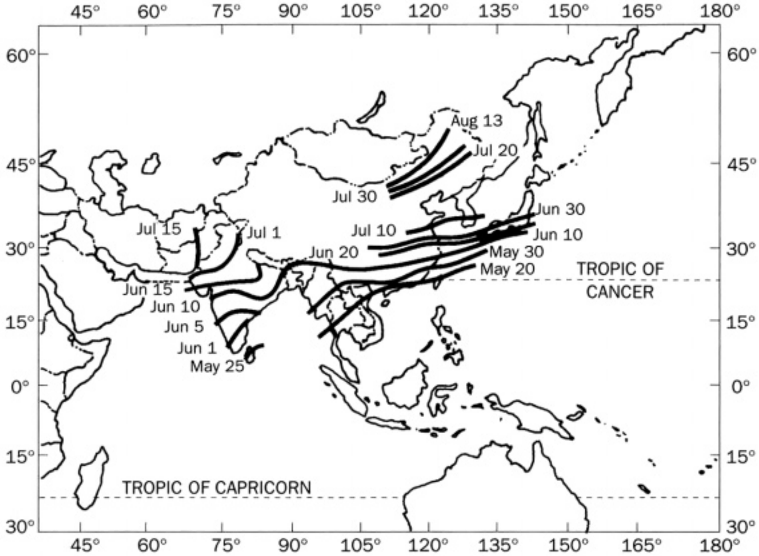
Land category	Rice area (%)	Duration (d)	Sowing Date	Sowing Method	Ripening date	Correlation and remarks
High *(Beali)*	15	<105	15–30 Jun	Broadcast line sown drilled	15 Sept	Rainfed shallow drought-prone; stress occurs for part or most of the season
Medium high *(Laghu-Sarad)*	20	105-120	10–15 Jun	Broadcast line sown transplanted	10 Oct	Rainfed shallow favorable; water control adequate; varieties developed for irrigated situations are suitable
Medium *(Sarad)*	27	120–135	8–10 Jun	Broadcast transplanted	25 Oct	Rainfed shallow drought- and submergence-prone
Low medium	23	135–150	4–14 Jun	Broadcast	20 Nov	Rainfed shallow submergence-prone: periods of heavy rainfall cause complete submergence of the crop for 10–25 d
Low *(Gaharipata)*	12	150–165	Before 10 Jun	Broadcast	30 Nov	Rainfed medium-deep, waterlogged; low-lying with drainage problems; water stagnation for 2–3 mo
Very low *(Pata)*	3	>165	25 May-5 Jun	Broadcast	20 Dec	Deepwater

been studied extensively; the *dambos* of eastern and central Africa by Mackel (1974), the *fadamas* of northern Nigeria by Saviddes (1981), the *bas-fonds* or *marigots* of francophone African countries by Kilian and Teissier (1973), and the *inland valley swamps* of Sierra Leone by Millington et al (1985). The catchments of these valleys range from 100 ha to 2,000 ha and vary in hydrological characteristics. Rainfed lowland rice also is grown in the floodplains of many African rivers.

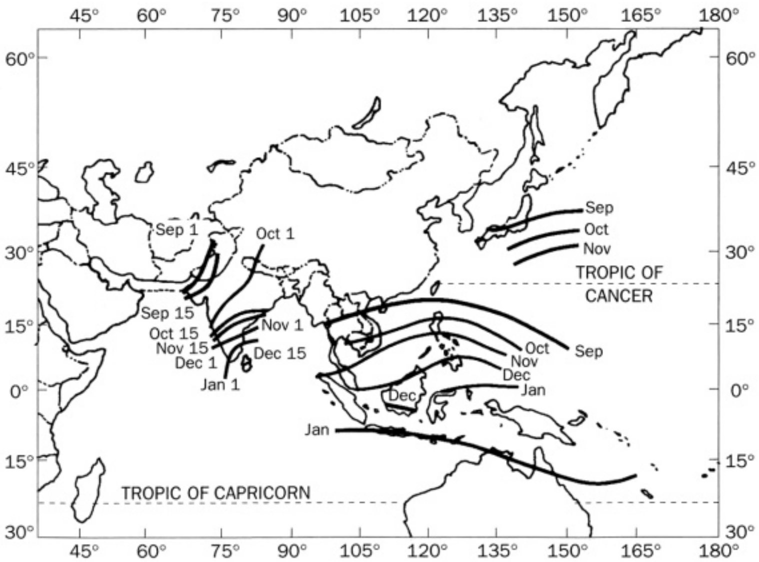
Rainfall and growing season length

In Asia, which grows 96% of the world's rainfed lowland rice, the monsoon is the source of precipitation and the ever variable factor to which rice cultivation is forced to accommodate. The atmospheric circulation characteristics of the southwest monsoon are unique to Asia. They are generated by the belt of intense radiational heat that builds up during the summer months (April to June) on the Asian land mass. The difference in temperature between the overheated land mass and the oceans to the south and east, which remain cool, creates the monsoon. The monsoon rains generated as a result of these air circulation patterns sweep broadly inland in a pattern of waves (Fig. 1.10).

The seasonal winds reverse themselves later in the year as the land mass cools faster than the oceans, so the monsoon recedes, again in waves (Fig. 1.11). There are three distinct monsoon patterns: the Indian monsoon (South Asia), the Malayan monsoon (Indonesia, the Philippines, most of



1.10. Average dates of the onset of the southwest monsoon in India and Southeast Asia (Tanaka 1980 as cited in Yoshino 1984).



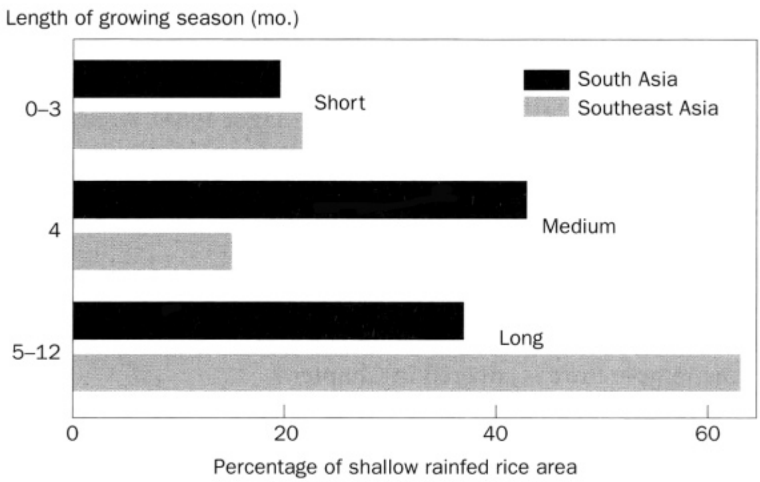
1.11. Normal dates that the southwest monsoon withdraws from India and southward migration of maximum rainfall from September to January in Southeast Asia (Tanaka 1980 as cited in Yoshino 1984).

mainland Southeast Asia, and most of China), and the Japanese monsoon (eastern Asia).

Farmers of rainfed lowland rice adjust their production systems to the local effects of these large-scale climatic processes. The time at which the monsoon arrives and the amount of rain that falls determine the fate of the rice crop. When the monsoon fails to bring adequate precipitation, as it does periodically, rice production falls short of needs, and the scale of human suffering is immense.

The length of the growing season in most parts of Asia is determined by the time of arrival and departure of the southwest monsoon. The agroclimatic classification system for rice developed by Huke (1982a) presumes that the rice-growing season consists of the months in which the mean rainfall exceeds 200 mm (Oldeman 1980). It assumes this average amount to be sufficient for wetland rice, considering the expected rates of evapotranspiration, seepage, and percolation commonly observed in rainfed lands. Maps of the agroclimates of South and Southeast Asia that use this system are available (Huke 1982a).

The number of months in which average rainfall exceeds 200 mm varies widely among rainfed lowlands (Garrity et al 1986b). South and Southeast Asia have similar proportions of ricelands that have short growing seasons; but Southeast Asia has a much larger proportion than South Asia of lands that have exceptionally long rice-growing seasons (Fig. 1.12). Growing-season length is related to the timing of drought stress experienced by the rice crop in different environments. (This point is further elaborated in Chapter 5.)



1.12. Proportions of shallow rainfed rice that have short (0-3 mo), medium (4 mo), and long (5-12 mo) growing seasons, South and Southeast Asia.

Temperature and radiation effects

One problem with the international terminology for rice environments (Table 1.1) is that it is based only on hydrology, yet areas that have similar hydrology may have different climates. For example, two *shallow, submergence-prone* areas may have quite different temperature regimes and radiation patterns. Because of these differences, a cultivar that is well adapted to one *shallow, submergence-prone* area may be unproductive in another. Further, the incidences of diseases and pests are influenced by the combination of temperature and humidity (amount, duration, and continuity of rainfall) that an environment experiences (Buddenhagen 1978).

High minimum temperatures and low solar radiation directly reduce rice's yield potential in many tropical areas (Seshu and Cady 1984). For instance, rainfed rice yields are low in eastern India and have not increased significantly in recent years. Researchers attribute these low yields, in part, to the area's high minimum night temperatures at tillering and floral initiation combined with low levels of solar radiation during the growing season (250-300 cal/m^2 daily) (Rao and Biswas 1979). While radiation levels are stable throughout eastern India's wet season, minimum temperatures begin to drop during the late months, and crops that mature during this cooler period have higher yields. For example, in a study of 27 eastern Indian locations, Garrity et al (1986b) found that crops harvested in September had a mean yield of 3.3 t / ha, but those harvested in late October had a mean yield of 4.5 t / ha.

While the productivity of rainfed lowland rice may be constrained by high temperatures at low latitudes, it may be limited by low temperatures at high latitudes. At latitudes greater than 17° N, temperatures are optimum for growing rainfed lowland rice only for a limited period: as minimum temperatures drop below 20 ºC, immature rice crops experience poor panicle emergence and high spikelet sterility. Thus farmers must use varieties that are sure to mature before the temperature drops. In northern Bangladesh, for instance, farmers recognize a critical flowering date and know that varieties flowering after this date have unstable yields (Magor 1984). At higher latitudes, photoperiod-sensitive cultivars, which flower according to daylengh rather than growth duration, consistently have more stable yields than insensitive cultivars, because they are sure to flower before the onset of cold stress.

Varietal differences in tolerance for high minimum temperatures and low solar radiation are not well understood. At present, these stresses have not received much attention in rainfed lowland breeding programs. Tolerance for low temperature is covered in Chapter 7.

Soil constraints

Many of the world's rainfed lowlands have serious soil constraints. The most widespread include salinity, alkalinity, iron toxicity, phosphorus deficiency, zinc deficiency, and organic and acid sulfate conditions. In some areas, these soil problems are exacerbated by poor water control.

In Southeast Asia, two-thirds of the rainfed area has soil-related constraints (Garrity et al 1986b). Poor cation exchange capacity is the most prominent condition, particularly in northeastern Thailand, where the sandy soils are highly infertile and drought prone. Acid sulfate soils are widespread in Vietnam. Thailand, Myanmar, and Vietnam all have large areas in which rainfed rice soils are saline. In South Asia also, poor capacity for cation exchange is the dominant soil problem; but salinity and alkalinity also are major constraints.

Because soil problems are so widespread, rice breeding programs of most countries must be sure that the varieties they develop are adapted to soil constraints. For more information about the distribution of problem soils in Asia, consult the work of Boje-Klein (1986), which provides detailed maps for the predominant adverse soil types. Chapter 8 addresses adverse soils in more detail.

Biological constraints

As noted earlier, climate influences the occurrence and severity of rice pests. In particular, the combination of temperature and humidity (amount, duration, and continuity of rainfall) that an environment experiences affects the incidence of diseases, insects, and weeds. Soil fertility is another important factor; rainfed lowlands generally receive lower fertilizer inputs than irrigated areas because the risk of water-related stress is high. By improving rainfed rice culture, can the present ecosystems be shifted from low to high productivity without encouraging the proliferation of diseases and insect pests?

Mew et al (1986) found that some rice diseases tend to be associated with certain hydrological situations. For example, viruses are more prominent in areas where rainfall is reliable in timing and amount than in areas where it is uncertain. Fungal diseases, particularly blast and brown spot, tend to domnate in areas where rainfall is unreliable.

The same insects damage rice in rainfed lowlands as in irrigated areas. However, certain pests, such as the brown planthopper, are more serious under irrigated conditions (Heinrichs et al 1986). While there is a clear association between environmental factors and disease and insect incidence, the complexity and diversity of rainfed environments makes it difficult to provide detailed information on the occurrence of biological stresses.

Currently, little or no pesticide is used in many rainfed areas. Integrated pest management can be developed for and applied in these areas before the use of pesticides becomes common. These rainfed areas then would avoid the problems associated with dependence on and misuse of pesticides. Host-plant resistance is an essential component of integrated pest management strategies (Teng 1994). Developing resistant rainfed rice cultivars is discussed in more detail in Chapter 9.

Rainfed ecogeographical regions

Experience with rice improvement over the past 25 years has made it possible to define broad geographical regions that have similar ecosystems and to determine their potential responses to efforts to improve rainfed lowland rice.

For example, the eastern part of South Asia—Bangladesh, eastern India, and the terai of Nepal—is a continuous floodplain in which certain combinations of hydrology and soil are repeated, and incidences of biological stress are similar. Thus improved varieties developed for one part of the zone are likely to perform successfully in other, similar parts of the zone.

Mainland Southeast Asia—centered in Thailand, Laos, and Cambodia—forms another zone. This region is more ecologically diverse and unique than eastern South Asia. Scientists have had little success so far in introducing foreign germplasm as replacements for the array of cultivars grown in this zone. The nature of this unique adaptation is not well understood.

A third integrated region comprises the islands and coastal areas of Southeast Asia. This zone includes Malaysia, coastal Vietnam, and the island countries of Indonesia and the Philippines. Cultivars have been shared successfully throughout this zone.

The definition of ecogeographical zones has not been rigorously tested. It is based, however, on considerable experience. It is particularly useful in research on biological stresses because insect biotypes and pathogen races frequently vary between regions. It also provides a useful framework for regional collaborative projects. The Rainfed Lowland Rice Research Consortium, for example, is focusing on two major regions: South Asia (located in eastern India) and Southeast Asia (located in Thailand) (IRRI 1993). The characteristics of local rice cultivars are explored further in Chapter 2.

Socioeconomic factors

In most rainfed lowlands, a single crop of rice is produced each year, and no other crops are planted before or after the rice crop. This cropping pattern is typical of the less favorable subecosystems, where long-duration, photoperiod-sensitive cultivars prevail.

As population density increases, farm size decreases, markets change, and new technologies are adopted. Farmers are pressured to use the land more intensively, even in less favorable areas. Those who have opportunities to add upland crops to their systems may have to change the varieties or cultural practices they use for their rice crop so they can manage both.

In many areas, the need to intensify cropping has encouraged farmers to switch to photoperiod-insensitive rices. Because these varieties can be harvested after a certain number of days, rather than only at a certain time of year, they facilitate double cropping of rice (Denning 1985).

The change to greater land use intensity often forces farmers to increase their expenditure for labor and capital. For example, an insensitive variety that ripens during the rainy season may be difficult to harvest; farmers must then use alternate, more costly methods to dry and store their harvest.

Rice ecosystems include the people who interact with the land. The perceived needs and preferences of the rice consumers and the cultural practices of the rice farmers are, therefore, critical factors in rice improvement. For instance, farmers are particularly concerned with grain quality in areas where, due to environmental stress, yields are difficult to increase. While farmers in these areas may not be able to increase their incomes by marketing more grain, they may be able to gain a comparative advantage in the marketplace by producing superior quality grain. Thus rice breeding programs must consider human preferences and practices of the target area for which a variety is being developed. Grain quality as an issue in rainfed rice improvement is covered in Chapter 10.

Tools for understanding rainfed environments

Breeders of rainfed lowland rice must have a solid understanding of the ecosystems of the target areas for which they are developing varieties, but environmental information may not be conveniently available. In many cases, they must gather this information themselves through direct interaction with farmers of the target area.

Practical, cost-effective tools have been developed for systematically gathering and interpreting critical information about ecosystems. Two of the most widely used approaches are *rapid rural appraisal* (Carruthers and Chambers 1981) and *agroecosystems analysis* (Conway 1986). Both were developed to aid researchers in diagnosing problems and identifying new, productive topics for research.

The rapid rural appraisal method helps researchers to elicit information from farmers. The researcher conducts open-ended interviews guided by a set of precise questions. The discussion generated by the questions provides insight into local knowledge and farmers' perspectives. For instance, farmers are keenly aware of differences in land characteristics and consider these differences when deciding to adopt or reject new cultivars (Morris et al 1986). Researchers need to elicit from farmers, through careful discussion, what varietal characteristics they consider desirable and why. Only then can breeders direct their efforts to producing varieties that will be appropriate and acceptable.

An example of rapid rural appraisal techniques applied to rainfed lowland rice has been presented by Fujisaka (1990b). Teams of researchers asked farmers to classify their environments and identify the associated production problems and potentials. They also asked about the farmers' management of inputs and outputs. The teams met daily to synthesize data and identify the research issues for subsequent interviews. Findings from each day were added to an evolving data set. Interviews with 100-300 farmers of five countries led to a better understanding of factors that influence varietal choice and associated management practices for different environments.

Agroecosystems analysis, an interdisciplinary technique, systematically compiles and interprets information about key aspects of an agricultural system (Conway 1986). To use this tool, a researcher does not need to have any specialized knowledge—only sharp observational and analytical skills. The strength of this activity is the framework it provides specialists of different disciplines to examine the whole agricultural system rather than focus on their areas of specialty. It may be especially helpful in identifying niches for existing cultivars and specifying the characteristics needed in the cultivars to be developed.

Rapid rural appraisal and agroecosystems analysis are local-level tools. To understand rainfed rice environments at the regional and national levels, a researcher must rely on some form of map technology. Thematic maps have been developed for display, overlay, and analysis on computers. *Geographic information systems* are now widely available and will be used increasingly by crop improvement programs to map and analyze environmental variations. For further information about these systems, consult the work of Borrough (1986).

Chapter 2

The cultivars

Traditional rainfed lowland cultivars number in the tens of thousands. They represent hundreds—possibly thousands—of years of evolution and selection for adaptation to their environment. Of the traditional varieties preserved in germplasm collections, some are no longer grown, having been replaced by newer varieties; many others, however, are still in use.

Over the past three decades, traditional lowland varieties generally have been rejected as sources of breeding material because their yield potential is limited even under favorable growing conditions. Breeders of rainfed lowland rices, however, need to embrace the traditional variety as an example to be emulated: it has enabled farmers to survive in inhospitable environments. Its shortcoming is that it cannot sustain an ever increasing population on a finite land base. In attempting to remedy that fault, breeders must seek to preserve its many desirable attributes.

How *Oryza* evolved

The evolution and taxonomy of the genus *Oryza* is complicated and controversial. It is beyond the scope of this book to explore its history in detail, but the following background helps to explain the diversity of and relationships among rice cultivars. Comprehensive treatment is available in Oka's *Origin of cultivated rice* (1988).

The genus *Oryza* comprises more than 20 species (Vaughan 1989). The basic haploid chromosome number is 12; and six genomes—designated A through F—have been identified, encompassing the diploids AA, BB, CC, EE, and FF and the tetraploids BBCC and CCDD.

The two cultivated species were domesticated independently: *O. sativa* L. in Asia and *O. glaberrima* in Africa. Both cultivated species and their progenitors have the same genome—AA. The wild ancestor of the Asian species (*O. rufipogon*) is distinct from that of the African species (*O. barthii*).

In the area that extends from the foothills of the Himalayas to the hilly regions of northern Thailand, Laos and southern China, a remarkable diversity of rices is cultivated. Scientists such as Chang (1976) and Oka (1988) consider this to be the area in which rice was domesticated. Second (1982), however, contends that rice was domesticated in the lowlands of China and South and Southeast Asia, and diversity accumulated in the intermediate hilly area.

Chang proposed that cultivated Asian rice was domesticated from an annual ancestor, *O. nivara.* Oka contended that the progenitor was more likely a perennial, *O. rufipogon,* because perennials offer greater genetic variability than do annuals. Since there is a general perennial-annual continuum, the two species probably are not biologically separate; but, because wild populations have been declining rapidly and the current populations probably differ from the ancestral populations, this issue is difficult to resolve. Domestication has involved selection for traits such as higher harvest index, increased self-pollination, reduced grain shattering, uniform seed maturity, and diversity of response to photoperiod (Oka 1988).

Wild populations of rice generally have greater genetic diversity than cultivated rices, as measured by isozyme polymorphism. Evidence favors gene flow between wild and cultivated rices. The common weedy rices, often termed red rice because of their pericarp color, probably are the result of such gene flow. These weedy rices are considered pests in many areas.

In Madhya Pradesh, India, purple-pigmented cultivars are used to help remove wild rices from the fields. Farmers periodically plant the purple varieties and then weed out all plants that are not purple. Prolonged use of this method could be expected to result in cross-pollination and the development of purple weedy rices. Oka (1988) found some evidence supporting such color transfer.

Wild rice is still harvested in some areas. In parts of India, it commands premium prices during the festival season (Fig. 2.1).

2.1. Women harvesting wild rice in Madhya Pradesh, India.

How subspecies are classified

All cultivated Asian rices belong to the same species. Understanding the classification of these rices into subspecies is of central importance to rice breeders: the classifications indicate cultivars' adaptation to specific environments and, therefore, influence breeders' strategies for utilizing the germplasm.

Rice scientists in Asia noticed that rice cultivars could be grouped into two basic types (reviewed by Oka 1988). The terms *indica* and *japonica* (corresponding to the Chinese terms *hsien* and *keng*) are widely used to distinguish these two types. For a while, the bold-grained rices of the Philippines and Indonesia were considered by many to be a third ecotype and were called *javanica.* Oka (1958), however, had earlier shown that the morphological and physiological characteristics of japonica and javanica types were essentially indistinguishable.

While the indica and japonica subspecies cannot be differentiated unambiguously by a single character, a combination of characters gives clear results (Table 2.1). The use of isozyme loci confirmed indica and japonica as the two major groups, with most upland and javanica cultivars falling into the japonica group (Second 1982). Intermediate cultivars also were observed.

A major isozyme study by Glaszmann (1987) surveyed 1,688 traditional Asian rice cultivars from the collection of the International Rice Germplasm Center. He examined the varieties for variation at 15 polymorphic isozyme loci via starch gel electrophoresis. Glaszmann's analysis confirmed the existence of two major subspecies, corresponding to the traditional indica and japonica classifications, and revealed four additional, smaller groups of varieties intermediate or peripheral to the two larger groups (Table 2.2).

Table 2.1. Characters used to classify varieties into two groups: indica or japonica (Oka 1958).

Character	Mode of variation	Typical reaction	
		Indica	Japonica
Phenol reaction	Discontinuous	Positive	Negative
KC10, resistance	Discontinuous	High	Low
Cold sensitivity	Discontinuous	High	Low
Drought resistance	Discontinuous	High	Low
Number of days to germination	Rather discontinuous	Low	High
Degree of seed shedding	Rather discontinuous	High	Low
Spikelet length-width ratio	Discontinuous	Higher	Lower
Apiculus hair length	Rather discontinuous	Lower	Higher
Awn length	Rather discontinuous	Shorter	Longer
Digestion of endosperm in KOH solution	Continuous	Easy	Hard
Hardening of endosperm	Continuous	Shorter	Longer
First internode length	Continuous	Short	Long

Table 2.2. ***Oryza sativa*** **L. classification by isozymes.**

Group	Designation	Description
I	Indica	Tropical cultivars, mostly lowland and deepwater; a few Asian upland cultivars; large, diverse group
II	Aus	Mostly very early cultivars from eastern India and Bangladesh; usually direct seeded; red pericarp
III		Rare group found only in Bangladesh; short duration
IV	Rayada	12-mo-duration. deepwater varieties grown in flood-prone regions of Bangladesh; strongly photoperiod-sensitive with long basic vegetative stage
V		Rices spread from Iran to Myanmar; usually characterized by high-quality grain; often slender grain with aroma and elongation when cooked
VI	Japonica Javanica Upland	Large group; dominant in temperate areas; Tropical examples include most upland varieties and javanica or bulu varieties

Source: Adapted from Glaszmann 1987.

Group VI represents traditional japonica cultivars. Javanica and most upland cultivars fit clearly into this group. Genetic distances between groups indicate that groups II and III show an affinity to group I (indica), and groups IV and V to group VI (japonica).

Cheng (1985) analyzed intermediate groups according to six traits: glume hairiness, phenol reaction, interval between first and second node of panicle axis, glume color at heading, leaf pubescence, and length-width ratio of spikelets. He found that many of the rices classified as intermediates by isozyme analysis could be grouped into the indica and japonica classifications; some intermediates remained, however.

Analyses using DNA markers such as restriction fragment length polymorphism (RFLP) have confirmed the existence of the two major groups (indica and japonica). In a survey using 10 RFLP markers, members of each isozyme group except group II clustered together; group II was split into two groups (Wang and Tanksley 1990). The smaller groups (II through V) usually are included in one of the two larger groups (I or VI) when cultivars are classified with DNA markers. For example, isozyme group II cultivars can be considered a subgroup of indica rice.

Isozyme analysis has reduced the ambiguity in designating racial types of Asian rice. The method, described in detail by Glaszmann et al (1988), makes it possible to determine a variety's isozyme group in a couple of weeks through a survey of five diagnostic isozyme loci. The classification terms used throughout this book correspond to isozyme classifications of Table 2.2.

There is some dispute over the origin of the two major subspecies of cultivated rice. Oka (1988) maintained that the indica-japonica differentiation is inherent in all wild rices because plants with both indica and japonica characteristics can be selected from the same weedy population and thus, he asserted, the indica-japonica divergence occurred during the process of domestication. He presumed that selection of indica or japonica characteristics is related to adaptation to environmental conditions. Second (1982) theorized that the large differences between the two subspecies, measured by isozymes or DNA markers, indicate that the divergence predated domestication. He has argued for independent domestication of the two subspecies: the japonica rices evolving in China and the indicas in South and Southeast Asia.

Traditional upland rices were thought, at first, to belong to the indica group because they originated in the tropics. Morphological, physiological, isozyme, and DNA-marker data, however, place them (along with javanica or *bulu* rices) in group VI. They are sometimes referred to as *tropical japonica* rices. Sato (1987) distinguished the two types according to morphological characteristics (Table 2.3). Glaszmann and Arraudeau (1986) showed that, based on morphological characteristics, temperate rices and Indonesian javanicas are at opposite extremes of a continuum that includes all japonica and javanica varieties. The rices of the hilly areas of South and Southeast Asia were at the midpoint of this continuum. Studies at the DNA level would be expected to differentiate the types more clearly. Sano and Sano (1990) noted that the two groups of japonicas were clearly differentiated by heterogeneity of the intergenic spacer region of DNA coding for ribosomal RNA.

Morphological and molecular diversity between groups I and VI is high, with differences at many loci. The indica-japonica divergence is important to breeders seeking varietal improvement because hybrids tend to be sterile. The major mechanism of sterility appears to be genic, and both one- and two-gene models have been proposed. lkehashi and Araki (1986) proposed a one-gene model, with the typical indica allele (S_5^i) and the japonica allele (S_5^j)

Table 2.3. Characters differentiating tropical and temperate japonica types (Sato 1987).

Character	Tropical japonica	Temperate japonica
First internode (mesocotyl) length, reared in dark	Long	Short
Digestion of endosperm in KOH	Easy	Difficult
Spikelet length-width ratio	Large	Small
Culm length	Long	Short
Panicle length	Long	Short
Panicle number/plant	Few	Many
Culm diameter	Thick	Thin
Flag leaf	Long, broad	Short, narrow
Basic vegetative period	Long	Short
Second leaf length	Long	Short

causing abortion of the female gamete when present in the heterozygous state. The F_1 generation of a typical indica × japonica cross will be semisterile, with about 50% of the spikelets not being fertilized. Several cultivars, however—mostly tropical japonicas—have a wide compatibility allele and, thus, produce fertile hybrids when crossed with indicas or japonicas. These cultivars are being used to develop indica-japonica hybrid rice in China and other countries.

Despite the presence of a gene with major effect, the sterility relationships among the groups are complicated (Oka 1958, Second 1982, Sano 1993). Indica × indica crosses and japonica × japonica crosses can produce sterile progeny, though indica hybrids rarely have high sterility rates. Aus rices may be partially sterile when crossed to indica rices; however, aus × japonica crosses usually have higher sterility rates. Crosses between the aromatic rices of group V and indicas usually produce progeny with high sterility.

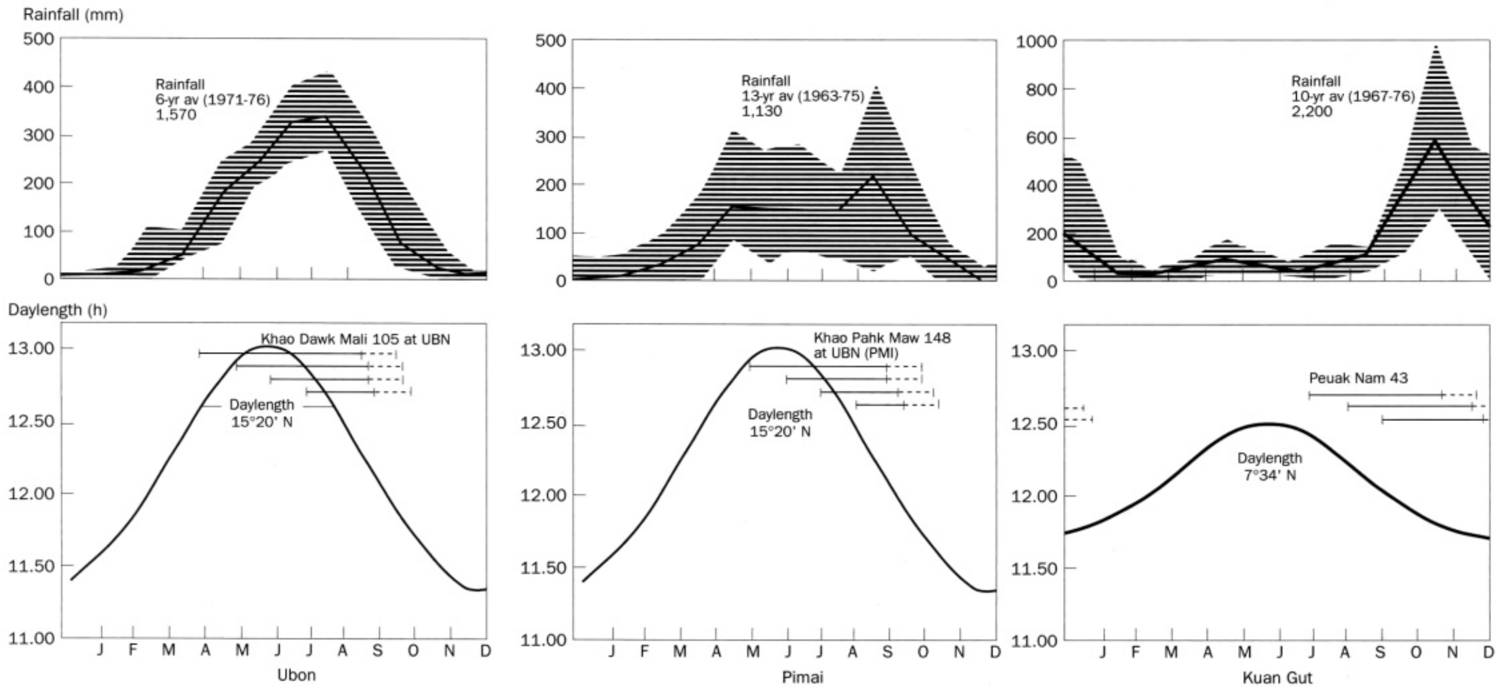
What traditional varieties have in common

The traditional rainfed lowland rices of Asia are predominantly group I (indica) cultivars. Some group II (aus) varieties have been classified as rainfed lowland rices, but these varieties usually are grown under typical upland conditions: dry seeding with growth in predominantly aerobic soils. Although they can be considered upland cultivars, they are closer to the indica group than to the japonica group by isozyme classification. Many of the group V cultivars, which are characterized by slender (and often aromatic) grains, are grown in the rainfed lowlands of eastern India, Bangladesh, and Myanmar.

Rainfed lowland rices are diverse, as later sections of this chapter show. Many of them, however, have the following features, which make them attractive components of unfavorable rainfed lowland environments.

Photoperiod sensitivity

Most traditional rainfed lowland rices are sensitive to photoperiod. Some that are weakly sensitive are grown where short-duration types are needed. Because photoperiod-sensitive cultivars flower at about the same date, regardless of seeding date, using such cultivars assures that the crops will be ready for harvest at the optimum time—after the peak rainfall period has passed and climatic conditions are favorable for the harvested grain to ripen and dry. Because the plants do not have a fixed growth period, the farmer has flexibility in choosing appropriate seeding and transplanting dates according to the availability of water or labor. When traditional photoperiod-sensitive rices are seeded before August or September, the seedlings can remain in the seedbed for 2 mo or more without a significant reduction in yield. Flowering dates, determined mostly by the critical daylength (see Chapter 4), differ widely between cultivars. Pushpavesa and Jackson (1979) showed that flowering dates for varieties adapted to different regions of Thailand are closely associated with rainfall patterns (Fig. 2.2).



2.2. Relation between rainfall distribution, daylength, and flowering dates of photoperiod-sensitive rice varieties grown at three locations in Thailand (Pushpavesa and Jackson 1979).

Plant height

Almost all traditional rainfed lowland rices are tall; that is, their height exceeds 140 cm. Tall plants with long leaves are favored in flood-prone areas because they are better able than short plants to survive submergence (see Chapter 6). Tall plants also are less stunted than short plants by drought and soil stresses. Further, they are more competitive with weeds than are modern semidwarfs.

While tall plants have these advantages, they also have serious productivity constraints. Most importantly, they are susceptible to lodging, and this tendency to lodge becomes more severe when soils are highly fertile or waterlogged (Fig. 2.3, see Chapter 3). It is said that some Thai farmers prefer tall varieties because they do not have to stoop to harvest them. Under favorable growing conditions, however, these tall varieties often lodge, so the farmer has to stoop to harvest them anyway (Fig. 2.4).

Yield stability

Traditional cultivars are both specifically and widely adapted to their environments.

A specifically adapted cultivar has characteristics that are appropriate for its particular growing environment. For example, its flowering date is related to the rainfall pattern and water regime of the area, and it is adapted to stresses that vary from region to region and field to field.

Widely adapted cultivars are grown over wide areas, having overriding traits—such as drought resistance, excellent grain quality, high yield, or tolerance for delayed transplanting—that make them popular with many farmers. Most popular cultivars have stable yields; that is, they can produce sufficient yields even under extremes of the conditions found in rainfed lowlands. This stability may be manifested as low variability over years (a characteristic considered critical by farmers) or low variability across locations (see Chapter 13). The two types of stability often are related and are due to the varieties' tolerance for stress.

Yield components

Generally, rice varieties can be categorized as high tillering with large numbers of panicles (*panicle number* types) or low tillering with fewer but larger panicles (*panicle weight* types). Modern semidwarf irrigated rices tend to have the highest tillering; tropical japonicas such as upland and bulu rices tend to be the lowest tillering; most traditional rainfed cultivars fall somewhere between these extremes. Thus, they tend to have lower tillering and larger panicles than modern irrigated rices, an important consideration for breeders seeking to develop modern rainfed lowland cultivars (see Chapter 3).

Grain size varies widely among traditional rainfed cultivars and is probably not a major determinant of yields. Many high-quality group V cultivars have extremely small grains, while high-quality Thai cultivars (group I) have very large grains (see Chapter 10).

2.3. A tall, traditional variety (foreground) lodges under increased nitrogen fertilizer, while a shorter variety (background) does not.

2.4. Harvesting tall, traditional varieties can be laborious when lodging is severe.

Disease and insect resistance

Traditional rainfed lowland varieties have been selected for performance under low-input management in areas where disease and insect pressure usually is not severe. Generally, these cultivars are resistant to the predominant pests; however, they can become susceptible when management or cropping systems are changed. For example, the incidence of rice blast increases when nitrogen levels increase.

The disease and insect resistance of traditional varieties varies. Some traditional varieties have served as donors of disease-resistance genes in rice breeding programs.

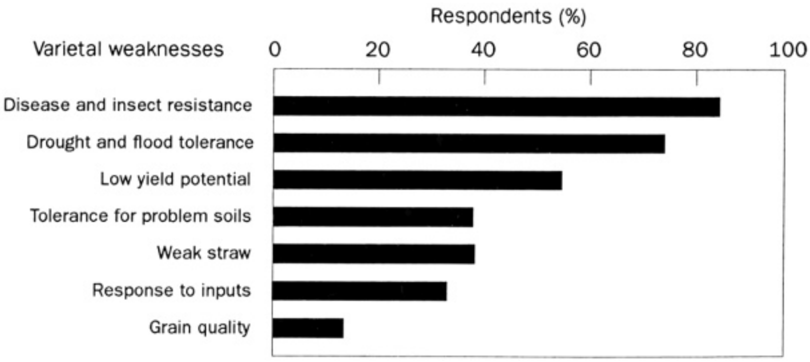
When Mackill (l986) asked rice breeders of South and Southeast Asia to rank the weaknesses of rainfed lowland cultivars currently grown in their areas, lack of disease and insect resistance emerged as the most significant shortcoming (Fig. 2.5).

How new data can be gathered

As germplasm has been collected, scientists have developed detailed descriptors for every morphological characteristic. These descriptors, though they are laborious to record, are useful for characterizing germplasm accessions.

Applied breeding programs can obtain data that are more pertinent to their needs by screening the germplasm collection for traits needed in the target area. For rainfed lowland rice breeding programs, the most relevant accessions are those that tolerate drought, submergence, and adverse soils.

Many important varietal characteristics, however, are not easily detected through large-scale germplasm screening:



2.5. Plant breeders' assessment of major weaknesses of varieties grown in rainfed lowland areas (Mackill 1986).

- wide adaptation,
- high yield,
- yield stability,
- tolerance for delayed transplanting,
- widely acceptable grain quality,
- acceptable performance in infertile soils, and
- suitability for direct seeding.

These traits, which determine farmers' adoption of rainfed lowland cultivars, are not clearly associated with striking morphological or physiological characteristics. Thus data about a rainfed lowland variety's desirable traits are best gathered from the farmers themselves.

Whenever possible, such data should be collected directly through interviews of farmers. Their intimate knowledge of local varieties can help breeders identify varietal constraints that could be alleviated through breeding and can assist in selecting promising parents for hybridization. For example, interviews conducted in the valleys of the central highlands of Madagascar revealed submergence to be a major stress in the area and identified the most promising varieties of the area for further improvement through hybridization (Fujisaka 1990a). And surveys conducted by Fujisaka (1990b) in the rainfed lowlands of five countries identified the varietal traits sought by farmers: high yields for all cultivars, drought tolerance and short duration for varieties to be grown in upper fields, and submergence tolerance for varieties to be grown in lower fields. From these results, Fujisaka learned that, if improved varieties were to be developed to replace the traditional varieties of the area, different varieties would be needed for upper and lower fields that were adapted to the differing conditions.

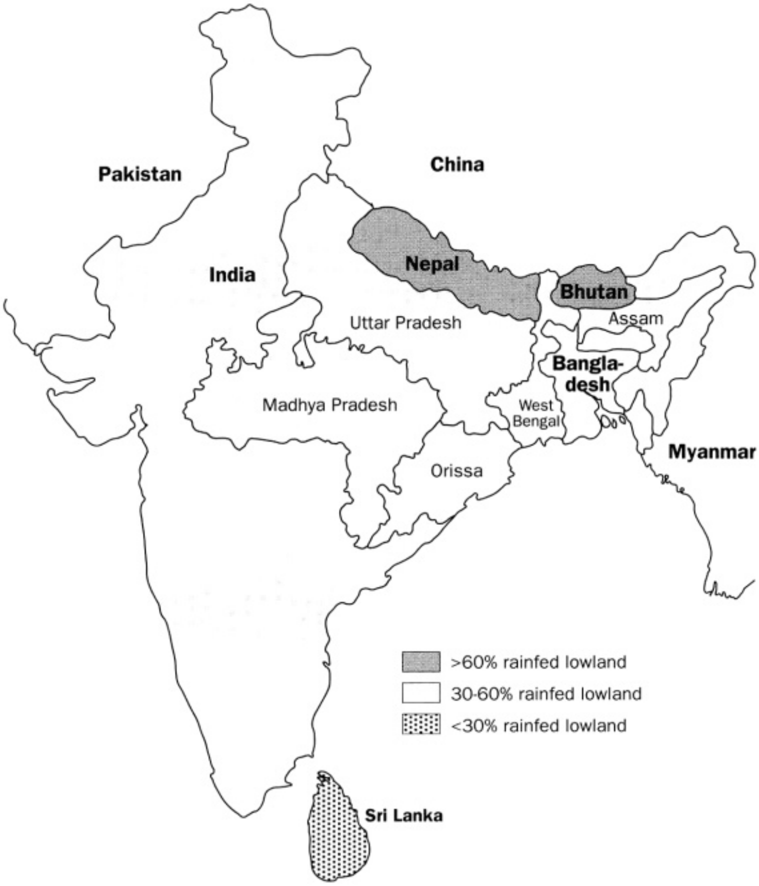
The work loads of most plant breeders, however, limit the time they can devote to exploring farm conditions in the target area. These breeders can rely on workers trained in rapid rural appraisal techniques to collect data about the extent and distribution of local and improved cultivars—an excellent means of identifying promising parents.

Examples of traditional South Asian varieties

Most traditional rainfed rices have limited geographical distributions; their ranges of adaptation often are confined to a state or country. Therefore, traditional cultivars can be described by region.

The great number and diversity of rainfed lowland cultivars warrant much more detailed coverage than is within the scope of this book. Monographs, such as one by Richharia (1966), describe traditional rice varieties in detail. This chapter considers only the most popular cultivars and those whose special attributes make them especially valuable to breeding programs.

In South Asia, the major concentration of rainfed lowland rice is in the eastern and northeastern portions of India and Bangladesh (Fig. 2.6). The major rainfed lowland belt includes the Indian states of Uttar Pradesh



2.6. Map of South Asia with percentage of area covered by rainfed lowland rice for each country.

(eastern), Bihar, Madhya Pradesh, Orissa, West Bengal, and Assam and the contiguous areas of southern Nepal and Bangladesh. Although they are generally considered to be outside the major rainfed belt, Sri Lanka and the southern Indian state of Tamil Nadu are home to some important rainfed lowland cultivars. The differences between upland, rainfed lowland, and deepwater rices often are not well delineated (see Chapter 1). More than 5 million hectares of upland rice are grown in this region in areas of high topography where moisture often is limiting. In most of this area, fields are direct seeded with very short-duration rices of isozyme group 11. The *gora* rices of the Chotanagpur plateau of Bihar and the *aus* rices of West Bengal and Bangladesh (also called *ahu* in Assam) are part of this group. These rices have exceptionally short duration—some can be harvested less than 80 d from seeding—and they have remarkable seedling vigor, which is essential in these intensely weed-competitive environments.

While the aus rices are usually considered to be upland varieties, their early vegetative vigor may make them useful as parents in rainfed lowland breeding programs, especially for areas in which fields are direct seeded. This group, however, has several undesirable characteristics:

- Their stems are weak, so the plants tend to lodge in fertile and moist soils.
- They tend to be more susceptible to blast than japonica upland rices.
- They seem to combine poorly with varieties of isozyme group I.

Most of the typical rainfed lowland rice of the region is grown in the river plains and delta of the Ganges-Brahmaputra river system extending from eastern Uttar Pradesh state in India to Bangladesh and including the terai of southern Nepal. Widely adapted rainfed lowland cultivars of eastern Uttar Pradesh include T9 and T100. N22 is a popular upland cultivar that also may be grown in shallow, drought-prone lowland environments.

Br8 is a widely adapted, photoperiod-sensitive variety of Bihar state that tolerates stagnant flooding at depths up to 50 cm. Br34, an early-flowering photoperiod-sensitive rice, is suitable for drought-prone rainfed lowland conditions. The variety Janki (formerly called 64-117), a selection from a local variety, was released for areas that are intermittently flooded. It is tall and tolerates both drought and submergence. The local selection TCA 72 is similar to Janki and has better grain quality. Sughandha is a group V photoperiod-sensitive cultivar with aroma. Both upland and rainfed lowland rices are common in the plateau area of southern Bihar. Brown Gora and Badsh Psand are popular varieties; Badsh Psand is both direct seeded and transplanted. Kalamdan is a popular lowland variety in the region.

The germplasm collection from Madhya Pradesh state in India is large, indicating the number and diversity of local varieties. Much of the area sown with traditional photoperiod-sensitive rices, however, is dominated by two cultivars. Safri 17 is the most popular—a hardy variety that does well under the harsh conditions of Madhya Pradesh. It has intermediate amylose content, good milling recovery (few broken grains), and is known for its drought resistance. It is grown under the direct seeded *biasi* or *beusani* system (see Chapter 1), and its strong photoperiod sensitivity allows it to flower on schedule, even when seeding is late due to delayed rains. The other popular variety, Dubraj, has lower yields than Safri 17 but is aromatic. In Madhya Pradesh, photoperiod-sensitive cultivars are seeded around 15-20 Jun and must flower by 15 Oct to avoid being damaged by low temperatures or drought. The Gurmatia rices are traditional photoperiod-insensitive cultivars that have bold grains, suitable for puffed rice (*poha*). Nagkesar is a typical purple variety planted to aid in weeding out green wild rice.

Some traditional varieties that are popular in Orissa state are Padmakesasi, Jhili, T141, T90, and SR26B. In the stagnant-flooded, medium-deep areas, T1242 and BAM6 are popular. Two selections from local cultivars, FR13A and FR34B, have become well known for their submergence tolerance. FR13A is one of the most outstanding cultivars for submergence tolerance of all varieties tested by IRRI (see Chapter 6).

Assam and West Bengal states of India and Bangladesh have similar designations for their main cropping seasons. Short-duration rices are direct seeded in the aus season (*ahu* in Assam); that is, they usually are seeded in March and April and harvested in July and August. Some of the aus crop may be transplanted and, therefore, would be considered shallow rainfed lowland rice (Miah et al 1986). Photoperiod-sensitive cultivars are transplanted or broadcast during the aman season (*sali* in Assam). In many areas, they are transplanted after the aus crop is harvested. Aman season fields in Assam are categorized according to water depth:

Category	Depth
Sali	Shallow rainfed lowland, the largest area
Asra	Deepwater (less than 1 m)
Bao	Very deepwater or floating

The dry season or boro crop usually consists of photoperiod-insensitive rices. Traditional cultivars are sown in low-lying areas where water remains after the rainy season. Modern varieties, now accounting for much of the boro crop, are irrigated.

Because of the diversity of Assam's rice cultivars, the Assam Rice Collection has become famous. (Members of this collection usually are identified by the prefix *ARC* followed by an accession number.) Of the traditional sali varieties, Monoharsali is the most popular because it is widely adapted and tolerates delayed transplanting; however, many other varieties also are grown (Table 2.4).

In West Bengal state and Bangladesh, rainfed lowland rice usually is referred to as *transplanted aman* (T. aman), and deepwater rice is called *broadcast aman* (B. aman). Some deepwater rice may be transplanted, however; and some of the rainfed lowland rice is direct seeded, especially in West Bengal. All traditional aman rices are photoperiod sensitive (Table 2.5). Their sensitivity can be classified as weak (such as DA31), intermediate (such as Latisail), or strong (such as Nizersail) (Ahmad 1979). Nizersail is the most popular traditional cultivar in Bangladesh. Because of its strong photoperiod sensitivity, it flowers on schedule and is ready for harvest before the onset of low temperatures or drought, even when it is transplanted late, after the harvest of an aus crop. In early November, almost all Nizersail fields are flowering; the variety's lax panicle is the striking feature of the T. aman landscape. Nizersail is reputed to be the same as the Indian cultivar GEB24, which was introduced to Bangladesh from Nigeria. GEB24 is a selection from the local Tamil Nadu cultivar Konamani.

Sri Lanka and southern India also have several important rainfed lowland varieties. Photoperiod-sensitive rices that respond to the small daylength changes of low-latitude Sri Lanka are grown during the *maha* season (August to February). Varieties such as Panduru Wee and Podiwee A8 normally flower in January and are harvested in February. Varieties such as Deveredderi and the salt-tolerant Pokkali rices are grown in stagnant flooded areas. Many rainfed lowlands of Sri Lanka are subject to flash floods (Jayawardena 1979); and traditional cultivars from these areas, such as Thavalu, Goda Heenati, and Kurkaruppan, have been excellent sources of submergence tolerance.

In Karnataka, traditional photoperiod-insensitive cultivars of about 135 days' duration (such as Halubbalu, Giddabyra, and Doddabyra) are grown in *Punaji* cultivation. That is, seed is broadcast in dry soil at about 100 kg/ha before the rains; the fields are irrigated later when sufficient rainfall has accumulated in ponds. For additional information about rice cultivars from

Table 2.4. Examples of rainfed lowland rice cultivars of Assam, India.

Name	Characteristics
Aborsali	Some flood tolerance
Biroi	Sali; some flood tolerance
Bordubi	Tolerates delayed transplanting well
Gobindabhog	Sali; high yields; fine grain
Lothasali	Coarse grain (that is, lower quality)
Manona Sali	Tolerates late transplanting
Misi	Sali; for medium lands
Monoharsali	Most popular traditional sali variety: tolerates late transplanting and low temperatures at reproductive stage
Prasadbhog	Can withstand delayed transplanting
Saragphala	Sali; some flood tolerance
Sialsali	High yielding
Solpona	Sali; some flood tolerance

Table 2.5. Popular (or once popular) photoperiod-sensitive transplanted aman rices of West Bengal, India, and Bangladesh.

Name	Characteristics
Badshabhog	
Batraj	Short duration
Biroi	High quality (unscented)
BR5	Blast-resistant selection from Badshabhog; aromatic; short-round grain with elongation
DA31	Very short duration
Dudmona	Tidal wetlands: late maturity
Garcha	Tidal wetlands
Getu	Salinity tolerance
Girmi	Tidal wetlands
Jhingasail	Good grain quality: wide adaptation
Kachamota	Tidal wetlands
Kalamadari	Tidal wetlands
Kataribhog	High quality (aromatic, short-slender grain); resistant to tungro virus
Karalsail	Grown in saline zone
Kumragoir	Tidal wetlands; long duratain
Latisail	Wide adaptation; 15 d earlier than Nizersail
Meghi (IET9003)	Submergence tolerance
Nizersail	Wide adaptation: tolerates delayed transplanting: long duration (flowers early in November)
Patnai 23	Tidal wetland: long-slender grain: grown in saline belt
Rajasad	Very short duration: tidal wetlands: grown in saline belt
Tilokkachari	Low-lylng areas: long duration

southern India, see Richharia (1966), Balakrjshna Rao and Biswas (1979), and Mohanty et a1 (1984).

Examples of traditional Southeast Asian varieties

Rainfed lowland rice is concentrated in the floodplains and deltas of the large river systems and inland valleys of continental Southeast Asia (Fig. 2.7).

Myanmar (formerly known as Burma) is dominated by the rainfed lowland ecosystem; thus many of its traditional cultivars are rainfed lowland varieties. These cultivars can be classified by maturity (Grant 1957):

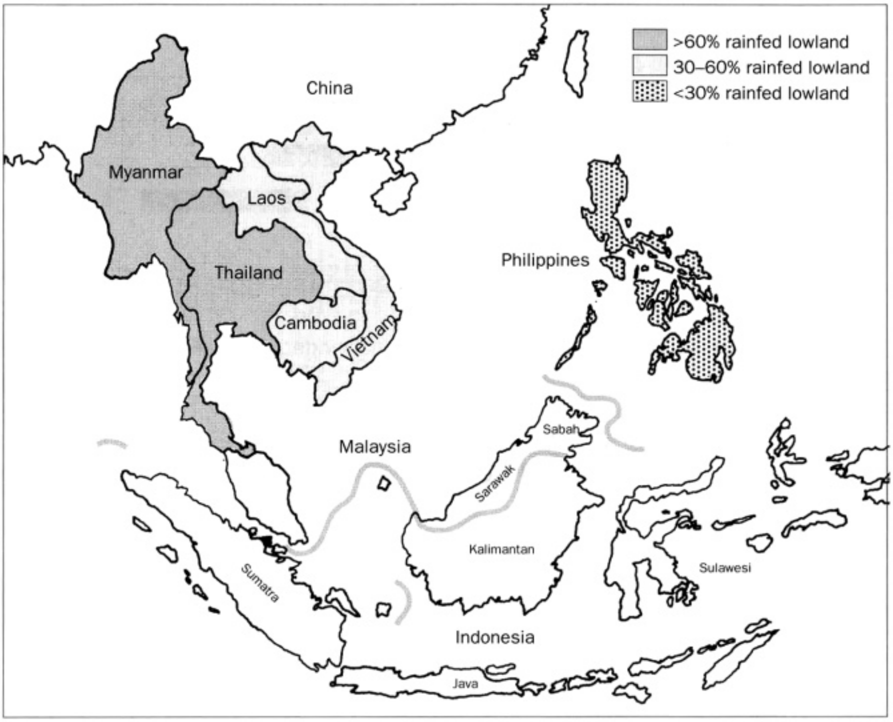
Maturity classification	Duration	Season
Kaukyin (early)	140-150 d	Harvested late October
Kauklat (medium)	150-170 d	Harvested late November
Kaukkyi (late)	170-200 d	Harvested early December
Mayin (spring)	140-150 d	Grown November to March

More varieties fall into the kauklat and kaukkyi classifications than into the kaukyin and mayin; and, together, kauklat and kaukkyi cultivars account for most of the rainfed lowland rice crops in Myanmar. The kaukkyi varieties are planted in areas that have deeper standing water.

Myanmar has a number of important rainfed lowland cultivars (Table 2.6). One of the most interesting is Ngwetoe, which is a rare example of a short (apparently semidwarf) photoperiod-sensitive cultivar. It can be planted in low-lying areas, it does not lodge, and it is responsive to inputs (Kyaw and Escuro 1979).

In Thailand, the government recommends for each region photoperiod-sensitive varieties that flower at the appropriate time (Fig. 2.8, Table 2.7). Farmers in the northern and northeastern regions grow many of the same varieties. In these areas, glutinous rice is grown primarily for consumption and nonglutinous rice primarily for market. Niaw Sanpatawng formerly was the dominant glutinous cultivar. Reputed to be a waxy mutant from the nonglutinous variety Leuang Yai 148, it flowers late (26 Oct) and is adapted to low-lying areas. It is being replaced, however, by the variety RD6, which has excellent grain quality and is well adapted to the problem soils of northeastern Thailand. Khao Dawk Mali 105 is the dominant nonglutinous variety in both the north and northeast. Because its grain quality is excellent (low amylose; desirable aroma; long, translucent grains), it is favored for export. It is drought-resistant and tolerates phosphorus-deficient, saline, and acid-phosphate soils. RD6 is an induced mutant of Khao Dawk Mali 105.

Many short-duration, photoperiod-insensitive (or weakly sensitive) cultivars are grown in northeastern Thailand. Notable among these is Nam Sagui 19, a nonglutinous variety with some tolerance for drought and salinity. Longer duration varieties such as Khao Pahk Maw 148 and Khao Tah Haeng 17 are popular in the Korat plateau of the northeastern region.

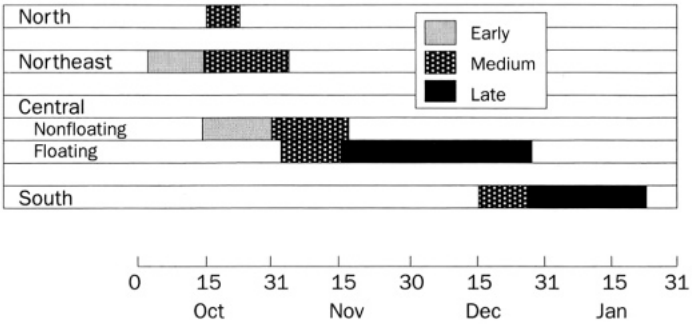


2.7. Map of Southeast Asia with percent of area covered by rainfed lowland rice for each country.

Table 2.6. Examples of traditional lowland rices of Myanmar.

Name	Characteristics
Hnan Wa Mee Gauk	Good quality
Hnanga	Short duration, traditional variety of delta area; export quality
In Ma Ya Baw	Popular in low-lying areas; high yielding; strong stems; good quality
Meedomhmwe	Excellent grain quality (especially grain elongation)
Meegauk	Export quality
Ngakywe (black)	Popular; excellent grain quality (aroma); long duration
Ngwetoe	Short-statured. photoperiod-sensitive
Pawsanhmwe	Excellent grain quality
Phokawgyi	Medium-long duration
Shwe Chi Gym	Low but stable yields: poor quality
Shwedinga	Export quality
Shwetasoke	Popular; high yielding

In Thailand's central plains, late-flowering varieties are favored because floods come later to the Chao Phrya Delta than to the northern and north-eastern regions. One of the most popular and widely known varieties, Leuang Pratew 123, normally flowers early in November. Because of the



2.8. Range of flowering dates of government-recommended varieties for the main rice-growing regions in Thailand (Pushpavesa and Jackson 1979).

Table 2.7. Government-recommended, tall, photoperiod-sensitive varieties of Thailand, by region (Awakul 1980).

Region	Name	Average harvest date	Endosperm type	Year of release
Northern	Muey Nawng 62M	20 Nov	Glutinous	1959
	RD6	21 Nov	Glutinous	1977
	Khao Dawk Mali 105	25 Nov	Nonglutinous	1959
	Leung Yai 148	25 Nov	Nonglutinous	1968
	Niaw Sanpatawng	26 Nov	Glutinous	1962
Northeastern	Hahng Yi 71	4 Nov	Glutinous	1968
	Nam Sagui 19	4 Nov	Nonglutinous	1968
	RD6	21 Nov	Glutinous	1977
	Khao Dawk Mali 105	25 Nov	Nonglutinous	1959
	Niaw Sanpatawng	26 Nov	Glutinous	1962
	Khao Pahk Maw 148	3 Dec	Nonglutinous	1965
Central plains	Gow Ruang 88	21 Nov	Nonglutinous	1962
	Nahng Mon S-4	26 Nov	Nonglutinous	1956
	Khao Pahk Maw 148	3 Dec	Nonglutinous	1965
	Leuang Pratew 123	11 Dec	Nonglutinous	1965
Southern	Puang Rai 2	6 Feb	Nonglutinous	1968
	Nahng Prayah 132	16 Feb	Nonglutinous	1962
	Peuak Nam 43	22 Feb	Nonglutinous	1968

rainfall and flooding patterns in southern Thailand (Fig. 2.2), local varieties flower late and are harvested in February.

The rainfed lowlands of Laos are contiguous to those of northeastern Thailand, across the Mekong River; so growing conditions and varietal choices in the two areas are similar. Almost all local varieties are glutinous. About 30% of the area is planted with short-duration varieties, which are weakly sensitive or insensitive to photoperiod. They are harvested early, when the supply of rice is low; thus they replenish depleted stocks and provide some security against damage to long-duration varieties by late-season drought. The longer duration photoperiod-sensitive varieties flower near the end of October.

In the rainfed lowlands of Cambodia, the dominant rice varieties are photoperiod sensitive and of long duration (Table 2.8), flowering from mid-November to mid-December. Many local cultivars are popular with farmers. Varietal choice usually reflects the water regime: Long-duration varieties are grown in low-lying areas, where flooding is deeper and more prolonged than in higher areas (Fujisaka 1988).

The two main rice-growing areas of Vietnam—the Red River Delta in the north and the Mekong Delta in the south—have greatly different growing conditions. The main photoperiod-sensitive crop, called *mua,* flowers earlier in the north (Fig. 2.9). *Late mua* usually refers to deepwater rice, which is common, particularly in southern Vietnam. Some of the traditional photo-period-sensitive varieties of southern Vietnam can produce yields of 5-6 t/ha and have good grain quality. Late-flowering rices grown near the Cambodian border tolerate acid sulfate conditions.

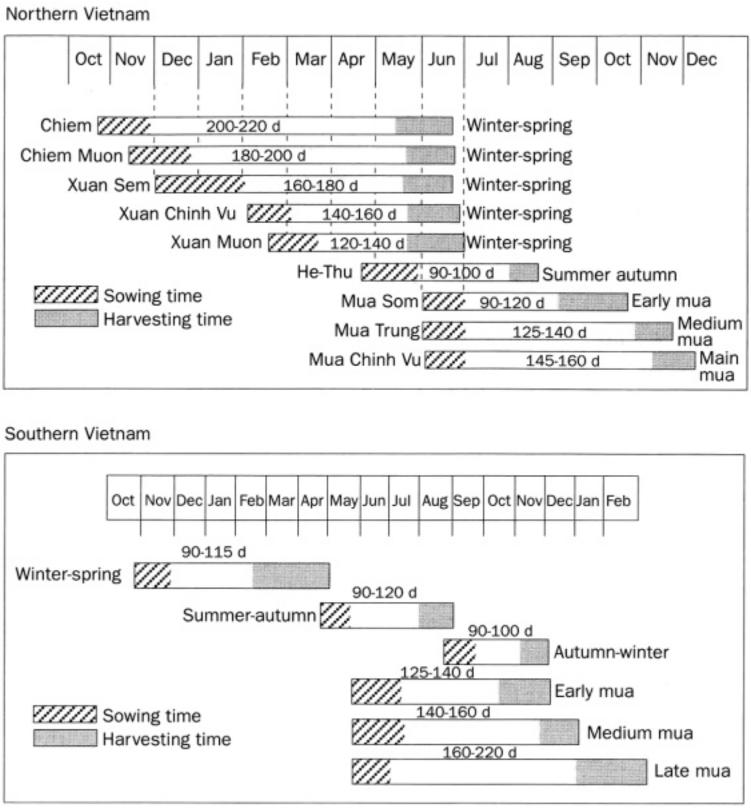
Many of the traditional Malaysian varieties have been replaced by modern cultivars. The traditional varieties are strongly sensitive to the small changes in daylength associated with low latitudes. In Sabah (eastern Malaysia), a tremendous diversity of local photoperiod-sensitive rices still are grown. Some of these varieties have growth durations of more than 180 d and usually are harvested from December to March.

In the Philippines, also, most of the traditional rainfed lowland varieties have been replaced by modern cultivars. As in southern Thailand and Malaysia, local varieties are photoperiod sensitive and tend to flower late (December to January). The Wagwag varieties of the Cagayan Valley of northern Luzon are some of the longest duration photoperiod-sensitive rices in the world: they flower later than the varieties of southern Thailand, Malaysia, and Sri Lanka. They are adapted to the rainfall pattern of most of the Philippines, where monsoons usually extend into January. These Wagwag rices tend to be hardy and vigorous, giving consistently good yields under adverse conditions. Similar varieties such as Lameo, Matsupal, and Okinawa are grown in other low-lying areas of Luzon.

Table 2.8. Varietal classes used in Cambodia (Fujisaka 1988).

Rice culture type	Area planted (ha) 1985	1986[a]	Remark
Early season	80,000	399,000	All photoperiod-sensitive types
Medium season	250,000		
Late season	1,000,000	937.000	
Deepwater	160,000	121,000	
Irrigated dry season	160,000	161,000	Modern varieties or traditional varieties in receding water
Total	1,650,000	1,618,000	

[a] Note: In 1986, 399,000 ha Includes early and medium; data were obtained from different sources.



2.9. The main rainfed lowland rice seasons in Vietnam (Ro and Hoang 1986).

Traditional varieties of Indonesia included tjereh (indica types), bulu (fully awned javanicas), and gundil (partly awned or awnless javanicas). Most have been replaced by modern cultivars. The rainfed lowland cultivars are predominately tjereh.

Traditional varieties still are grown in some unfavorable rainfed lowlands. In southern Sumatra and southern Kalimantan, some traditional varieties are used in the *lebak* system in low-lying areas in the dry season. In this system, plants are transplanted two and, in some cases, three times. Photoperiod-insensitive cultivars are used (Catling 1992).

Examples of popular modern varieties

Because the development of improved cultivars is a continuous process, any comprehensive survey would soon be outdated. Yet some improved cultivars have had a major impact on rainfed lowland rice production, and these examples can be important to rice breeders in formulating strategies for varietal improvement. Here, the term *improved cultivars* generally refers to those that differ from the traditional plant type. (However, for instance, the tall, photoperiod-sensitive cultivars developed to replace local varieties can be considered *improved*.)

Paramount among improved rainfed lowland varieties is Mahsuri, one of the most widely grown rice cultivars in the world. The Food and Agriculture Organization of the United Nations sponsored a large indica × japonica crossing program centered at Cuttack, India, in the early 1950s. The objective of this program was to introduce characters such as responsiveness to fertilizer and sturdy (nonlodging) culms into the tropically adapted indica germplasm. F_2 populations from some of the crosses were grown in Malaysia in 1958 (Samoto 1965). After selection of progeny for better performance under improved management, a breeding line from the cross Taichung 65/ Mayang Ebos 80*2 was released as Mahsuri in 1965. (Taichung 65 was the high-yielding japonica parent; Mayang Ebos 80 was a tall indica variety from Malaysia.) Of the few varieties resulting from this indica × japonica crossing program, only Mahsuri was widely adopted.

The phenomenal success of Mahsuri was unexpected by plant breeders. While originally intended to be an irrigated variety, it was not appropriate for high-input conditions. Because it was tall and had long, yellowish leaves, it did not appear to represent the new plant type sought by rice breeders (Jennings 1964). In fertile soils, it lodged severely, and the grains often germinated on the panicle. Plant breeders were slow to recognize its virtues because it consistently performed poorly at Los Baños and other Philippine sites. Many eastern Indian breeders, likewise, were unimpressed after its introduction.

The Mahsuri variety was spread almost entirely by the farmers themselves. It was not strongly promoted by major research institutions because it was bred outside the rainfed lowland belt of eastern India and Bangladesh. Although it was released in Malaysia, it achieved its greatest success in the eastern Indian states of Uttar Pradesh, Bihar, Assam, Orissa, and West Bengal; in the terai of Nepal; and in Bangladesh and upper Myanmar. It also is cultivated in southern India; and it probably would have been successful in Thailand if it had not had short grains. (Thais prefer long-grained rices.) The success of Mahsuri proves that rainfed lowland varieties can be widely adapted.

Mahsuri's popularity is attributed to several characteristics including, primarily, its productivity under low inputs. It is not responsive to nitrogen fertilizers; but in infertile soils it almost always outperforms both traditional and modern varieties. It seems to be adapted to some adverse soils, particularly acid lowland soils, perhaps because of its tolerance for phosphorus deficiency (Chaubey et al 1994). It has a highly desirable grain type: slender grains and good cooking quality. It is weakly photoperiod sensitive (about 150-170 d growth duration) and performs well under delayed transplanting. It can tolerate water depths of up to 70 cm during its later growth stages.

Breeders have cited its weak photoperiod sensitivity as a hindrance to more widespread adoption. Traditional photoperiod-sensitive cultivars are still preferred where adverse water conditions cause frequent, prolonged delays in transplanting. If seeded and planted too late, Mahsuri flowers and ripens after the optimum time. Its susceptibility to blast, especially in the seedbed, is a serious problem in cool areas such as Nepal. Mahsuri also is susceptible to bacterial blight, and it can be damaged by both drought and submergence. (Nevertheless, it often is grown in drought- and submergence-prone areas because it is productive under low inputs and farmers are reluctant to apply fertilizer in these risky areas.) It lacks dormancy, and its grains tend to sprout on the panicle when rainfall is heavy or the crop is severely lodged. Despite its obvious drawbacks, many farmers prefer not to replace it with higher yielding alternatives.

While no other improved rainfed lowland cultivar has achieved the widespread success of Mahsuri, several have succeeded regionally, particularly where rainfed lowland conditions are more favorable. Many of these successful cultivars were byproducts of breeding programs directed to irrigated or highly favorable rainfed lowland conditions.

A striking example is Pankaj, released from a sister line of IR5 in India. Pankaj's plant type is excellent for rainfed lowland conditions. Selected from the cross Peta/Tangkai Rotan, it has intermediate plant height without a semidwarf gene. It does not lodge, its growth duration is long (about 150 d), and it produces excellent yields in the monsoonal climates of South Asia. It has been grown widely in eastern India, usually in areas that do not have serious water control problems.

IR20, a long-duration cultivar developed mainly for resistance to stem borer, was popular in the rainfed lowlands of southern and eastern India, although its planted area has decreased in recent years. It was nicknamed Irrisail in Bangladesh, the *sail* suffix indicating its suitability for the T. aman crop.

Bangladesh breeders developed BR4 from the cross IR20/Pankaj in 1979. BR4 has shown excellent adaptation to T. aman conditions in Bangladesh and has consistently performed well in international rainfed lowland nurseries. It has the favorable plant type of Pankaj and long duration with weak response to photoperiod. It can tolerate moderate submergence and delayed transplanting. BR4 (and the related cultivars BR10 and BR11) replaced many of the traditional varieties grown in the aman season in Bangladesh.

Indian breeders developed Jagannath, a short mutant of the popular cultivar T141, in 1969 (Mohanty et al 1984). It has the photoperiod sensitivity of the parent and does not lodge, being only about 100 cm tall. The long-duration cultivar CR1014, developed from a cross between an indica variety (T90) and a bulu (Uran Urangan), has been popular in many areas of eastern India. Other photoperiod-sensitive cultivars with improved plant types that have been released in eastern India include CR1009 (Sabitri) in Orissa and Jogen in West Bengal.

Several varieties emanating from IRRI's breeding program have been successful in rainfed lowlands. IR5 and IR20 already have been mentioned. IR36 has been successful in some drought-prone areas that require short-duration varieties. It has excellent disease and insect resistance and is particularly well adapted to direct seeding, as in the *gogo-rancah* system used in Indonesia. Its longer duration sister line IR42 also has been successful. IR46 and IR48 both had excellent adaptation to rainfed lowland conditions but achieved limited success. IR52 was released specifically for rainfed lowland conditions, It inherited drought resistance from the Thai cultivar Nam Sagui 19; however, its susceptibility to blast limited its adoption.

Using germplasm collections

Obtaining seed of local varieties usually presents few problems; however, obtaining seed of exotic varieties may be more difficult. The best source for such cultivars is the research station or national improvement program of the country or province of origin. If seed is not available from these sources, the International Rice Germplasm Center (IRGC) at IRRI can provide seed.

Accessions of this germplasm bank are routinely screened at IRRI and other sites for traits such as resistance to biological and physicochemical stresses, grain quality, and important morphoagronomic characters. Breeders can request accessions that excel in any of these characters and can generally be assured the seed that is distributed comes from the same source as the seed that was screened.

Sometimes, a breeder is interested in obtaining seed of a variety that is known to have a specific characteristic—for example, a variety that was reported in a published paper to be submergence tolerant. Requesting the seed by name may produce unexpected results. Many accessions in the germplasm bank are sent in by individuals without being examined in advance by trained germplasm workers. These individuals may make mistakes in identification, and those mistakes sometimes are not detected. Furthermore, farmers may use the same name for several varieties or use several names for the same variety. Accessions that have the same name but obviously different morphological or other characters are maintained under different accession numbers; therefore, it is advisable to request all accessions of the variety to increase the chance that the strain of interest is included. And, since the name of a variety may be spelled several ways (for example, *Latisail, Latisali, Lattisail, Lati Sail*), it is wise to list possible alternate spellings in the request for samples. In some cases, the samples may be identical—they were merely collected at different times or by different researchers. In other cases, they may differ due to variability within the cultivar or other causes.

The IRGC will supply about 5-10 g of seed of each variety for research purposes. Thus the seed must be multiplied (and purified if necessary) if the variety is to be evaluated in several replications or trials.

Chapter 3

Agronomic traits

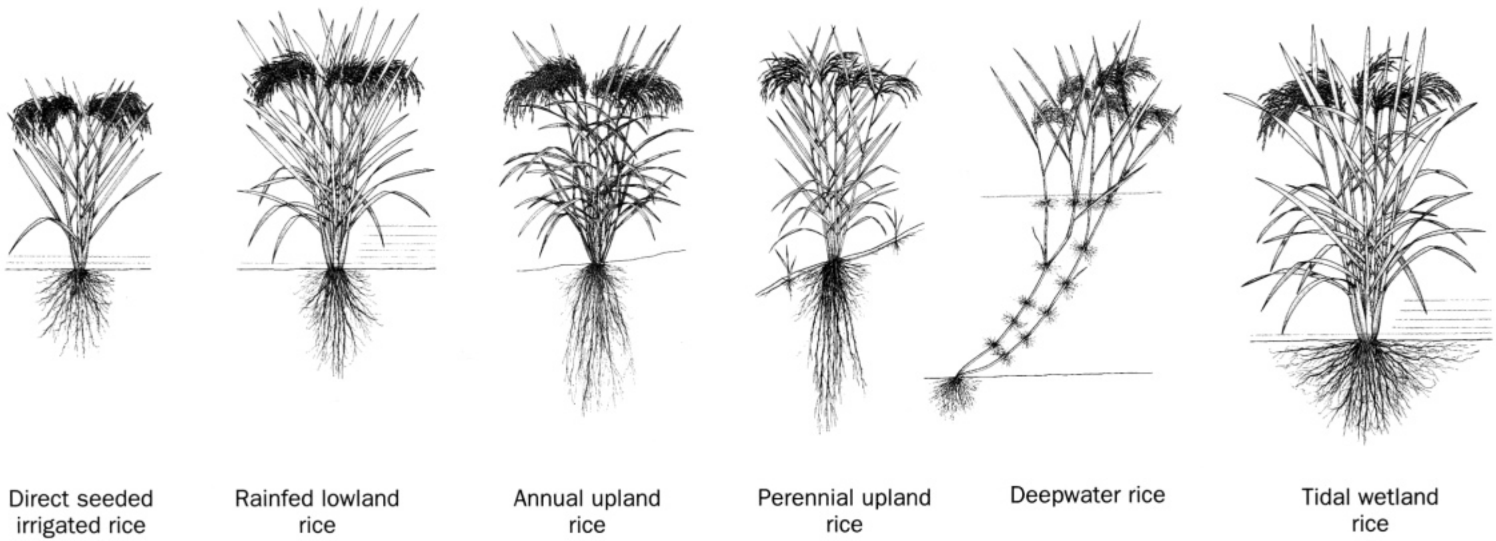
The fundamental concern of rice breeders is producing varieties with superior yields. Breeders therefore are concerned with agronomic traits—the morphological characteristics that make a plant suitable for a particular production method or growing environment—because those traits are related to yield.

Sometimes, however, breeders get caught up in the pursuit of the ideal plant type. They become distracted by the aesthetic appeal of the breeding line or cultivar and fail to give sufficient attention to the plant's potential to be productive in farmers' fields. Conversely, some breeders tend to reject cultivars that have unappealing physical characteristics, even though some aesthetically unattractive varieties are popular among farmers and highly productive, In fact, breeders and farmers often find different plant characteristics appealing. A prime example is the cultivar Mahsuri, which appeared to breeders to have many undesirable features (tall stature, weak stems, yellowish leaves, brown hulls) but was widely accepted by rainfed lowland farmers because it tended to have higher yields than their traditional cultivars and had a preferred grain type.

Different agronomic traits are needed for each type of rice culture. In fact, IRRI (1989c) has identified sets of morphological characteristics that are appropriate for each of the major types of rice culture—irrigated, rainfed lowland, upland, deepwater, and tidal wetland (Fig. 3.1)—and has targeted its rice breeding programs to developing varieties with these characteristics.

For irrigated rice, the search for an improved indica plant type dominated breeders' efforts in the early 1960s, with most breeders using the highly productive Japanese japonica cultivars as models for the new tropical rices (Jennings 1964). Because widespread attention and effort were concentrated on irrigated rice, a consensus developed within the scientific community about what morphological characteristics were needed to produce high yields in the irrigated environment.

So far, rainfed lowland rice has not been the focus of such attention. Scientists disagree about what constitutes the optimum plant type for rainfed lowlands, and too few data have yet been collected to resolve the conflict. Most breeders concerned with producing varieties for this environment have carefully observed traditional cultivars and speculated about how closely they can be made to resemble irrigated cultivars without losing their adaptation to rainfed lowlands. In the future, much more attention must be given to identifying the morphological characteristics that confer higher, more stable yields under rainfed lowland conditions.



3.1. Rice plants of the future: optimum plant types for the major types of rice culture as envisioned by IRRI (IRRI 1989c).

Nanda and Coffman (1979a) developed a list of "base characteristics" needed in all rainfed lowland rices. A slightly modified version of that list follows:

- moderately high yield potential,
- intermediate height,
- sturdy culms,
- moderately long, erect leaves,
- moderate to high tillering,
- large panicles with many grains,
- complete panicle exsertion,
- low tiller mortality, and
- sufficient grain dormancy to prevent preharvest sprouting.

Other characteristics also are needed under certain conditions:

- seedling vigor,
- early vegetative vigor,
- leaf sheath and blade elongation, and
- tolerance for delayed transplanting.

Most of the characteristics in these two lists are discussed in the following sections. Grain dormancy, however, is covered in Chapter 10.

For a comprehensive description of the morphological characteristics of rice, see *The morphology and varietal characteristics of —the rice plant* by Chang and Bardenas (1965).

Yield and yield stability

In developing improved cultivars for rainfed lowlands, the breeder must seek to raise yields and make them more stable. One issue that complicates breeding for rainfed lowlands is determining what constitutes a realistic yield for these areas. A variety's yield under rainfed lowland conditions almost always will be lower than under irrigated or otherwise optimum conditions because of the many constraints in rainfed lowlands:

- stresses related to shortages and excesses of water,
- nutrient stress,
- low solar radiation (because rainfed lowland rice is grown during the rainy season), and
- high night temperatures.

Low solar radiation and high night temperatures, combined, severely limit yields for areas of the tropics where rainfed lowland rice is grown during the monsoon (Seshu and Cady 1984) (see Chapter 1).

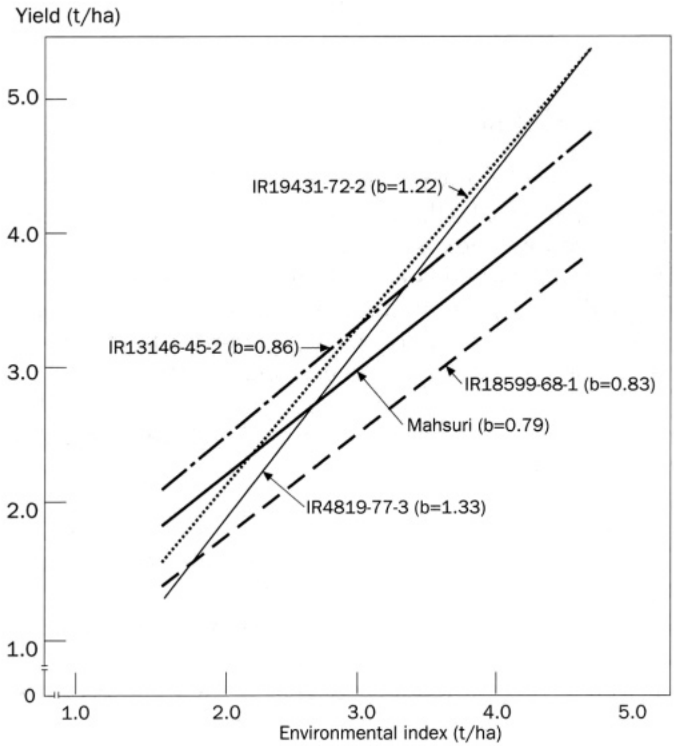
Due to these constraints, the target yield for most rainfed lowland rice crops must be lower than for most irrigated rice crops, and breeders can be more flexible in selecting for plant type. That is, the traits associated with high yields under irrigated conditions—short stature; narrow, erect leaves; high tillering—are less important under rainfed lowland conditions.

In developing varieties for rainfed lowlands, breeders must be less concerned with maximum yield under optimum conditions than with yield stability. A variety that has stable yield is one that maintains its productivity under unfavorable conditions. Yield stability can be measured by growing a variety at several locations and then regressing its yield at each location onto the mean yield of all varieties grown at that location (Fig. 3.2). Varieties that have lower regression coefficients (b<1) are more stable than varieties that have higher regression coefficients.

A variety usually has a stable yield when it is able to resist the environmental stresses that limit productivity. Traditional rice cultivars are noted for their high yield stability; however, this quality often is associated with low yield potential. Breeders aim to increase yields while maintaining yield stability.

In rainfed lowlands, rice farmers use little or no fertilizer. Traditional cultivars are well suited to soils that have low fertility; in fact, they do not respond well to higher soil fertility.

The higher yields of improved rices usually are obtained by using modestly higher levels of inputs than are typical of traditional cultivation systems. The improved cultivars are not generally accepted by farmers, however, unless they are at least as productive as traditional varieties when environmental stresses limit yields. In other words, they must have higher yield potential and equal or better yield stability in comparison with traditional varieties to be preferred by farmers.



3.2. Regression of the yields of five rice lines on mean site yields for 24 varieties included in the 1983 International Rainfed Rice Shallow Water Yield Nursery. Varieties that have lower regression coefficients (b) are considered to be more stable (Seshu 1986).

Plant height and lodging resistance

Many rainfed lowland farmers prefer traditional varieties because they are taller than modern semidwarf cultivars. (Traditional varieties usually are taller than 140 cm; modern semidwarf cultivars are shorter than 120 cm.) Farmers have found that taller plants usually are better able to compete with weeds and tolerate environmental stresses.

Most rice breeders, however, believe plants with intermediate height (120-140 cm) are most appropriate for rainfed lowlands (Mackill 1986) because they tend to be more resistant to lodging and have higher harvest indexes than taller plants. Both of these qualities are related to the plant's response to nutrients, particularly nitrogen. Traditional cultivars respond to increases in nitrogen with excessive vegetative growth, which makes them more susceptible to lodging; and lodged plants have reduced yields.

Lodging can be especially severe under *medium-deep* conditions (Fig. 3.3). As the water level rises, tall plants tend to elongate rapidly at the basal internodes; then, as the water recedes, the elongated plants topple over (Balakrishna Rao et al 1971, Lim and Yamamoto 1978, Srivastava and De 1982). The widely grown cultivar Mahsuri, for example, is particularly prone to lodging due to elongation of the lower internodes (Taniyama et al 1988). Shorter rice cultivars usually elongate less at the basal internodes (IRRI 1964) and, thus, probably are more lodging resistant under these conditions.

3.3. Tall varieties tend to lodge in this medium-deep rainfed lowland nursery at IRRI. Deep water (40-50 cm) promotes rapid internodal elongation. When the water is drained, the elongated plants lodge.

Shorter rice cultivars usually have higher harvest indexes than taller varieties. (Harvest index is the ratio of grain yield to total dry matter.) When traditional cultivars are grown in fertile soils, they become leafy—they use the extra nutrients to produce more dry matter but not more grain. Modern rices, on the other hand, usually use the extra nutrients to produce more grain rather than more vegetative material (Evans et al 1984).

Semidwarf rices have higher harvest indexes than rices of intermediate height (Yoshida 1977) and, therefore, have higher yields. These cultivars, however, are less able than intermediate-height plants to compete against weeds and resist stresses. In areas such as rainfed lowlands, where maximum yields are 6 t/ha or less, intermediate height is not a disadvantage (Yoshida 1977). Indeed, in the international rainfed lowland trials, which generally do not include tall cultivars, plant height has been positively correlated with yield (Seshu 1986). Rainfed lowland breeding programs should concentrate on developing stress-resistant intermediate-height rices, as these will be suitable for most if not all rainfed lowland conditions.

Plant height is controlled by both major and minor genes. The recessive semidwarf gene *sd-1* has been used extensively to develop improved irrigated rices, and some other semidwarf genes have been used to some extent. In addition to these major genes, genes of lesser effect, often termed *modifying genes,* affect plant height. For example, some varieties that have a semidwarf gene also have modifying genes that result in plants of intermediate height. (Other intermediate-height cultivars, such as Pankaj and IR5, do not have a semidwarf gene.) In crosses involving a semidwarf gene, the F_2 population includes plants that segregate 3 tall to 1 semidwarf. The tall and semidwarf plants resemble the two parents in height, although there is some variation within each type. In crosses that do not involve a semidwarf gene, plant height behaves as a typical quantitative trait. The trait has a continuous distribution in the F_2, so the breeder can select progeny with a range of heights.

Strong competition in bulk populations may obscure the potential height of plants. That is, if a tall parent was included in the cross, intermediate-height plants may appear to be stunted. Care must be taken not to discard these plants before they can be evaluated more realistically: In later-generation progeny rows, competition is less intense because height is not segregating, so plants are better able to achieve their potential. In crosses that are segregating for photoperiod sensitivity, the height of sensitive plants is strongly influenced by growth duration, which depends on daylength: longer duration plants are taller (see Chapter 4).

Even when plant height is under simple genetic control, it is affected by environmental conditions. An intermediate-height cultivar may seem too short for typical rainfed lowland conditions if it is grown under water- or nutrient-related stress; and a line that is too short for rainfed lowlands may seem to have intermediate height if it is grown in an especially fertile nursery plot.

Besides plant height, the literature (IRRI 1964, Wang and Hoshikawa 1991, Ookawa and Ishihara 1993) mentions other factors that contribute to lodging resistance, such as

- thickness of the culm wall,
- diameter of the culm,
- amount by which the internodes are overlapped by the leaf sheaths, and
- density of lignin.

Under most rainfed lowland conditions, short to intermediate stature should confer sufficient lodging resistance. Under *medium-deep* conditions, however, even semidwarfs may lodge. Unfortunately, strong selection for lodging resistance under these conditions may result in reduced yield because plants with lower yields are less prone to lodge. Thus yield and lodging resistance should be selected for simultaneously.

Scores for lodging resistance usually are based on visual inspection (Table 3.1). The scores are affected, however, by the growth duration of the test entries. That is, short-duration entries tend to lodge more easily than long-duration entries, especially if they flower while rainfall is abundant. Therefore, lodging scores should be compared only for entries of similar duration.

A more objective measure of lodging resistance is bending resistance (O'Toole 1984). Many breeders evaluate bending resistance by bending the culm halfway over, releasing it, and observing the speed with which it returns upright (Jennings et al 1979). In *medium-deep* trials at IRRI, Amante and Mackill (l988) found that plants with high bending resistance were much less likely to lodge than those with low bending resistance.

Table 3.1. System for scoring lodging resistance and culm strength (IRRI 1988d).

Type of score	Score	Description	Characteristics
Lodging resistance	0		No plants are lodged
	1		Less than 20% of plants are lodged
	3		20-40% of plants are lodged
	5		41-60% of plants are lodged
	7		61-80% of plants are lodged
	9		More than 80% of plants are lodged
Culm strength	1	Strong	No plants are bending
	3	Moderately strong	Most plants are bending
	5	Intermediate	Most plants are moderately bending
	7	Weak	Most plants are nearly flat
	9	Very weak	All plants are flat

Vegetative vigor and leaf characteristics

Seedling and vegetative vigor (rapid leaf elongation and abundant tiller production) are useful characteristics in most rice-growing environments but are especially important in rainfed lowlands.

In direct seeded rainfed lowland ricefields, weed competition is intense. When water is scarce, nonvigorous genotypes can be overcome completely by weeds. The direct seeded aus and gora rices of eastern India and Bangladesh are some of the most vigorous rice cultivars in the world. They can compete with weeds even during droughts. In transplanted crops, too, vegetative vigor helps rice plants to compete against weeds.

In rainfed lowlands, rice often must be transplanted into fields that are flooded as deep as 30 cm. To survive in these fields, seedlings must be tall—a difference in height of just 10 cm can mean the difference between survival and death (Bhattacharya and Vergara 1979). Seedling height has proved to be related to submergence survival in many trials at IRRI. Both seedling height and vegetative vigor are closely and positively related to mature plant height, which implies that it may be difficult to combine shorter stature with seedling vigor. Cultivars such as Chandina of Bangladesh, however, are known to be vigorous at the vegetative stage even though they are short at maturity (Nanda and Coffman 1979a).

Data on seedling vigor are available from the International Rice Observational Nursery. Many short and intermediate-height lines have excellent seedling vigor when measured over many locations. The cultivar BG850, with an average height of 100 cm, had the best score in IRON in 1988 (IRRI 1989b).

Scoring for seedling and vegetative vigor is partially subjective, taking into account factors such as (Jennings et al 1979)

- rate at which the seedling emerges,
- rate at which the seedling increases in height,
- length and erectness of leaves, and
- number of tillers.

Early vegetative vigor may be related to germination rate, a trait that varies greatly among rice cultivars (Krishnasamy and Seshu 1989). Usually, vigor is scored about 40-50 d after germination (Table 3.2). Seedling vigor also can be scored in the seedbed just before transplanting.

Characteristics of the leaves, particularly the flag leaf, are closely associated with high yields in irrigated rice. According to Jennings et al (1979), plants with narrow, erect leaves produce the highest yields under irrigated conditions because such leaves do not shade one another. Some breeders have advocated narrow, erect leaves for rainfed lowland conditions also (Balakrishna Rao 1973), but others have recommended long, droopy leaves (Nanda and Coffman 1979a). So far, few hard data are available to support either of these views. Although plants with long, droopy leaves may not produce the highest yields under optimum irrigated conditions, they may be appropriate for rainfed lowlands: since the leaves are long, the plants may be

Table 3.2. System for scoring seedling vigor (IRRI 1988d).

Score[a]	Description	Characteristics
1	Extra vigorous	Very fast growing; majority of seedlings have two or more tillers at five-leaf stage
3	Vigorous	Fast growing; majority of seedlings have one or two tillers at the four- to five-leaf stage.
5	Normal	Seedlings are at the four-leaf stage
7	Weak	Seedlings are somewhat stunted, having three to four leaves; no tillers have formed: population is thin
9	Very weak	Seedlings are stunted and leaves are yellowing

[a]Note: A cultivar's rating depends on how long after seedling or transplanting scores are taken.

better able to survive submergence (see Chapter 6); and since the leaves are droopy, the plants may be better able to intercept sunlight at early growth stages (Yoshida 1977).

Nevertheless, breeders for rainfed lowlands should try to develop improved lines with diverse leaf characteristics because it is difficult to determine in advance what leaf architecture is best suited to a certain growing environment.

Yield components and panicle characteristics

Grain yield is the result of several components that are determined at various stages in the growth of rice (Yoshida 1981):

Yield component	**Determined during**
number of panicles per m^2	tillering
number of spikelets per panicle	panicle differentiation and development
percentage of filled spikelets	meiosis, anthesis, and early ripening
mean grain weight	ripening

While changes to each component can affect yield, the correlations between the components are highly negative. It is possible, for instance, for a cultivar to have a low number of panicles and yet be high yielding because it compensates by having a high number of spikelets per panicle.

Number of panicles

De Datta (1981) emphasized that the number of panicles per square meter is an important determinant of rice yields. Although panicle number varies between varieties—and within the same variety grown under differing conditions—the optimum number for transplanted, high-yielding varieties is about 300 panicles / m^2 (Yoshida 1981). For direct seeded rice, the optimum number could be as high as 600 panicles/m^2 (Yoshida 1981). For rainfed lowland rice, no firm data are available on optimum tiller number. Considering the lower yields of rainfed lowland rice, the optimum probably would be lower than for irrigated rice.

In transplanted rice, panicle number is determined largely by tillering ability; thus breeding cultivars that can produce large numbers of tillers has become an important objective for both irrigated and rainfed lowland programs (Jennings et al 1979, Nanda and Coffman 1979a). Yoshida (1981) asserted, furthermore, that high tillering ability is more important when environmental conditions are poor—as they are in most rainfed lowlands—than when they are optimum. Mahapatra and Reddy (1982) concluded that reduced tillering is a major cause of lower yields in *medium-deep* conditions.

While abundant tillering is generally considered important for most rice-growing environments, some evidence indicates that excessively high tillering, as found in many indica semidwarf varieties, may not be optimum for rainfed lowland conditions. For example, Srivastava (1984) found that high tillering may not be necessary for rainfed lowland cultivars to be productive, even in *medium-deep* areas. At IRRI, no relationship has been found between yield and tiller number under *medium-deep* conditions, even though varieties differed significantly for tiller number (Amante and Mackill 1988). High tillering ability may actually be a disadvantage during drought because not enough water may be available to support the development of many panicles per square meter. Many widely grown rainfed lowland cultivars compensate for lower tiller number with larger panicle size. Breeding for large panicles has thus been seen by many rainfed lowland breeders as a more important objective than breeding for abundant tillering. Large panicles also have become an increasingly important goal in breeding for higher yields in irrigated rice, particularly when that rice is direct seeded (Akita 1989, Dingkuhn et al 1990, IRRI 1990).

Number of spikelets

Some breeders of rainfed lowland rice prefer to develop cultivars that have moderate tillering ability but produce large panicles with many grains per panicle (*panicle weight* types) rather than cultivars that produce many tillers and many small panicles (*panicle number* types). Their rationale incorporates the following observations:

- Panicle weight types often are preferred by farmers who harvest individual panicles rather than plants.
- Panicle weight types may be less affected than panicle number types by certain stresses such as drought.
- Panicle weight types may have a higher ratio of productive to unproductive tillers than panicle number types.
- Panicle weight types are less likely than panicle number types to produce late tillers. Because cultivars that produce late tillers are more likely to have underdeveloped root systems, they generally are less able to resist drought.

While large panicle size is a desirable breeding objective, breeders should avoid being too rigid in selecting for panicle and tillering characteristics. A range of plant types is preferable for advanced yield testing because more information can be derived from such a range about the plant characteristics that are optimum for the target area.

Percentage of filled spikelets

The percentage of filled grains is determined largely by the number of spikelets that are fertilized and the ability of the plant to fill the fertile spikelets. Environmental stresses such as drought, salinity, low and high temperatures, and low solar radiation increase the number of unfilled grains. Lodging also can increase unfilled grains, especially if it occurs before flowering. Under normal growing conditions, the percentage of filled grains usually is high and is not a major factor affecting yield (Yoshida 1981).

Grain size and weight

Grain size or weight varies widely among rice cultivars. When a certain grain weight becomes an objective of a breeding program, it usually is because of consumers' preferences, not because of any relationship between grain weight and yield.

Grain weight is related to hull size, which is determined during panicle development; however, environmental conditions after flowering (such as temperature) determine the extent to which the grains are filled. Recently, scientists have been giving greater attention than in the past to grain density or weight per volume. Some morphological characteristics, such as predominance of primary panicle branches and low tillering ability, are associated with higher percentages of high-density grains (IRRI 1987). While grain density is difficult to select for in a breeding program, efforts are being made to incorporate it into high-yielding rices.

Other panicle and grain characteristics

Panicle and spikelet characteristics such as panicle compactness, presence or absence of awns, and hull color are not directly related to yield. Farmers' preferences regarding these components vary from one location to another.

Panicle exsertion, however, is universally regarded as an important trait. *Panicle exsertion* is the emergence of the neck node from the flag leaf collar. When the panicle does not emerge completely, some spikelets remain within the sheath, and these spikelets tend to have high sterility rates. Environmental factors such as drought, low temperature, and certain diseases can impair panicle exsertion. Breeders always should select for complete panicle exsertion in the F_2 and pedigree nurseries.

Threshability is an important characteristic for most breeding programs. Many traditional rainfed lowland cultivars shatter easily. Farmers who harvest by panicle and who transport rice before threshing need cultivars that resist shattering. See Jennings et al (1979) for guidelines to selecting for threshability.

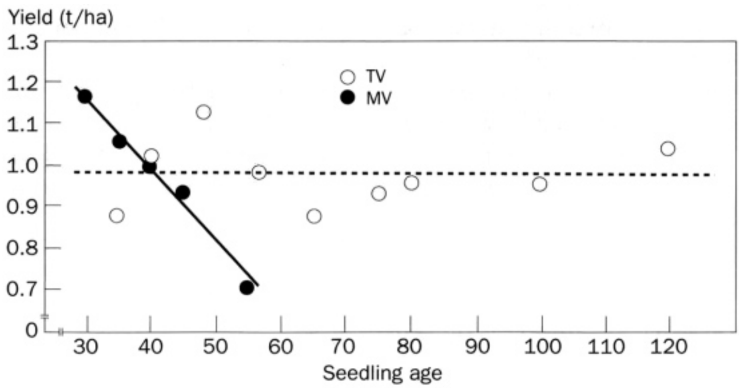
Tolerance for delayed transplanting

Transplanting is the most widely used method by which rainfed lowland rice crops are established. Most agronomists consider 3-4 wk as the optimum age at which seedlings may be transplanted (De Datta 1981). In rainfed lowlands, however, drought or flooding often makes it impossible to transplant within 4 wk of seeding. In fact, in more than 50% of the rainfed lowland rice area, transplanting is frequently delayed (Mackill 1986).

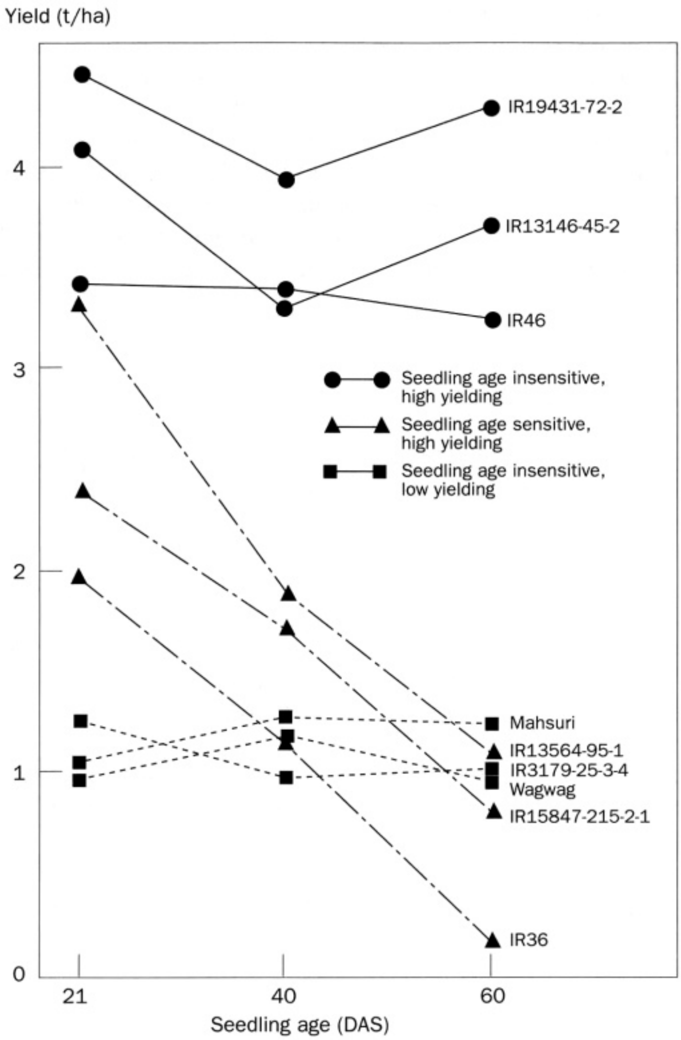
Direct seeded crops usually cope with water-related stresses better than transplanted crops do. At present, however, many farmers are unable to direct seed their rice crops because they lack suitable weed control methods. Breeders therefore should concentrate on developing cultivars that tolerate delayed transplanting.

One advantage of transplanting is that it allows farmers to be flexible in dealing with water-related stresses. If a drought occurs just after seeding, the plants can be left in the seedbed until sufficient water is available for transplanting. In *medium-deep* areas, farmers use older seedlings because they are better able than young seedlings to survive flood damage. In some low-lying areas, rice is grown in the dry season as floodwaters recede. Farmers in these areas usually use older seedlings, which are better able than young seedlings to tolerate the high water levels at transplanting time. For example, a study conducted by Pande et al (1979) showed that flood survival of the modern cultivar Jaya increased from zero for 18-d-old seedlings to more than 60% for 46-d-old seedlings. This tolerance for high water may result from the higher carbohydrate content or greater height of older seedlings (Bhattacharya and Vergara 1979).

Traditional photoperiod-sensitive cultivars usually are more tolerant of delayed transplanting than are modern cultivars (Fig. 3.4). Modern rices have been identified, however, that tolerate transplanting up to 60 d after seeding (Fig. 3.5). C4-63 is an example of a tolerant cultivar that has been adopted in some *medium-deep* areas (Bhattacharya and Vergara 1979). Tolerance for delayed transplanting is related to growth duration; that is, cultivars that mature in fewer than 120 d are less tolerant than longer duration cultivars. Tolerance also differs within maturity groups. In some rainfed



3.4. Grain yields of traditional (TV) and modern (MV) varieties, expressed as ratio of yield to yield of 40-d-old seedlings (Gines et al 1985).



3.5. Yield of rice cultivars and breeding lines at three seedling ages: 21, 40, and 60 d after seeding (IRRI 1985).

lowland nurseries in Cagayan Valley, Philippines, transplanting has been delayed up to 90 d after seeding. Most modern rices flowered or initiated panicles while in the seedbed. Nevertheless, a few genotypes still were able to recover and produce acceptable yields after transplanting (IRRI 1989a). In some cases, tolerance seems to reside in the ability of the plant to postpone panicle initiation until after transplanting; in others, it appears to come from the plants' ability to initiate new panicles after transplanting, even though some panicles already have initiated.

Other than growth duration, the morphological and physiological characteristics that confer tolerance for delayed transplanting are unknown. Likewise, the inheritance of this tolerance has not been studied. Considerable genetic variation exists for the trait, and tolerant lines usually can be identified among breeding materials not previously selected for tolerance. Selection for this trait in early generations is easy: bulk populations and pedigree nurseries can be left in the seedbed for extended periods before transplanting. In some cases, transplanters may find it difficult to transplant large nurseries because greater exertion is required to pull older seedlings from the seedbed.

Ratooning ability

Ratooning is the practice of harvesting an additional rice crop from tillers produced by the stubble of the main crop. Ratooning is common only in limited areas of Asia; however, it has been advocated as a low-cost alternative to double cropping (Krishnamurthy 1988). While the ratoon yield almost always is much lower than the yield of the main crop, it is produced quickly and with few inputs.

In most rainfed lowlands, the water available is insufficient to support double cropping of rice but may be sufficient to support ratooning; thus ratooning may be a useful strategy for increasing rice production in these areas. A ratoon crop can be produced if

- sufficient water is available after the main crop is harvested,
- temperatures are not so low as to constrain the growth of the ratoon crop,
- the land is not needed for an important postrice crop, and
- large pest populations have not built up during the main cropping season.

The success of a ratoon crop depends primarily on a favorable environment and effective management practices (Vergara et al 1988). In fact, the performance of the ratoon crop is affected by the practices used with the main crop, such as

- plowing depth,
- time of transplanting,
- plant spacing,
- crop establishment method,
- fertilizer management, and
- water management.

There are some genotypic differences, however, for ratooning ability. Abundant production of ratoon tillers has been observed in the cultivars Mahsuri and Intan, and many other cultivars with ratooning ability have been identified (IRRI 1988c). Some evidence suggests that ratooning ability is related to delayed leaf senescence after the main harvest and high carbohydrate levels in the stubble (Vergara et al 1988, Ichii 1988). Other studies, such as one conducted in the state of Texas, USA, found correlations between ratooning ability and other traits to be low (Bollich et al 1988).

Few studies have been made of the genetics of ratooning ability. Cuevas-Pérez (1980) found the heritability of this trait to be low; Li and Chen (1988) measured a range of heritability values in different crosses; Chauhan et a1 (1989) measured heritability values of 0.66 to 0.88 for the ratio of ratoon tillers to main crop tillers, and they noted that the trait is recessive. While these genetic studies indicate that early-generation selection for ratooning can be effective, most breeders consider the trait to be difficult to measure accurately. Selection in advanced generations or fixed lines is generally believed to be more reliable (Bollich et al 1988). Because ratooning is strongly influenced by environmental conditions and agronomic practices, selection trials should be replicated within a season and over years.

Bardhan Roy et a1 (1988) suggested that ratooning of photoperiod-sensitive varieties could increase rice production in submergence-prone areas of West Bengal, India. They seeded photoperiod-sensitive cultivars in early November so the main crop could be harvested in late March or April. The ratoon crop, harvested in October, produced yields of up to 4 t / ha—about the same as the main crop. They observed varietal differences in regularity of flowering during the main crop, so they seeded the F_2 plants in November to select for optimum main crop flowering time. According to their findings, the traits required for optimum productivity under this system include

- photoperiod sensitivity,
- submergence tolerance (or elongation ability),
- drought resistance,
- semidwarf height,
- nitrogen responsiveness,
- disease and insect resistance, and
- ability to produce many ratoon tillers.

The procedure of Bardhan Roy et al (1988) for selecting for ratooning ability could be used effectively in other areas that are similar in climate to West Bengal, but it is not appropriate for areas where water is scarce or temperatures are low after the main cropping season.

Chapter 4

Growth duration

Growth duration is an agronomic trait; but, because it is a crucial factor in the choice and success of rainfed lowland rice varieties, it merits more in-depth coverage than other agronomic traits.

For most farmers of rainfed lowland rice, growth duration (or flowering date) is the most important characteristic differentiating rice cultivars and their adaptation to particular growing conditions. The vast majority of traditional rainfed lowland rice cultivars are photoperiod sensitive, and many farmers still prefer to use these traditional varieties. Although improved varieties have increased yields in some situations and offer agronomists greater flexibility in devising intensified cropping systems, most improved varieties are photoperiod insensitive. According to farmers, this lack of photoperiod response is the primary hindrance to their adoption of improved varieties.

Rice breeding programs have found it easy to change plant maturity, particularly of photoperiod-insensitive lines. Developing improved photoperiod-sensitive cultivars has not been so easy, partly due to the difficulty in making crosses and managing nurseries, as discussed in this chapter, and partly due to the scarcity of productive photoperiod-sensitive donors.

Components of growth duration

Rice is a short-day plant; that is, flowering is hastened by longer dark periods (shorter days). The two major components of the vegetative growth phase are the *basic vegetative phase* (BVP) and the *photoperiod-sensitive phase* (PSP). The end of the vegetative growth phase coincides with panicle initiation and the beginning of the reproductive phase. In the tropics, the *reproductive phase*—between panicle initiation and flowering—is about 35 d long and is believed not to vary appreciably among cultivars. The *ripening phase,* from flowering to full maturity, is about 30 d long. In the tropics, most variation in growth duration among cultivars can be explained by differences in BVP and PSP.

BVP, also known as the *juvenile* stage, is the initial period of growth. During this period, the plant does not respond to changes in daylength. A cultivar's BVP can be estimated by growing the plants under the *optimum photoperiod* — the daylength that minimizes growth duration. Optimum photoperiod varies between cultivars, but 10 h often is used in experimental situations. Since flowering usually occurs about 35 d after panicle initiation, BVP is estimated by subtracting 35 from days to flowering. In the tropics, BVP values for rice range from 10 to 85 d (Vergara and Chang 1985).

The effect of BVP can be seen when rice is planted during the time of year in which days are naturally short (September to December in the northern hemisphere). In this season, differences in days to flowering among photoperiod-sensitive cultivars are related mostly to differences in BVP length: cultivars with longer BVP flower later than those with short BVP.

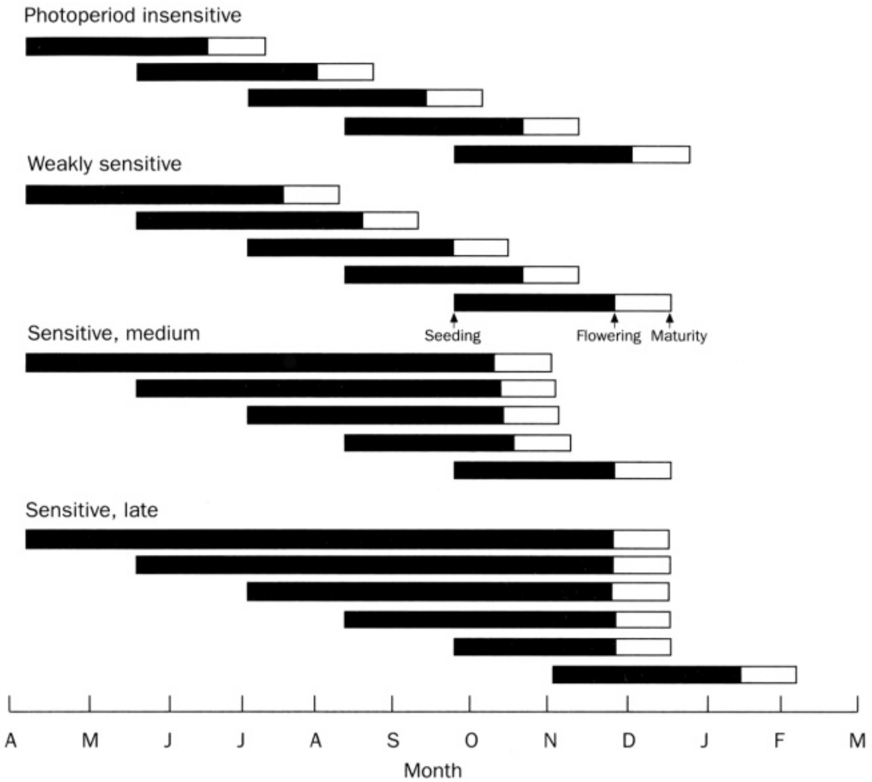
The PSP can range from near zero in photoperiod-insensitive rices to more than 165 d in those that are strongly sensitive. PSP is estimated by subtracting minimum growth duration (at optimum photoperiod) from maximum growth duration (usually at a 14- or 16-h photoperiod). Strongly sensitive cultivars do not flower at long daylengths, so experiments usually are terminated 200 d after seeding.

Vergara and Chang (1985) used PSP to classify rices according to their photoperiod response. They classified insensitive rices as those with a PSP of 30 d or less; sensitive rices have PSP of more than 30 d. While this method of classification is appropriate for weakly sensitive cultivars, it is not satisfactory for more strongly sensitive cultivars, which all have PSPs of more than 100 d.

Critical photoperiod is the shortest daylength under which strongly sensitive cultivars will not flower. It can be measured by subjecting the plants to several photoperiods ranging from 12 to 16 h. If a plant flowers within 200 d when grown under a 12-h daylength but not when grown under a 12.5-h daylength, its critical photoperiod is between 12 and 12.5 h. Most strongly sensitive cultivars have critical photoperiods of 12-14 h.

The critical photoperiod largely determines the normal flowering date of a photoperiod-sensitive cultivar when it is planted under natural daylength conditions before daylength begins to shorten (Fig. 4.1). The cultivar will not flower until daylength reaches the critical photoperiod. Planting dates for the rainfed lowland belt of South and Southeast Asia coincide with the beginning of the monsoon (usually April to July). During early vegetative growth, days are long; daylength begins to decrease after June 21. Therefore, cultivars with longer critical photoperiods flower earlier than do those with shorter critical photoperiods. Cultivars from lower latitudes (for example, southern Vietnam, Borneo, Sumatra, southern Thailand, and Sri Lanka) generally have very short critical photoperiods—near 12 h. They can flower as late as January, which means they initiate panicles when daylength is shortest (Fig. 4.1).

The number of short-day treatments required to induce flowering in photoperiod-sensitive rices ranges from 4 to 24 (Vergara and Chang 1985). Irregular flowering is commonly observed in rices that are planted as daylength is increasing (Vergara and Lilis 1966). Thus the flowering stimulus apparently is not transmitted between tillers; so culms that are mature enough to be induced produce panicles, but later tillers flowering under longer photoperiods are not induced.



4.1. Relation between daylength and flowering date for cultivars of different growth durations and degrees of photoperiod sensitivity in a hypothetical date-of-planting experiment. Medium- and long-duration cultivars differ in critical photoperiod.

For a comprehensive review of the components of growth duration in rice, see Vergara and Chang (1985).

Measuring photoperiod sensitivity

The growth duration of a cultivar results from the complex interaction among its BVP, critical photoperiod, and strength of response to changing photoperiods. Rice cultivars show considerable variation in these traits, so measuring a cultivar's sensitivity to photoperiod is not simple.

Temperature and daylength are the primary environmental determinants of growth duration. Since temperature variation is limited in the tropics, daylength is the overriding environmental factor in growth duration in these regions.

The most accurate estimate of photoperiod sensitivity can be obtained by measuring the growth duration of plants under a range of artificial photoperiods. (See Figure 4.2 for examples of the types of responses that can be expected.) This type of experiment makes it possible to estimate the following parameters:

Parameter	Measured as
BVP	Shortest duration to flowering minus 35
PSP	Difference between shortest and longest duration
Optimum photoperiod	Photoperiod for shortest duration
Critical photoperiod	Shortest photoperiod at which cultivar does not flower
Rate of response	Shape or slope of response curve

Rate of response is the most difficult parameter to estimate because for many cultivars it is not linear. The slope of the portion of the curve at which there is maximum change of duration with changing daylength (that is, 10-13 h) indicates the photoperiod response. Cultivars that are strongly sensitive have larger regression coefficients than those that are weakly sensitive (Fig. 4.2).

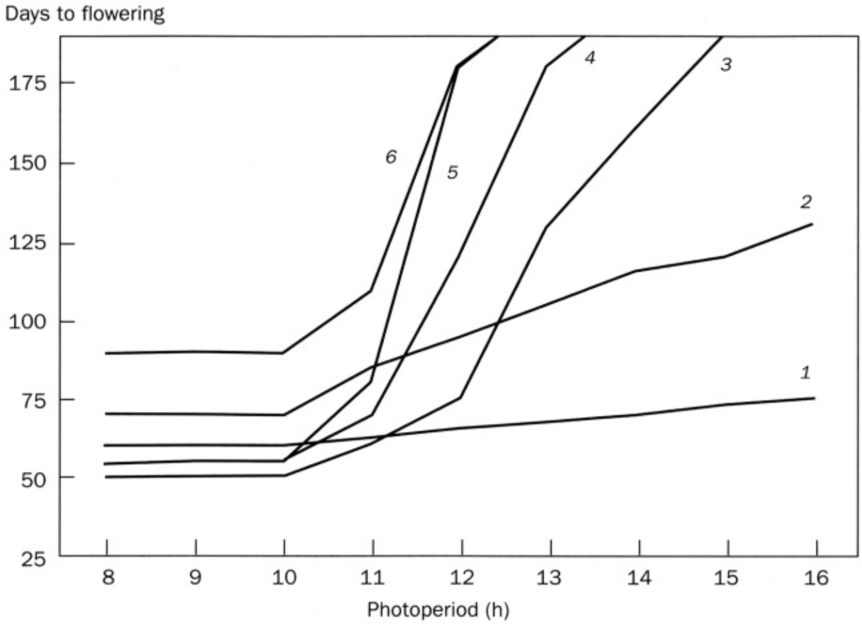
Short-duration, photoperiod-insensitive cultivars behave, typically, as cultivar 1 in Figure 4.2. These cultivars show a slight response to photoperiod.

Many long-duration cultivars that are considered to be photoperiod insensitive respond similarly as cultivar 2. Although they respond more strongly to photoperiod than short-duration cultivars, they flower under all daylengths common in the tropics (11-13 h) with moderate change in growth duration.

Some short-duration, photoperiod-sensitive cultivars, such as Nam Sagui 19 of Thailand, respond as cultivar 3. These cultivars can flower under most tropical daylengths, but their growth duration is strongly affected by photoperiod. Either they have a long critical photoperiod (greater than 14 h) or they do not have a critical photoperiod (that is, they flower at all photoperiods tested).

The behavior of cultivar 4 is typical of medium-duration, photoperiod-sensitive cultivars that have distinct critical photoperiods. Cultivar 5 represents long-duration, photoperiod-sensitive cultivars that have very short critical photoperiods. These types of cultivars are common near the equator, where very long-duration varieties are grown. Cultivar 6 represents photoperiod-sensitive varieties that have long BVP. These cultivars, such as the Rayada deepwater rices of Bangladesh, are rare.

Unfortunately, it is time consuming and expensive to conduct experiments that expose a cultivar to a variety of photoperiods; so such detailed data are available for few rice cultivars. Vergara and Chang (1985) listed the growth durations of a large number of cultivars tested at IRRI under four photoperiods: 10, 12, 14, and 16 h. For convenience, cultivars usually are classed as either photoperiod sensitive or insensitive; however, responses to photoperiod actually form a continuum, with many cultivars having intermediate responses.



No.	BVP (d)	PSP (d)	Optimum photoperiod (h)	Critical photoperiod (h)	Response (b)[a]	Description
1	25	15	10		0.02	veryearly.insensitive
2	35	60	10		0.11	late, slightly sensitive
3	15	170	10	(16)	0.25	early, weakly sensitive
4	20	>170	10	13.0-13.5	0.40	medium, strongly sensitve
5	20	>170	10	12.0-12.5	0.53	late, strongly sensitive
6	55	>170	10	12.0-12.5	0.40	late, strongly sensitive, long BVP (e.g., Rayada cultivars)

[a] Regression of days to flowering on photoperiod for photoperiods of 10-13 h.

4.2. Hypothetical response curves for six cultivars with different growth duration characteristics.

While testing under artificial photoperiods produces the most accurate estimates of photoperiod sensitivity, useful approximations can be obtained more easily by planting samples of the cultivars in the field at different dates. Photoperiod-insensitive cultivars show little change in growth duration when planted in different months (Fig. 4.1). Since days are longer at the beginning of the growing season and shorter at the end, sensitive cultivars with longer critical photoperiods flower earlier than those with shorter critical photoperiods.

Response to photoperiod can be calculated by regressing the days to flowering on seeding date (Katayama 1963). (Seeding dates can be measured as days from the first seeding date of the experiment.) Photoperiod-insensitive cultivars have regression coefficients near zero. Poonyarit et a1 (1989) calculated regression coefficients of -0.57 and -0.64 for two strongly sensitive cultivars. They found that the weakly sensitive cultivar Nam Sagui 19 had a regression coefficient of -0.26. One breeding line, IR26760-27, flowered later than Nam Sagui 19 at all seeding dates, yet its regression coefficient was only -0.12, indicating that it was less sensitive to photoperiod. Thus sensitivity is not directly related to lateness of flowering, as some have assumed.

The more planting dates that can be used for each cultivar, the more accurate will be the estimate of photoperiod sensitivity. An index of photoperiod response can be obtained, however, by using only two planting dates during the main wet season. To derive such an index, note the days to flowering (DF) at two seeding dates (SD) and apply the following formula (Nwe and Mackill 1986):

$$(DF_1 - DF_2) / (SD - SD_1)$$

The result will be close to zero for insensitive cultivars and close to one for strongly sensitive cultivars.

A third method of testing for photoperiod sensitivity can be used in the tropics. At Los Baños, Philippines, (15°N latitude) strongly sensitive cultivars can be identified by seeding in February. At this seeding date, the daylengths are becoming too long for these cultivars to initiate panicles. Sensitive cultivars can easily be identified as those that remain vegetative even 6 mo after seeding.

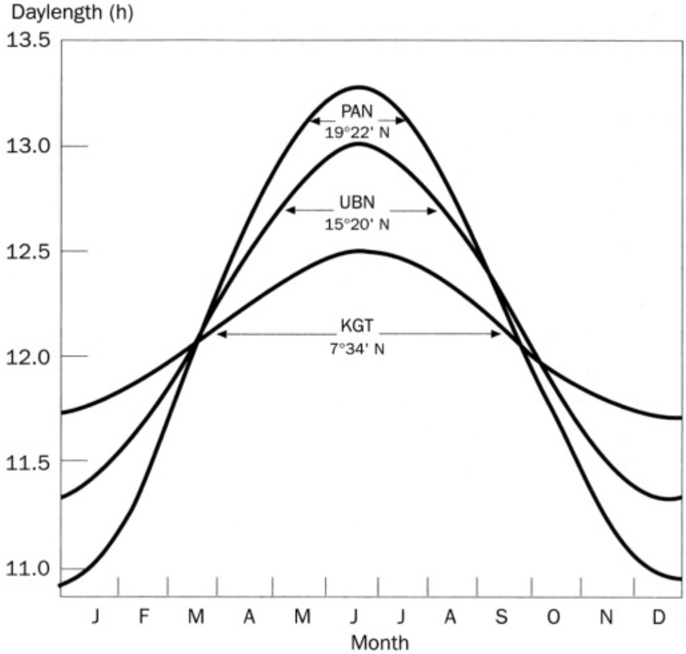
The advantage of this method is that it does not require much field space: the entries can be planted at close spacing in short rows (about 1 m). One disadvantage is that this method is not suitable for sites at higher latitudes because temperatures at the time of seeding may be too low for optimum results. Further, reliable data on photoperiod sensitivity are not available until at least 5 mo after seeding.

The behavior of photoperiod-sensitive cultivars under field conditions is strongly influenced by the latitude of the research site. Daylength changes are more pronounced at higher latitudes than at lower latitudes (Fig. 4.3). Daylength is the same for all sites at the September equinox (about 21 Sep), so cultivars that initiate panicles near this date and flower at the end of October should behave similarly at different latitudes.

Some traditional cultivars grown near the equator have long growth duration when planted in September. Even though the shortest daylength occurs on 21 Dec, they often flower in February. This response indicates that panicle initiation can occur a month or more after the short-day treatment starts. These cultivars probably require many cycles of short days to stimulate panicle initiation.

Genetics of photoperiod sensitivity

The growth duration of segregating progeny reflects the complex interaction of BVP, degree of photoperiod sensitivity, critical photoperiod, and the photoperiods under which the plants are grown.



4.3. Daylength patterns at different latitudes in Thailand (Pushpavesa and Jackson 1979).

Inheritance of BVP characteristics must be studied under the optimum photoperiod—10 h is suitable for experimentation. The length of the BVP is generally controlled by two or three genes of cumulative effect (Chang et al 1969). Short duration is dominant to long duration.

The presence or absence of photoperiod response usually is controlled by one or two dominant or recessive genes (Vergara and Chang 1985). A major gene controlling photoperiod sensitivity is designated *Se-1* (or *Lm*) and is located on rice chromosome 6 (Yokoo and Fujimaki 1971, Yokoo et al 1980, Mackill et al 1993). This gene seems to be present in many sensitive cultivars. A recessive gene, *se-2,* has been mapped to chromosome 7 (Yu and Yao 1968) but has not received much attention. Another major gene, *Se-3,* which is independent of *Se-1,* has been identified in some very long-duration sensitive cultivars (Poonyarit et al 1989). The two dominant genes seem to have a cumulative effect in conditioning photoperiod sensitivity. For instance, they combine to condition a very short critical photoperiod in very long-duration cultivars such as Puang Rai 2 (Thailand) and Soc Nau (Vietnam). The breeding line IR26760-27, which has the dominant sensitivity gene *Se-3* and the recessive allele of *se-1,* has a weak response to photoperiod. A gene from the wild species *O. rufipogon,* which has an effect similar to that of *Se-3,* was designated *En-Se-1* by Sano (1992). Several "late-heading genes"———designated *E1, E2,* and *E3* — have been shown to differ from *Se-1* (Yokoo and Kikuchi 1992). More photoperiod sensitivity genes are being identified, such as *Se-4* (Oshima et al 1993) and *Se-5* (Yokoo and Okuno 1993). It is still not clear whether all these genes are at different loci.

The genetics of critical photoperiod, which is the main determinant of flowering date, is less well understood than that of photoperiod sensitivity, although the two are definitely related. Some evidence indicates that different alleles at the *Se-1* locus control critical photoperiod (Yokoo and Kikuchi 1977). If this is the case, then sensitive segregates in a cross between a sensitive and an insensitive parent should have the same flowering date as the sensitive parent. In some crosses, however, sensitive segregates have been recovered that have different critical photoperiods than the sensitive parents (Pushpavesa and Jackson 1979, Nwe and Mackill 1986). Thus it seems that genes independent from *Se-1* can influence flowering date, and a range of flowering dates usually can be obtained from a sensitive x insensitive cross. Nevertheless, it is rare to recover sensitive progeny that flower later than the sensitive parent. This situation occurs only if each of the two parents has a complementary photoperiod sensitivity gene, such as *Se-1* and *Se-3*.

Some cultivars, especially semidwarf rices, have genes that inhibit photoperiod sensitivity (Vergara and Chang 1985, Oshima et a1 1993). Crosses between photoperiod-sensitive cultivars and short-duration semidwarf rices often yield many fewer sensitive recombinants than expected for a single gene trait (Nwe and Mackill1986). When sensitive recombinants are desired and insensitive donors are required, longer duration parents should be used.

Photoperiod-insensitive cultivars

Traditional photoperiod-insensitive cultivars seldom are grown in rainfed lowlands (see Chapter 2). Short-duration cultivars of eastern India and Bangladesh, which belong to isozyme group II (aus), are frequently identified as rainfed lowland cultivars; these areas, however, have growing conditions that are closer to those of uplands, being flooded only periodically and usually late in the season. Improved photoperiod-insensitive cultivars have been introduced successfully into many rainfed lowlands, particularly where favorable conditions prevail.

Very short-duration cultivars almost always are byproducts of irrigated breeding programs and rarely have been developed for rainfed conditions. Short duration offers two major benefits:

- It reduces the risk of drought injury in areas where the amount or duration of rainfall is limiting; in particular, plants are spared from terminal drought stress at the reproductive stage (see Chapter 5).
- Where rainfall is sufficient, it allows intensification of the cropping system through double cropping rice or producing a pre- or postrice upland crop.

Very short-duration cultivars have been successful in areas where they can be direct seeded. They are not suitable for most conditions, however, because

- They are sensitive to delayed transplanting, which is common under rainfed lowland conditions.
- They mature during periods of heavy rainfall, which makes proper harvesting and drying difficult.
- They compete poorly with weeds as they tend to be very short.
- They are not adapted specifically to the stresses that are common in rainfed lowlands, particularly drought.

Very short-duration cultivars probably would be adopted more widely if efforts were stepped up to develop varieties that are adapted to rainfed lowland conditions.

Since heritability for flowering date is high, breeders can select for short duration beginning in the F_2 generation, or even in the F_1 generation of multiple crosses (Jennings et al 1979). Selecting short-duration recombinants is easy; but recombining short duration with other desirable plant characters, such as intermediate height and sturdy culms, is more difficult.

Medium- and long-duration cultivars are more useful than short-duration varieties in rainfed lowlands: they are less sensitive to delayed transplanting, and their height is more suitable for rainfed lowland conditions. Many breeding programs have developed productive cultivars that are weakly sensitive or insensitive to photoperiod and have intermediate height. An outstanding example is BR4 (and related cultivars), which was developed in Bangladesh (Miah et al 1986). These cultivars descended from the sister lines IR5 and Pankaj, which have been adopted by many rainfed lowland farmers (see Chapter 2). Many medium- and long-duration, photoperiod-insensitive varieties are available for use in breeding programs, and they are among the highest yielding lines in the international rainfed lowland nurseries.

Photoperiod-sensitive cultivars

Photoperiod-sensitive cultivars have many advantages for typical rainfed lowland conditions. There appears to be no genetic barrier to developing sensitive rices with improved height and yield potential (Salam and Mackill 1993).

The types of parents used for crossing must be chosen according to a breeding program's objectives, particularly desired growth duration (Table 4.1). Weak sensitivity to photoperiod may be a logical objective, especially considering the popularity of the cultivar Mahsuri (see Chapter 2). On the other hand, some of Mahsuri's disadvantages are linked to its weak photoperiod sensitivity, and these disadvantages are of greater consequence in unfavorable rainfed lowlands.

At least one photoperiod-sensitive parent with the optimum flowering date should be used in crosses because it is difficult to recover sensitive progeny that have longer duration than the sensitive parent. If a sensitive parent is crossed with an insensitive parent, it usually is possible to select sensitive progeny with shorter duration than the sensitive parent—an important consideration for programs that seek to obtain lines that mature earlier than the prevalent cultivars.

If two or more photoperiod-sensitive cultivars are crossed, most or all of the progeny are sensitive, making it easier to obtain desirable recombinants. In most cases, insensitive donors also are included in crosses. The expected proportion of sensitive F_2 recombinants varies with the type of cross as follows:

Type of cross	**Sensitive**		**Insensitive**
	Se-1 Se-1	Se-1 se-1	se-1 se-1
Sensitive/insensitive	0.250	0.500	0.250
Sensitive/insensitive//insensitive	0.125	0.250	0.625
Sensitive/insensitive//sensitive	0.625	0.250	0.125

These estimates assume that sensitivity is controlled by the major gene *Se-1* and that the insensitive parent does not have inhibitor genes.

Making crosses with photoperiod-sensitive cultivars may require special nursery management. Normally, staggered plantings are used to synchronize the flowering dates of short- and long-duration varieties. Sensitive varieties, however, usually flower at the same time regardless of planting date; so crosses between two sensitive cultivars with different flowering dates can be difficult to make. By planting them late in the season (September to November), their flowering periods can be made to overlap (Fig. 4.1). If they are planted too late, however, (December to February, depending on the variety), they will not flower at all (Herrera and HilleRisLambers 1984). At higher latitudes, it may be difficult to use late planting dates because low temperatures may interfere with crossing and seed set. In these areas, plants can be potted and subjected to artificial short days, moving the pots into a dark room at about 1600 h each day until panicles initiate.

Table 4.1. Guidelines for selecting photoperiod-insensitive and -sensitive parents in breeding photoperiod-sensitive rices.

Response to photoperiod	Considerations in selecting parents
Insensitive	Avoid very short-duration parents unless early flowering or weakly sensitive recombinants are desired. Productive, medium- or long-duration lines with intermediate plant height are desirable. Use long-duration lines (>140 d) if very late-flowering recombinants are desired.
Sensitive	Use traditional cultivars with wide adaptability, stress tolerance, or other desirable traits. Choose a parent that has a flowering date the same as or later than the desired flowering date. Use the traditional cultivar as the female parent to help diversify the cytoplasm sources.

Once crosses have been produced, the F_1 plants must be seeded so that daylengths will be short enough to induce flowering. If the F_1 generation is seeded during the normal growing season, which usually is June to July, daylength should not be a problem. If the cross is made during the wet season, the F_1 generation should be planted during the off season so the F_2 seed will be available for planting during the next wet season. (It is better to plant the F_2 in the wet season, which corresponds to normal timing of rainfed lowland crops in farmers' fields. This timing ensures that selections will be made under typical environmental conditions of the rainfed crops.) It is important not to seed the F_1 plants too late: if they are seeded from January to April, they will take much longer to produce seed. At IRRI, F_1 seed from crosses made during the wet season are germinated by mid-December; thus they flower in time to seed the wet-season F_2 populations in June. Where off-season planting is not possible, the F_1 generation, like the crosses, can be grown in pots and subjected to artificial short days.

The F_2 generation and the pedigree nursery can be handled normally (see Chapter 12). For most crosses in which photoperiod sensitivity is emphasized, insensitive progeny should be eliminated at an early stage. Sensitive progeny can be identified in several ways:

- When seeded early (April to early June), insensitive plants or pedigree lines flower earlier than the sensitive parents (before October) because the growth duration of insensitive plants does not exceed 150 or 160 d.
- When two generations per year are grown, the sensitive pedigree lines have much longer growth duration in the wet season than in the dry season if wet-season nurseries are planted by July.
- When a special nursery is planted in the dry season (February), sensitive lines are those that do not flower in 140-150 d.

These identification methods usually yield unambiguous results for strongly photoperiod-sensitive progeny. Weakly sensitive plants may not be so easy to identify.

Two generations a year should be grown wherever possible. At tropical locations, such as Los Baños, rice may be grown year-round; so producing two generations a year presents few problems (Table 4.2). Selections should be made from the F_2 generation during the wet season to ensure that the

Table 4.2. Breeding scheme for developing photoperiod-sensitive rices where two generations a year can be grown.

Year	Season	Generation	Activities
1	Wet	F_2	Select for plant type
2	Wet	F_3	Select for plant type
	Dry	F_4	Advance generation, screen
3	Wet	F_5	Select for plant type
	Dry	F_6	Advance generation, screen
4	Wet	F_7	Bulk best rows
	Dry	F_8	Increase seed
5	Wet	Fixed lines	Conduct observation trials and replicated yield trials

normal phenotypes are expressed. Since the F_2 generation is critical for selection (see Chapter 12), it is important for the plants to be grown under the photoperiod and temperature regime common in the rainfed lowland crop, allowing them to express their normal plant type. The F_3 generation should be grown during the following wet season because, if it is grown during the dry season, photoperiod-sensitive plants will appear stunted and have few tillers and small panicles; thus, it will not be possible to select for the desired phenotype. The F_4 generation can be grown during the dry season, provided that seeding is early enough to enable sensitive plants to flower. Phenotypic selection of photoperiod-sensitive pedigree lines is not possible in the dry season as the plants are induced to flower too early and do not have sufficient vegetative growth to express their normal plant type. These lines can be screened simultaneously for other traits such as disease or insect resistance, grain quality, or submergence tolerance, providing data on which to base future selections. Otherwise, the F_4 can be considered a generation-advance nursery. The F_5 generation should be grown during the wet season to allow another round of selection for desired phenotype. The F_6 generation can be grown during the dry season for generation advance. Most likely, the lines still will be segregating; if so, F_7 lines should be grown during the following wet season.

Plants seeded in off-season nurseries that do not flower tend to be strongly sensitive to photoperiod and, thus, may give useful recombinants. They can be lifted from the field, and the tillers can be removed and replanted in short rows. The seed harvested from these rows at the end of the wet season represents clones of the rescued plant and can be planted during the following wet season.

At locations where off-season nurseries cannot be grown, it may be possible to arrange a *shuttle breeding program* for advancing generations. In Thailand, for example, alternate generations of photoperiod-sensitive populations from the northeast are grown at a lower latitude—near Bangkok or in the central plains—during the off season. In some cases, institutions such as IRRI assist in growing off-season nurseries. One difficulty of shuttle breeding sensitive populations is the need for rapid turnaround between harvest of the wet-season crop in November and seeding of the dry-season crop in December.

An alternative to off-season nurseries is rapid generation advance (RGA), a method used extensively in some temperate countries in which only one crop a year can be grown. In the RGA facility at IRRI, photoperiod-sensitive populations are given artificial short-day treatments to induce flowering. Three generations a year can be obtained through this method (see Chapter 12).

For breeding programs that grow only one generation per year, operations are similar for breeding photoperiod-sensitive and -insensitive rices; thus these programs take twice as long to produce fixed lines for advanced tests than those in which two generations can be produced. Yet many programs find it easier to manage a single generation per year, especially when labor and facilities are insufficient for growing off-season nurseries. An advantage is that all generations are grown under realistic rainfed lowland conditions. Fixed pedigree lines will therefore have passed through at least four generations of rigorous phenotypic selection before they are advanced to more intensive evaluation trials.

Progress in developing improved photoperiod-sensitive types

Because of the difficulty of working with photoperiod-sensitive rices and a perception that they are less productive than insensitive rices, many breeders have concentrated on developing improved insensitive varieties. Since sensitive varieties are better adapted to rainfed lowlands, greater effort needs to be applied to developing improved sensitive cultivars.

Traditional rainfed lowland cultivars usually are tall and low yielding. So far, breeding for rainfed lowlands has focused on developing lines that combine strong photoperiod sensitivity with shorter stature.

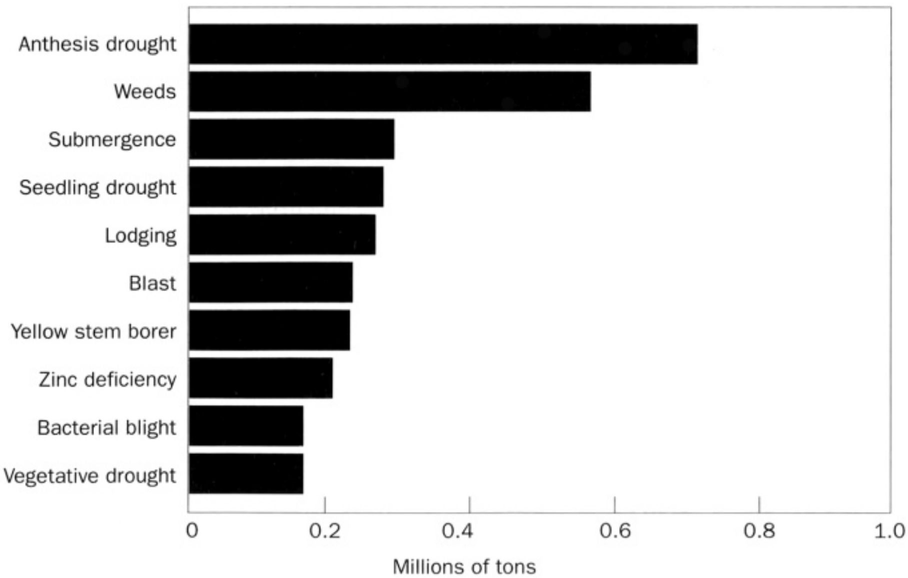
It has been easiest to develop lines with flowering dates in October. Some programs have worked to develop cultivars with shorter duration; but these cultivars tend to have longer critical photoperiods, a characteristic that is difficult to combine with strong photoperiod sensitivity. Other programs have focused on cultivars with later maturity, which have shorter critical photoperiods (IRRI 1988b). Some lines with flowering dates in November and December have been developed, but progress has been slower than for the October-flowering rices. Cultivars that flower this late require at least two photoperiod sensitivity genes, as discussed earlier in this chapter. Recombinants in crosses between long-duration traditional varieties and insensitive parents usually flower earlier than the long-duration parent.

CHAPTER 5

Drought resistance

Drought has long been recognized as the primary constraint to rainfed rice production. For example, a massive study conducted in eastern India showed that drought was the primary factor limiting rice yields based on the extent of losses and priority in breeding programs (Widawsky and O'Toole 1990). Yield losses caused by drought at the anthesis and seedling stages combined were about double those caused by weeds, which was the second-ranked constraint (Fig. 5.1). Throughout Asia, rice breeders are keenly aware of farmers' need to cope with drought.

Many agricultural scientists have sought to overcome this constraint by finding ways to increase the water supply to crops in drought-prone areas rather than developing crops that are adapted to water shortages. Their rationale is that rice, which is a semiaquatic species, has not developed many of the adaptations—deep rooting habit and thick epicuticular wax, for instance—that have evolved in upland crops such as wheat, sorghum, and maize. However, it would be impossible to provide sufficient water throughout the huge rainfed areas; thus rice breeders are challenged to improve varietal resistance to drought.



5.1. Top 10 causes of yield losses in rainfed lowland rice, eastern India (Widawsky and O'Toole 1990).

Although considerable research into drought resistance is under way, many of the research methods used are not practical for applied breeding programs. For the near future, breeding programs need to focus on understanding the genetics and physiology of adaptive traits and developing new selection tools. Breeders, agronomists, and physiologists must cooperate closely in the development of improved, drought-resistant cultivars.

This chapter introduces the principles of plant-water relations and plant adaptation to drought stress. These principles are followed by practical information about screening methods and breeding strategies for drought resistance.

Plants and water

Water is transported from a plant's roots to its shoots through conduits called the *xylem vessels.* The plant loses water primarily through pores in its stem and leaves, known as *stomata,* as a consequence of *transpiration.* That is, carbon dioxide (which is needed for photosynthesis) moves from the atmosphere into the plant through the open stomata, which simultaneously allow water and oxygen to diffuse to the atmosphere.

The concept of *water potential* helps to clarify the movement of water in plants. (See Kramer 1983 for a full discussion of this concept.) Any type of reaction or movement requires energy. Water potential, often designated $y_{w,}$ is the energy available for water to react or move. Because objects always move from higher to lower levels of energy (that is, they move down an energy gradient), water moves in the direction of lower potential (that is, energy is lost during movement).

The potential of pure water is defined as zero. The potential is lowered when substances are dissolved in water. This reduction is referred to as the *solute potential* (y_s), which becomes more negative as the concentration of solutes increases.

Water potential also is influenced by pressure. The *pressure potential* (y_p) increases as pressure increases. When water is under tension, as occurs in the xylem vessels, the pressure potential becomes negative.

Plant water potential is the sum of the solute and pressure potentials:

$$\Psi_w = \Psi_s + \Psi_p$$

Soil water potential includes another factor, *matric potential* (y_M): an expression of the strong attraction between water and the soil particles. As soil dries, the soil water potential decreases. Water potential is easier to measure than solute or pressure potential. It is measured in bars (b) or megapascals (MPa), where 1b = 0.1 MPa.

The opening and closing of stomata is influenced by leaf water potential. When water potential is high, the stomata remain open, and transpiration and photosynthesis continue. As soil water potential declines, the flow of water also declines, reducing the leaf water potential. When the water potential of the leaves reaches a certain level — usually -1.2 to -1.6 MPa — the stomata close, and the exchange of gas and water through the stomata decreases or ceases (Hsiao 1982). This response helps the plant to conserve water, but it also decreases photosynthesis. Further, when the water potential of the leaves is low, the pressure potential of the cells drops, constraining cell expansion and retarding plant growth.

In unflooded soil, water potential varies according to depth. Most of the rice plants' roots are in the top 20 cm of soil, so the plants extract water first from this depth, causing the soil water potential to decline rapidly. When the soil water potential of the upper soil becomes so low that the roots no longer can take up water, deeper roots still may extract water from deeper soil if the soil water potential is adequate at that level of the soil profile. Lowland rice varieties are especially vulnerable to drought stress because their roots tend to be concentrated in the upper soil layers.

Drought stress affects the rice crop directly, reducing growth rate and tillering and, when severe, killing the leaves and then the plants. It also affects the crop indirectly: it causes the plants to decrease their rate of transpiration, which results in reduced nutrient uptake (O'Toole and Baldia 1982). Drought stress also increases weed competition because

- Many weeds exceed rice plants in their ability to maintain plant water potential under stress, and maintain much faster growth rates during a drought.
- Weeds transpire, just as rice plants do; so their presence hastens water loss from the soil (Cruz et al 1983).

Drought stress is less damaging during the vegetative phase than during the reproductive phase because younger plants are better able to recover when the stress is relieved (O'Toole and Chang 1979). However, drought stress during the vegetative phase can permanently strain the plants—even if it is relieved before they flower—resulting in reduced leaf area, tiller number, and yield (Cruz et al 1986). Drought stress during the reproductive phase—which is particularly damaging during booting and flowering — desiccates spikelets and anthers, reduces pollen shedding, inhibits panicle exsertion, and increases sterility rates (O'Toole and Chang 1979, O'Toole and Namuco 1983, Ekanayake et al 1989).

The effects of drought stress on plant growth are complicated by many interacting environmental and agronomic factors. For instance, the properties and condition of the soil affect root growth and thus the plant's potential for water uptake during a drought. The concentration of oxygen in the soil, which is reflected in the reduction-oxidation (redox) potential, affect root growth (OToole and Chang 1979). Root growth is inhibited in soils that have impervious layers, such as hardpans and plowpans (Ghildyal and Tomar 1982, O'Toole and De Datta 1986).

Most studies of drought resistance have focused on upland rice and, thus, the results may not always be useful to breeders of lowland rice. Uplands tend to have aerobic soils that offer little resistance to root penetration. Rainfed lowland rice crops usually are transplanted after the soil is puddled; and the plow layer tends to be shallow, underlain by a hardpan, so root growth is restricted. Drought stress takes longer to develop in the flooded lowlands than in the uplands; however, it is more damaging to lowland varieties because they are not conditioned for it. Thus plants whose drought resistance mechanisms are appropriate for upland systems may not be suitable for rainfed lowlands, and vice versa. And different mechanisms require different screening methods.

Types of drought resistance

Resistance can be described agronomically as the yield of a genotype when stressed compared with the yield when not stressed (Blum 1982). Stability analysis (Eberhart and Russell 1967), which uses site mean yields as an environmental index, can be used to measure agronomic drought resistance. While breeders may find this analysis useful, they must be aware of its limitations: many environmental factors other than drought stress influence yield, and these other factors cannot be excluded.

While the degree to which a variety resists yield reduction under drought stress is the ultimate criterion for drought resistance, in practice it is expensive to obtain such data. More commonly, breeders evaluate drought resistance by rating the symptoms, in particular, degree of leaf drying experienced by plants during screening. Resistance is commonly rated on a scale of 1 (most resistant) to 9 (most susceptible) (Table 5.1).

Table 5.1. Scoring system used for evaluating resistance to and recovery from drought in upland screening at IRRI.

Response to drought	Score	Description
Resistance	0	No symptoms of stress
	1	Slight drying of leaf tips
	2	25% of the length of 25% of all leaves (normally, the older leaves) is dry
	3	At least 25% of the length of not more than 50% of all leaves is dry
	4	At least 25% of the length of 50% of all leaves is dry; 25% of leaves are fully dried
	5	50% of all leaves are fully dried
	6	51%–69% of all leaves are fully dried
	7	70% of all leaves are fully dried
	8	More than 70% of all leaves are fully dried
	9	All plants are apparently dead
Recovery[a]	1	90-100% of plants have recovered
	3	70-89% of plants have recovered
	5	40-69% of plants have recovered
	7	20-39% of plants have recovered
	9	0-19% of plants have recovered

[a]Standard *evaluation scoring system for rice* (IRRI 1988d).

Most plant physiologists have adopted the terminology for drought resistance developed by Levitt (1980), which is based on engineering terminology that describes the mechanics of strains and stresses. Under this system of terminology, *drought resistance* refers generally to the plant's response to drought stress. Its two major components are *avoidance* and *tolerance.* Avoidance mechanisms enable a plant to maintain high plant water potential and thus avoid physiological stress. Tolerance mechanisms let a plant maintain vital physiological functions and growth while plant water potential is reduced. Avoidance, therefore, limits the stress experienced by the plant tissue, whereas tolerance reduces the effects of the stress experienced by the plant tissue.

Most of the drought resistance traits that have been studied in rice are avoidance mechanisms: first, a mechanism (such as an effective root system) lets the plant maintain water uptake; later, another mechanism (such as effective stomatal control) reduces water loss from the leaves (O'Toole and Chang 1979). Dehydration tolerance helps a plant to remain productive when drought is prolonged (Turner 1982).

A third strategy for dealing with drought is *evasion,* in which the plant completes yield-determining processes while drought stress is not present. For example, upland rices and some lowland rices evade drought stress by maturing early. That is, in areas where the rainy season is short, plants that have short growth duration may complete the reproductive stage before drought stress becomes severe.

Photoperiod sensitivity is a common evasion tactic of lowland rice. Regardless of the seeding or transplanting date, a photoperiod-sensitive cultivar flowers on a certain calendar date—usually when the probability of drought is low. In many cases, lowland farmers help their crops to evade drought stress by leaving the seedlings in the seedbed until the fields have accumulated sufficient water for transplanting.

Drought resistance mechanisms

Many adaptive traits have been proposed for use in breeding programs for drought-prone areas: leaf rolling, epicuticular wax, amino acid accumulation, and so on. Unfortunately, few hard data are available about the contributions of these traits to drought resistance.

Although a genotype may have one or more adaptive traits, it still may not be agronomically drought resistant (Blum 1982). Some resistance mechanisms may be effective only in certain environments; for example, Turner (1982) identified the combinations of traits a plant needs to survive three kinds of drought: terminal, unpredictable, and terminal plus unpredictable. And all resistance mechanisms probably have costs in terms of overall productivity (Hsiao 1982). Rosielle and Hamblin (1981) reasoned that all advances in stress adaptation are at some expense of yield potential.

Table 5.2. Adaptive traits for drought resistance in rice (adapted from O'Toole 1982).

Type of trait	Mechanism	Effect
Root related	Deeper or denser root system	Increased water uptake with large soil water reservoir
	Increased root penetration of hardpan	Increased water uptake under restricted soil water reservoir
	Root osmotic adjustment (desiccation tolerance)	Expanded crop-available soil water under restricted soil water reservoir
Shoot related	Stomatal closure	Maintenance of leaf water potential
	Leaf rolling	Maintenance of leaf water potential
	Thicker epicuticular wax layer	Maintenance of leaf water potential
	Osmotic adjustment	Maintenance of turgor potential
	Accumulation of amino acids or growth regulators	Physiological adjustment
Reproductive stage specific	Increased panicle diffusive resistance	Flower at higher panicle water potential
	Early morning anthesis	Flower at higher panicle water potential
	Tolerance for high spikelet temperature	Decreased sterility
	Emergence of new panicles from internodes	Recovery of lost yield component
	Remobilization and translocation of stored reserves	Maximization of potential harvest index
	Nonsynchronous tiller development	Lower probability of catastrophic yield loss

Resistance mechanisms can be classified as root related, shoot related, and reproductive stage specific (Table 5.2).

Root-related traits

Because rice plants take up moisture primarily through their roots, and because the root systems of rice plants vary according to genotype, root-related characteristics have received more attention from rice scientists than other drought resistance traits.

Since root systems usually are hidden from view in the soil, they cannot easily be studied. Hydroponic and aeroponic systems have been employed to study root growth. In the hydroponic system, plants are grown in PVC tubes that are 50-100 cm long (Ekanayake et al 1985b, Haque et al 1989a). The plants are held above the tubes with baskets or plastic-foam holders. The aeroponic system was used by Armenta-Soto et al (1983) to study the genetics of root characteristics. O'Toole and Wolfe (1990) have described how to construct aeroponic systems. Basically, plants are suspended by plastic-foam holders above tanks in which nutrient solution is sprayed as a fine mist. The advantages of this system are (O'Toole and Wolfe 1990):

- The researcher can observe the root system directly.
- Measurement and periodic sampling are easy.

- The root material is clean, simplifying detailed analysis.
- The roots are not mechanically damaged.
- The quantity of plant material supplied is large relative to the space required for the experiments.

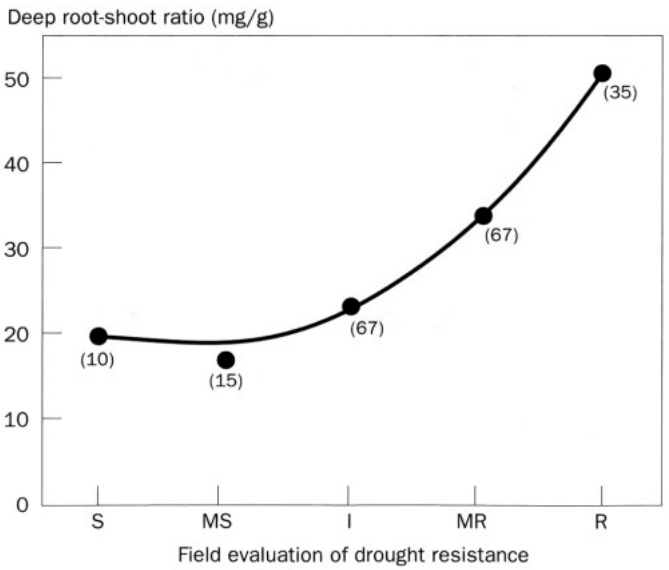
Roots may respond differently to field conditions, however, than to these artificial growing conditions.

Root-related characters have been shown to be related to drought resistance under upland field conditions (Ekanayake et al 1985b). Their association with drought resistance under rainfed lowland conditions, however, is less certain (Chang et al 1982).

Differences in root systems are related to the ability to maintain adequate leaf water potential and resist drought under upland conditions. Varieties with longer, thicker roots or denser root systems had higher resistance as measured by less leaf death under drought stress (Ekanayake et al 1985b).

The ratio of deep roots to shoots also is positively correlated with upland rice drought resistance scores (Fig. 5.2). Yoshida and Hasegawa (1982) asserted that this ratio is a measure of a plant's ability to absorb water from deep soil layers. They also found that upland rices generally have deeper root systems and thicker roots than lowland varieties. The root length density of upland rices in the upper soil profile is comparable to those of other upland crops (Fig. 5.3).

A plant's leaf water potential at dawn is a measure of the plant's ability to rehydrate overnight. It is an indicator of root system development



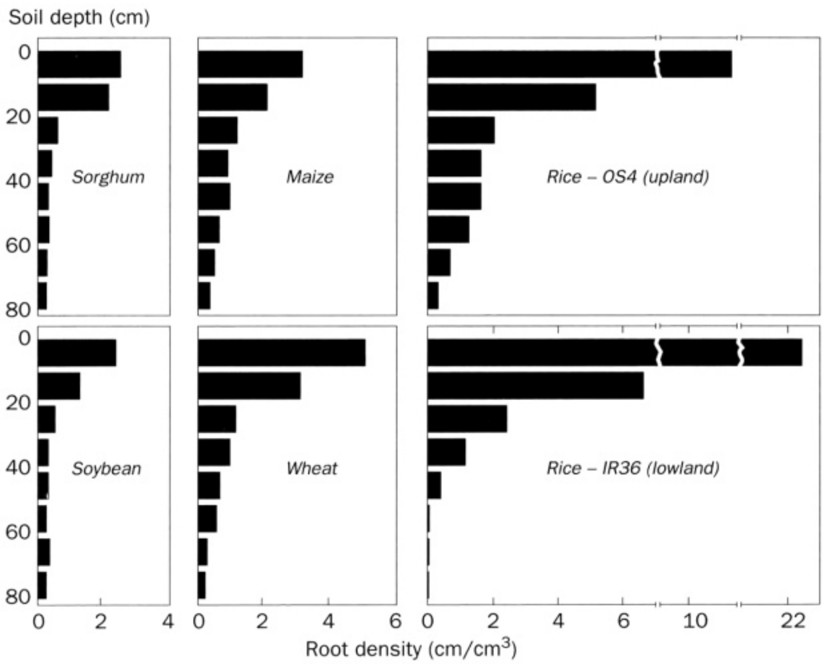
5.2. Relationship between ratio of deep roots to shoots and scores for drought resistance in upland field evaluation. S = susceptible, MS = moderately susceptible, I = intermediate, MR = moderately resistant, R = resistant. In parentheses are numbers of genotypes in each class (Yoshida and Hasegawa 1982).

(O'Toole and Chang 1979) and, like the characteristics mentioned above, is highly correlated with visual scores for drought resistance. Thicker roots tend to have larger diameter xylem vessels (Yambao et al 1992), which allow more water to be conducted from the roots to the shoots—with less flow resistance—in a given time.

Root system depth is related to tiller number but not to plant height. Early tillers have longer and larger roots than late tillers; plants with more tillers tend to have more late tillers and, thus, a shallower root system (Yoshida and Hasegawa 1982). The lack of correlation with plant height indicates that deeper roots can be combined with shorter stature.

Root length, thickness, dry weight, and length density are polygenic traits that are moderately to highly heritable (Armenta-Soto et al 1983, Ekanayake et al 1985b). Xylem vessel cross-sectional area seems to be controlled by a few genes with additive effect; the moderate level of broad-sense heritability (45%) indicates that roughly half of the variation observed is genetic as opposed to environmental.

Champoux et al (1995) used restriction fragment length polymorphism (RFLP) analysis to study the genetics of drought resistance and root morphology in the cross Moroberekan (upland japonica) × CO 39 (lowland indica). They found that 27 marker loci were associated with at least one root characteristic. Of 14 chromosomal regions containing loci associated with drought resistance under field conditions, 12 also were associated with root



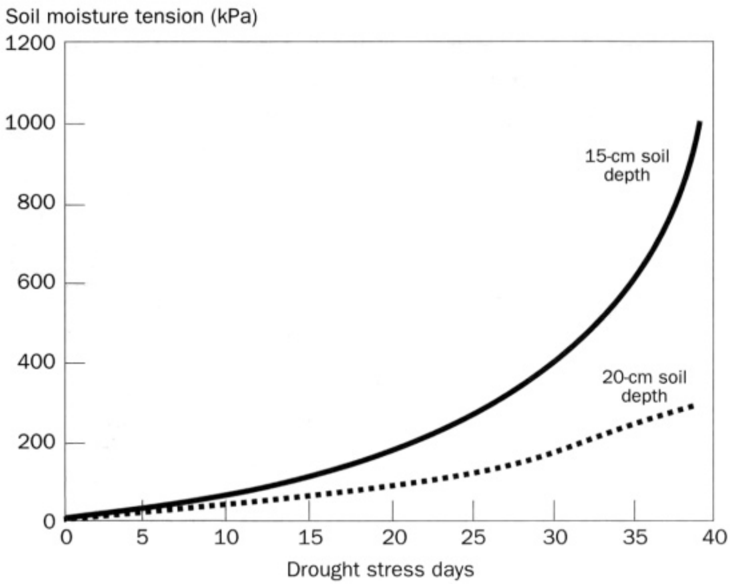
5.3. Root distribution for four upland crops and two rice cultivars grown in upland conditions (Yoshida and Hasegawa 1982).

morphology. Thus Moroberekan genes that were associated with a thicker or more extensive root system also were associated with greater drought resistance under field conditions.

The studies cited above indicate that root-related characters, the most important factors conferring drought resistance, are inherited polygenically. Therefore, few resistant progeny should be recovered from a resistant by susceptible cross. Experience at IRRI, however, has shown that resistant progeny are readily obtained from crosses that include one strongly resistant parent. Genetic studies of resistant by susceptible crosses have indicated that one or more major genes were involved in conferring drought resistance (Singh and Mackill 1991). This finding indicates that inheritance of resistance may not always be as complicated as is frequently assumed. Further evidence supporting the involvement of major genes in root growth of rice comes from the discovery of a mutant gene (*rt*) that inhibits root growth (Futsuhara and Kitano 1985).

While there appears to be no genetic barrier to selecting for deeper and thicker roots, the trait is difficult to measure. Because depth and thickness of roots are positively correlated with drought resistance scores under upland screening conditions, such scores are indicators for differences in root depth. Plants with deep roots avoid stress because, during a drought, they can tap the water stored in lower layers of the soil (Fig. 5.4).

Most studies of drought resistance in rice have been conducted under upland conditions or in aeroponic systems. In both cases, the roots are in an aerobic environment that does not restrict rooting depth. Upland rice cultivars



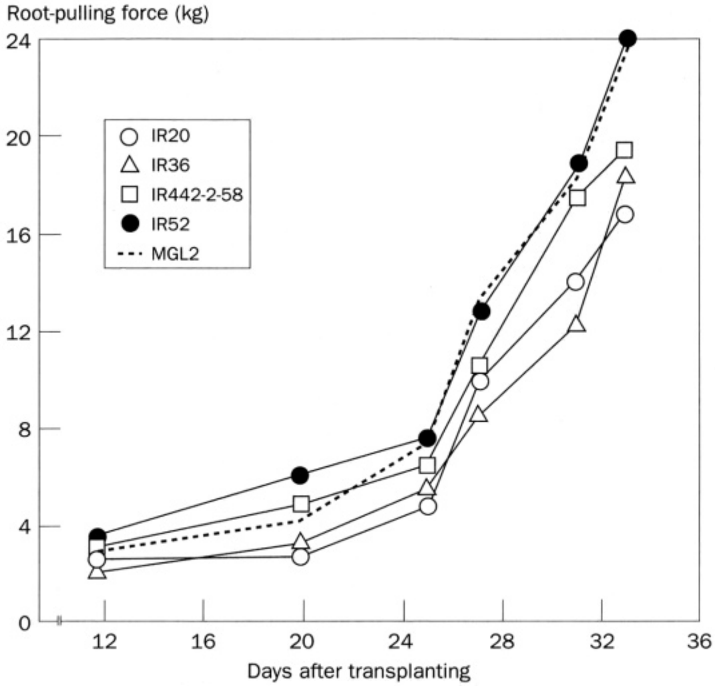
5.4. Development of soil-water deficit during upland field drought screening at 15 and 20 cm soil depth at IRRI (De Datta et al 1988).

generally excel in root characteristics associated with resistance, and they are more likely to perform well under drought screening than lowland rices. Upland rices, however, are not well adapted to transplanted, anaerobic lowland conditions. Thus varieties proposed for release to rainfed lowlands must be screened under conditions similar to those found in lowland fields.

In the lowlands, the land is prepared for planting while it is wet, so a massive hardpan is formed. The roots of rice plants are confined to the shallow layer of soil overlying the hardpan. While the roots of some lowland varieties may be capable of penetrating the hardpan, this capability may not be expressed. When the soil is submerged, the rice plants have little compulsion to develop deeper roots because sufficient water is available near the soil's surface.

Root-pulling force (RPF) has been used to study variations in rooting depth under lowland conditions (O'Toole and Soemartono 1981). About 5 wk after transplanting, plants are lifted from the field using a device that clamps to the base of the plant and is attached to a force meter or scale (Fig. 5.5). The force required to pull the plant is positively correlated with root length density of the portion of the root system that remains in the soil (Ekanayake et al 1986). RPF often is low for upland rices grown under lowland conditions (O'Toole and Soemartono 1981), but it is positively correlated with scores for drought screening under upland conditions (Ekanayake et al 1985a). Some rice cultivars that are known for their drought resistance (e.g., IR52 and MGL2) have high RPF scores (Fig. 5.6). A genetic study

5.5. Measuring root-pulling force. (a) The lateral roots are cut off with a coring device, and the force required to uproot the plants is measured. (b) This force results from breakage of roots and is related to the root mass remaining in the soil.



5.6. Root-pulling force of five rice cultivars from 12 to 32 d after transplanting (Ekanayake et al 1986).

conducted at IRRI showed heritability for this trait to be relatively low (Ekanayake et a1 1985a), suggesting that selection based on a plant's RPF may not always produce progeny with high RPF. Progeny with high RPF can be recovered in crosses involving one high-RPF parent and in crosses between two parents with moderate RPF.

While transplanting is the predominant method of crop establishment, at least 25% of the total rainfed lowland area is direct seeded (Mackill 1986). In direct seeded areas, conditions are similar to those found in uplands. The resistance mechanisms of upland rice, in particular the deep root system, are more effective in direct seeded than in transplanted rainfed lowland rice. The large differences in drought resistance observed among varieties under upland drought screening indicate that the scope is substantial for breeding more resistant cultivars (Ekanayake et al 1985a, De Datta et al 1988).

Shoot-related traits

Three mechanisms limit water loss from rice leaves (Table 5.2):

- stomatal closure,
- leaf rolling, and
- leaf epicuticular wax.

While stomatal closure, described earlier, limits water loss, it also reduces uptake of carbon dioxide from the atmosphere and, consequently, reduces the rate of photosynthesis.

As a rice plant's leaf water potential decreases, its leaves begin to roll or curl. Leaf rolling can be considered both a symptom of drought stress and an adaptive response by the plant. Leaf rolling reduces the area of leaf exposed to the atmosphere and increases resistance to transpiration on the upper surface of the leaf (O'Toole and Cruz 1980). The level of leaf water potential at which leaves begin to roll varies between cultivars. Contrary to what would be expected, the leaves of some drought-resistant upland rices begin to roll at a higher leaf water potential than do those of lowland rices (Dingkuhn et al 1989). Although leaf rolling reduces gas exchange and photosynthesis, it improves a plant's *water use efficiency* — the ratio of carbon dioxide assimilated to water transpired. While plants use leaf rolling to avoid drought stress, those with leaves that roll at high leaf water potential may have reduced yields during periods of only moderate stress (Dingkuhn et al 1989).

Drought-resistant cultivars are better able than susceptible cultivars to maintain water uptake; thus their leaves remain unrolled longer. Results of drought screening tests generally show delayed leaf rolling to be associated with resistance (Singh and Mackill 1990). Some scientists, however, have urged breeders to be cautious in using leaf rolling to score plants for drought resistance (Dingkhun et al 1989, Turner et al 1986). If plants are prevented from increasing their water uptake to avoid stress (for example, when they are grown as potted plants with confined rooting volume), then leaf rolling may help the plants to avoid drought by limiting water loss.

Most water that is lost from the leaves escapes through the stomata. Much less is lost through the cuticle, which is covered with a layer of epicuticular wax. When leaf water potential drops and the stomata close, however, transpiration through the cuticle continues. Thus during severe drought, epicuticular transpiration accounts for a greater proportion of total leaf water loss than does stomatal transpiration.

Differences in cuticular resistance to water loss are related to the amount of wax n the leaf surface (O'Toole et al 1979). Upland cultivars usually have more epicuticular wax than do lowland cultivars (O'Toole et al 1979). Transferring this trait into lowland cultivars could increase drought resistance because it would be effective whether the rice were transplanted or direct seeded. Unfortunately, rice has only a fraction of the wax of upland crops; for example, the waxiest rice leaves observed so far have less than 5% of the epicuticular wax of sorghum (O'Toole et al 1979).

The amount of leaf wax appears to be polygenically inherited in rice (Haque et al 1992). Considering that the heritability of this trait is quite low and its measurement is expensive and time consuming, it is unlikely to be used to select for drought resistance in breeding nurseries.

When leaf water potential is low, cell turgor (or pressure potential) is reduced, so cells are less able to expand. Plants frequently respond to a drop in water potential by increasing the concentration of cell solutes, thus reducing the solute potential. The process may be passive: as the cells dehydrate, the concentration of solutes naturally increases. Additionally, solutes may be actively synthesized that further lower the solute potential. At a constant leaf water potential, a reduction in solute potential increases turgor, allowing the plant to maintain growth at a lower leaf water potential (Steponkus et al 1982). This process is called *osmotic adjustment.* Hsiao et al (1984) showed that, when tissues experience osmotic adjustment, the leaves roll and dry at a lower leaf water potential than when tissues do not adjust; thus osmotic adjustment allows photosynthesis to be maintained longer under stress.

Turner (1986) observed varietal differences in osmotic adjustment under drought stress. Lowland (indica) cultivars adjusted more—about 0.5-0.6 MPa under severe stress—than did drought-resistant upland cultivars. The level of osmotic adjustment was related, however, to the cumulative amount of stress as measured by number of days below a threshold leaf water potential.

For other crops, much research has focused on the accumulation of certain amino acids (such as proline) or growth regulators (such as abscisic acid) in cells exposed to drought stress. It is not clear whether these accumulations are resistance mechanisms or symptoms of stress. In general, scientists believe they are a consequence of drought injury and, therefore, selection for them has not been shown to be useful.

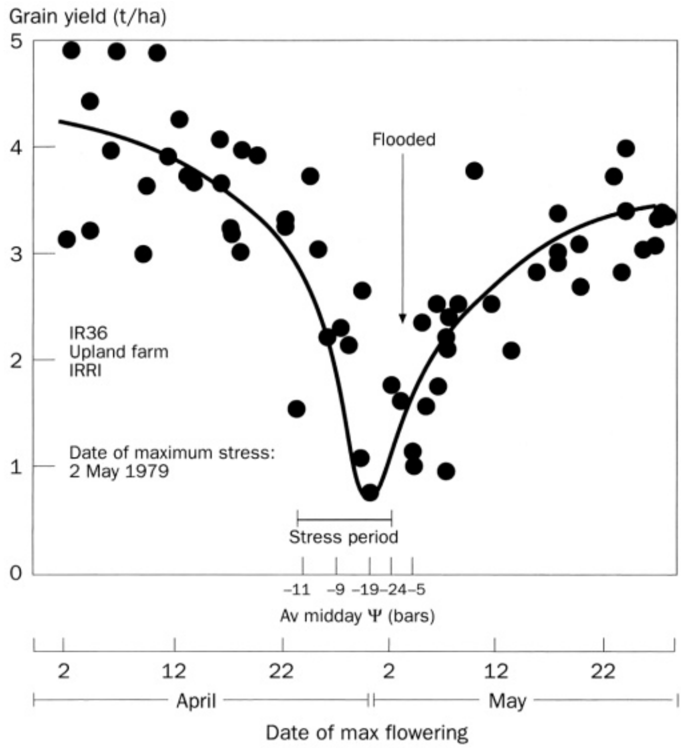
Reproductive-stage traits

Rice is most sensitive to drought during its reproductive stage (Fig. 5.7) (Matsushima 1966, Hsiao 1982, O'Toole 1982); however, less research has been done on the effects of drought at this growth stage than on those at the vegetative stage. Most root- and shoot-related traits continue to function during the reproductive phase because, although the vegetative tissues are not growing, they are still active. Further, several flowering characteristics play important roles in drought resistance at this stage (Table 5.2).

When drought occurs during rice's reproductive stage, panicle exsertion and anthesis are inhibited (Ekanayake et al 1989), so the spikelets are not fertilized. The result can be drastic yield reduction.

The effects of high-temperature stress on a rice plant's reproductive system are similar to the effects of drought. Plants that are able to resist high-temperature stress usually are those in which anther dehiscence is more complete. This ability to maintain anther dehiscence under exposure to high temperatures is controlled by a few genes of mostly additive effect (Mackill and Coffman 1983). And the mechanism that controls this trait appears also to confer resistance to drought-induced spikelet sterility (Mackill and Ekanayake 1986).

Genotypes differ in drought resistance at the reproductive stage; however, it is difficult to screen for drought resistance under field conditions because plants that flower on different days experience different amounts of stress. Some upland rices appear to be drought resistant during the reproductive stage (Garrity and O'Toole 1994), but the mechanisms of that resistance are not fully understood. It is not clear whether these mechanisms can be applied to rainfed lowland varieties.



5.7. Grain yield of IR36 planted at 16 dates in relation to a single drought-stress period. Crops that flowered on 2 Apr were near maturity during the stress period, and those that flowered after 22 May were near panicle initiation during stress (IRRI 1980).

Flowering rice panicles have little resistance to water loss even when they are being severely desiccated. O'Toole et al (1984) reported that the diffusive resistance of spikelets at flowering remained 1.5 s/cm across a wide range of panicle water contents. This finding suggests that, unlike leaf tissue, rice panicles have no mechanism for inhibiting water loss and thus stabilizing water content and water potential.

Panicle and leaf water potentials follow similar diurnal trends under both normal and stress conditions. Panicle water potential tends to be slightly higher than leaf water potential during the early and middle flowering periods (IRRI 1983a). Rice panicles, however, may become completely desiccated during a drought that is short enough or mild enough to leave leaf tissue unaffected (O'Toole et al 1984). Rice's behavior under these circumstances contrasts dramatically with that of wheat, in which spikelets die only when the drought is so severe as to kill all of the leaves (Morgan 1971).

Considering the sensitivity of rice panicles to drought stress, it would seem practical to breed for morphological adaptations that increase panicle resistance to water loss. A number of panicle traits have been suggested, however, as mechanisms that, when genetically manipulated, could increase the resistance of the panicle to water loss (O'Toole 1982, Garrity et al 1986a) such as

- a thicker cuticular wax or silica layer on the spikelet epidermis;
- dense trichome development on the lemma and palea; that is, hairy or velvety glumes;
- presence of awns;
- erect leaf structure, which limits the panicle's exposure to the atmosphere;
- partial rather than complete exsertion of the panicle.

The utility of such traits in improving the drought resistance of the rice panicle was investigated by Garrity et al (1986a). Shielding emerging rice panicles to reduce their transpiration was expected to increase spikelet fertility during drought stress. When various panicle shields were applied to the emerging panicles of drought-stressed plants, panicle transpiration was greatly reduced, but spikelet fertility did not increase. They concluded that even when the emerging panicle is well protected, its water potential equilibrates with the rest of the plant, which has a much larger surface area. Thus genetically increasing panicle resistance through breeding is unlikely to produce significant benefits.

Several reproductive-stage traits may allow rice plants to recover from drought (Table 5.2):

- The formation of new panicles that develop from buds at the rice plant's internodes may help the plant to recover lost yield components. These panicles, however, will differ considerably in flowering date and thus not all of the grain will be mature at the same time.
- Plants that can translocate more carbohydrates from vegetative tissues to the grain may be able to recover from drought that occurs before or during flowering (Reyniers et al 1982). The ability to accumulate and translocate stored carbohydrates to the grain differs among genotypes and is directly related to grain yields under drought stress (Chaturvedi and Ingram 1989).
- Plants that can develop tillers asynchronously may be able to avoid catastrophic yield loss caused by short, intense drought during flowering. Since not all of the tillers are flowering at the same time, only some of them are killed by the drought. But asynchronous tillering is usually undesirable because the grain does not ripen uniformly. At harvest, some grains may be immature while others are overripe. This trait, however, may decrease risk in highly drought-prone environments.

Screening methods

Many methods are available for screening plant populations for drought resistance. Deciding which method is most suitable and effective for a particular program is challenging because

- a large number of traits are related to drought resistance,
- the relationships between those traits are complex,
- different traits are needed for different soil and hydrological environments, and
- breeding programs must work within financial constraints.

Therefore, in choosing an appropriate screening method, a breeder must consider

- the growing conditions of the test plot compared with those of the target environment,
- the growth phase at which the rice crop is most likely to be exposed to drought in the target environment,
- the intensity of stress that is appropriate to the screening,
- the plant characteristics that are to be monitored, and
- the techniques that will be used to measure those characteristics.

In early generations, screening methods should be used that apply to a large number of genotypes. As lines advance, or as you try to identify new donors, methods that require more time and resources become more appropriate.

IRRI has found several methods of drought screening to be useful in breeding improved varieties; however, each of these methods has some limitations.

Upland field screening at the vegetative stage

At IRRI, an upland nursery that is used for drought screening during the dry season was refined and used extensively since 1978 (De Datta et a1 1988). Through these screening trials, breeders identify cultivars that retain a high proportion of living biomass when the young plants are subjected to progressively more intense soil-water deficit during the vegetative stage. Upland field screening also lets breeders identify cultivars that can rapidly resume leaf production and growth when the drought stress is relieved through irrigation. Using this method, thousands of cultivars can be evaluated each year.

The entries are dry seeded on a granular clay soil in a well-tilled upland field that drains freely and is not influenced by subsurface groundwater. This planting takes place after the onset of the dry season, when rainfall is dependably low (in January at IRRI). For each entry, 10 g of seed is hand drilled in unreplicated two-row plots. The rows are spaced 30 cm apart and are 2.5 m long. A total of 60 kg/ha of nitrogen fertilizer is applied in two equal doses by topdressing at 10 and 20 d after seedlings emerge. Mercury tensiometers are installed at several locations in the field. (Directions for fabricating tensiometers and interpreting the readings are given in Appendix 1.) The field is sprinkler-irrigated at 4-d intervals, or when the soil matric potential (SMP) at a 10-cm depth approaches −0.03 MPa (0.3 bars).

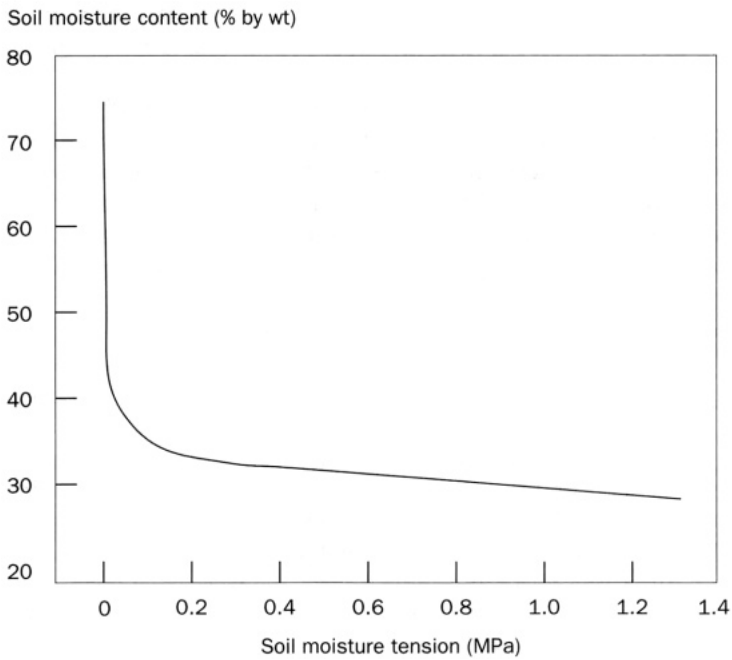
Irrigation ends 30 d after seeding. Soil moisture is monitored at 0 and 20 cm depth as the soil dries. At the same time, the tensiometers are monitored until average SMP at 10 cm reaches −0.08 MPa (the device's limit for accurate measurement). Then soil samples are gathered at 0 to 20 cm depth every other day, and the average gravimetric moisture content of the samples is determined; that is, the samples are oven dried, and the soil moisture content is calculated as a percentage of soil dry weight. A curve relating SMP and soil moisture content is derived by using both techniques simultaneously (Fig. 5.8). The curve is then used to calculate SMP values from soil moisture content and thereby determine the date at which SMP reaches -0.5 MPa and -1.0 MPa.

The use of tensiometers helps breeders

- make sure the irrigation schedule is controlled and uniform,
- score the entries each year at the same precise levels of soil water potential.

Because the use of tensiometers improves the precision and consistency of screening trials, data gathered in separate years can be compared reliably. Three times during the dry-down phase, each entry is inspected and given a score representing its reaction to drought—when SMP reaches -0.2, -0.5, and -1.0 MPa. Generally, these levels are reached about 2 d after SMP reaches -0.1, -0.4, and -0.8 MPa, respectively. After the final drought screening at -1.0 MPa SMP, the field is twice sprinkler-irrigated to saturation; and, after about 10 d, the entries are inspected and their recovery is scored (Table 5.1).

Such screening at the vegetative stage has identified a number of cultivars and breeding lines that consistently score high in drought resistance



5.8. Desorption curve of soil (0-20 cm depth) for the drought-screening site used at IRRI (De Datta et al 1988).

(Fig. 5.9, Table 5.3). It has let breeders screen large numbers of lines at early stages of the breeding program. And it has been especially useful in letting breeders evaluate cultivars' ability to recover from drought.

The method, however, looks at recovery from prolonged drought stress that reaches -1.0 MPa (Malabuyoc et al 1985). This water deficit is so severe that the plants' viable leaf area is drastically reduced and many entries nearly die. It is not yet clear how a plant's ability to recover from such conditions is related to its ability to recover from the less severe stress that is typical of field conditions. Scores for drought resistance are only moderately correlated with scores for drought recovery (r = 0.55**) (Malabuyoc et al 1985). Thus, many varieties that resist drought well are unable to recover from prolonged drought. But some are able to recover.

Chang et al (1974) used another method for mass screening entries in the field during the dry season. They placed pairs of check varieties—one that was resistant to drought and one that was susceptible—at regular intervals throughout the test plot. The plots were irrigated until 40 d after seeding; then water was withheld for about 20 d. Entries were scored when the leaves of the susceptible checks began to roll but those of the resistant checks still were unfurled. Then irrigation was resumed, and the entries were scored for recovery ability.

Variability within the field for soil factors such as moisture-holding capacity can decrease the accuracy of drought screening, so the most uniform field possible should be used for such screening. One way to assess a field's uniformity is to plant a single crop of a drought-susceptible cultivar and observe the progress of drought symptoms. If the onset of drought symptoms differs by several days among parts of the field, it is not suitable for drought screening.

Even in fields that seem uniform, check varieties should be planted at regular intervals to monitor this variability. A check variety in every 10 plots is recommended if field space and seed of the check variety are sufficient. All entries are scored for drought resistance, and the scores for the checks are used to adjust the scores of the nearest plots.

Supapoj et al (1982) proposed using the average deviation in the score of each check from the mean score of all checks to adjust the scores of adjacent entries. Performing these calculations takes time and effort; so, in practice, many breeders do not often adjust scores. A computer can handle the calculations quickly and easily. As more breeding programs gain access to computers, adjustment of scores is bound to become more common.

Dry-season field screening methods have a number of limitations:

- They depend on the ability to grow a large number of lines in the field during a period of little rain. Thus a sprinkler irrigation system usually must be installed to deliver water uniformly over the entire field.
- It is difficult to apply the same degree of stress each year. In Los Baños, for example, unseasonable rainfall and cloudy weather during the dry season create year-to-year environmental variability.
- In some areas, dry-season soil moisture is difficult to control due to seepage from canals or adjacent irrigated plots.

5.9. Promising lines are identified in an upland drought-screening nursery in the dry season at IRRI.

Table 5.3. Best performers in upland drought-screening nursery, IRRI, 1978-85 (De Datta et al 1988).

Designation	Accession number	Origin/ resistant source	Drought score		Recovery score
			-0.5 MPa	-1.0 MPa	
Germplasm bank entries					
ARC10372	20884	India	3.2	5.0	2.4
BKN6986-108-2	39171	Thailand	2.9	4.7	2.5
RD19	39174	Thailand	2.4	3.6	2.4
Carreon	05993	Philippines	3.3	5.0	2.7
IRAT133	55683	Ivory Coast	2.2	3.9	2.2
IRAT144	55685	Ivory Coast	0.7	4.0	2.3
Leb Mue Nahng 111	07819	Thailand	3.1	5.1	2.6
Moroberekan	12048	Guinea	2.1	4.3	3.0
Nam Sagui 19	11462	Thailand	4.2	5.9	3.1
NCS 116	51866	India	1.5	3.5	1.0
NCS 130	51879	India	2.0	3.5	1.0
IRRI breeding lines					
IR5178-1-1-4		LMN 111	3.2	4.7	2.7
IR5624-110-2		KDML 105	2.4	4.2	2.5
IR52		Nam Sagui 19	3.3	4.6	2.4
IR9560-2-6-3-1		Carreon	3.7	5.0	3.0
IR9669 Sel		Carreon	2.1	4.2	2.0
IR9782-111-2-1-2		Nam Sagui 19	2.2	4.5	2.7
IR9995-96-2		Nam Sagui 19	3.2	4.9	3.1
IR65		Nam Sagui 19	2.5	4.0	2.0
IR24761-35-3		Nam Sagui 19	2.2	4.0	1.9
IR24761-156-3		Nam Sagui 19	2.2	4.5	1.4

Note: See Table 5.1 for the scorlng system used. 1 = best, 9 = worst.

- For breeding programs that focus on photoperiod-sensitive cultivars, dry-season screening may not realistically evaluate a cultivar's potential. Under the shorter daylength of the dry season, these cultivars often are forced to initiate panicles and flower within a month or two of seeding, so normal vegetative growth is likely to be inhibited.

Drought screening in the greenhouse

Breeders can screen plants in the greenhouse at any time of year, even during the rainy season. A number of methods have been developed for vegetative-stage screening in the greenhouse (O'Toole and Maguling 1981). The primary differences in the methods concern rooting environment: some grow the plants in pots, where the roots are confined to a limited volume of soil; others grow them in deep tanks so that deep rooting is not restricted. Screening in pots is inappropriate for upland rices, which rely on deep root growth as a major mechanism of drought avoidance. For rainfed lowland rices, however, which often are grown in soils that resist deep root penetration, screening in pots may produce satisfactory results. When the plants to be screened are grown in pots, the breeder can select genotypes that make best use of the limited supply of soil water either by limiting their transpiration losses or by tolerating intense deficits of tissue water without dying.

De Datta et al (1988) planted large numbers of rice varieties in drums (50 cm tall and holding 100 liters) to compare their ability to survive and recover from drought. Kandasamy (1981) developed a greenhouse method that lets breeders compare varieties' ability to force their roots through a uniformly compacted subsoil of known penetration resistance. This method is useful for comparing small numbers of genotypes but is not suitable for large-scale screening.

Thus field screening is the easiest approach: more lines can be tested simultaneously. Since field screening may not give the whole picture for rainfed lowland rice, greenhouse screening can also be informative.

Reproductive-stage screening

As was mentioned earlier, rice is most sensitive to drought during the reproductive stage, when stress may drastically reduce grain yields (Namuco et al 1980). Geneticists have not yet discovered whether the same genes control drought resistance at the vegetative stage and at the reproductive stage. It is plausible that some characteristics are important at both stages—for instance, a root system that has superior ability to exploit soil moisture or shoots that have excellent water conservation mechanisms are useful at any growth stage. Nevertheless, the reproductive stage includes unique events such as meiosis, panicle exsertion, anthesis, and caryopsis growth; and the complex mechanisms that control these functions complicate the genotype's interaction with water deficits.

Long-term research at IRRI (Garrity et al 1982; Novero et al 1983; IRRI 1984a, 1985) resulted in the development of a program that screens rice for drought resistance during flowering. The three-tiered program is simple and practical (Garrity and O'Toole 1994); but because screening during reproductive stage poses unique difficulties, the program requires more management than those that screen plants at the vegetative stage.

Tier one: vegetative-stage screening. The first tier of screening takes place during the vegetative stage using methods described in the previous section. Cultivars that are susceptible to drought at this stage are eliminated because experience has shown they are unlikely to have superior resistance at the reproductive stage.

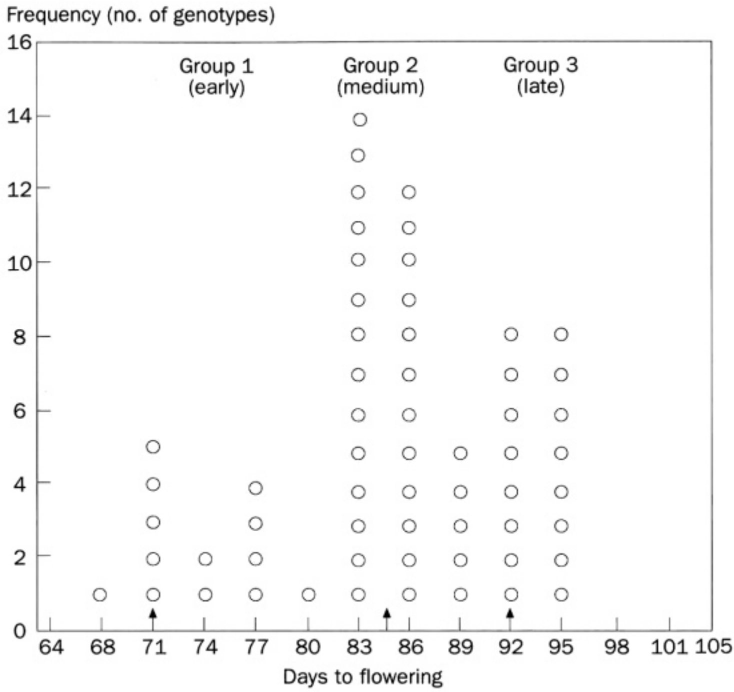
Tier two: mass screening. Many of the same mechanisms of drought avoidance and tolerance are responsible for overall resistance at both the vegetative and reproductive stages; however, cultivars that have similar vegetative-stage resistance may have significantly different resistance at the reproductive stage. Therefore, the second tier of screening—mass screening at flowering—helps breeders to identify, from among the remaining entries, the cultivars that are able to maintain spikelet fertility when exposed to drought.

The mass-screening method includes (Garrity and O'Toole 1994)

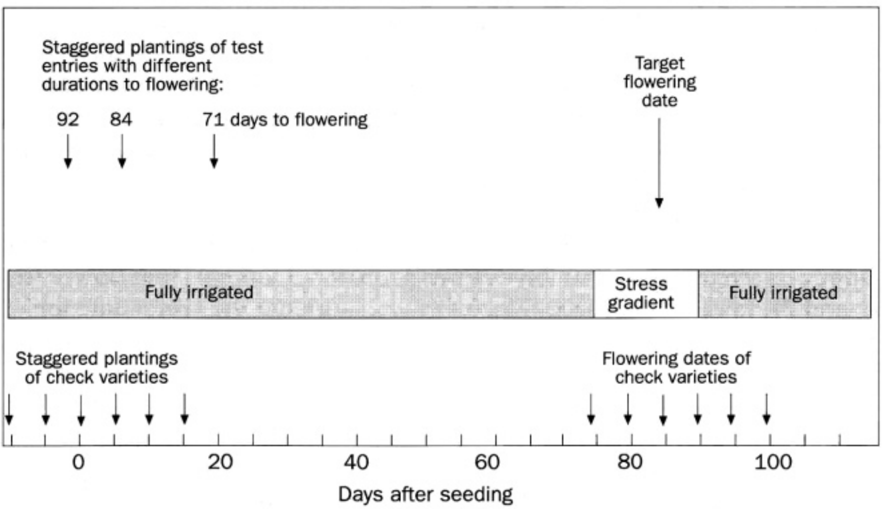
- staggering the planting of genetic material during the dry season to synchronize flowering dates,
- generating water deficits by interrupting irrigation during the flowering period, and
- scoring for spikelet fertility.

The planting materials are assembled, and the flowering date of each line is estimated. The frequency distribution of days from seeding to flowering is plotted (Fig. 5.10). From this information and climate data for the research site, the optimum period in which to generate a controlled drought is chosen. At IRRI, the ideal period comes in the first half of April, when the days are most likely to be dry and clear. In some locations, it may not be possible to plant the nursery at the appropriate time for plants to flower at this optimum date. For example, it may be difficult to seed early enough to obtain the appropriate flowering dates because wet weather at the end of the rainy season prevents land preparation. Likewise, at higher latitudes, low temperatures from December to February delay flowering until the end of the dry season, when rains can interrupt the stress period.

The planting materials are divided into three to five groups based on days to flowering, and dates for staggered planting are selected. For example, suppose a screening trial involves three groups of materials that flower 92, 84, and 71 days after seeding (Fig. 5.11). And suppose the target date for imposing drought conditions is 14 Apr. To assure that all of these materials flower at the same time and, therefore, can be tested for drought resistance simultaneously, the first group must be seeded on 13 Jan (92 days before the target date), the second group on 21 Jan (84 days before the target date), and the last group on 3 Feb (71 days before the target date). Using more groups makes it possible to target the flowering of each genotype more precisely, but usually there is some uncertainty in the estimated flowering dates of many of the lines (especially when data about a variety's flowering date have been collected only during the wet season). However, as data from dry-season screening trials accumulate, flowering dates become more predictable.



5.10. Frequency distribution of a set of rice culitvars nominated for flowering-stage drought screening. These entries are divided into three groups. The arrows indicate the recommended number of days before the target date that each group should be planted.



5.11. Scheme of planting dates for synchronizing the flowering periods of test entries. Check varieties are planted every 5 d so they will flower throughout the stress period. Test entries are planted according to their expected growth duration. Those that take the longest to flower are planted first. The objective is for all of the plants to flower as near the target date as possible.

A *blocks-within-reps experimental design* (referred to as the *group balanced block design* by Gomez and Gomez 1984) is most suitable for the mass screening trials. Under this design, the members of each group are planted together in a block. This arrangement is convenient because the different maturity groups must be seeded on different dates; so for each seeding date, all the entries can be seeded together in contiguous plots within each replication. This greatly simplifies field management. Plot size is 1.0 m (four rows 25 cm apart) × 1.5 m in three replications—that is, three identical plots are planted for each group. Each plot is seeded at a rate of 75 kg/ha, so 34 g of seed is needed for each entry.

Because the mass screening trial is conducted during the dry season, it is sometimes difficult to avoid exposing the crop to unwanted drought stress during vegetative growth. To prevent such stress, enough water must be applied to compensate for the high level of evapotranspiration demand. Plots should be sprinkler-irrigated every 3-4 d at a rate equal to 1.4 times the amount of water evaporated in a Class A evaporation pan during that period (1.4 × Epan). At IRRI, when irrigation rates fall below this level, even fully irrigated dry-season controls show greater-than-normal levels of panicle sterility.

For any trial, the amount of irrigation needed depends on site conditions and on the length of the period of induced drought stress. Tensiometers (see Appendix 1) can be installed in each replication at depths of 10 and 30 cm and can be monitored daily. The data produced can be used to assess soil-water conditions and to schedule irrigation.

During the stress period, the water supply can be interrupted, or partial irrigation can continue. A sprinkler irrigation system is used, with pipelines spaced 12 m apart and sprinklers set at 12-m intervals, to provide a uniform amount of water over each part of the field.

To use mass screening in a lowland environment, a bunded field must be chosen where the water table is deep enough that it cannot be reached by the crop's roots. The field is flooded continuously or intermittently during vegetative growth; then it is drained during the flowering stage to induce drought stress.

The following data should be collected during mass screening:

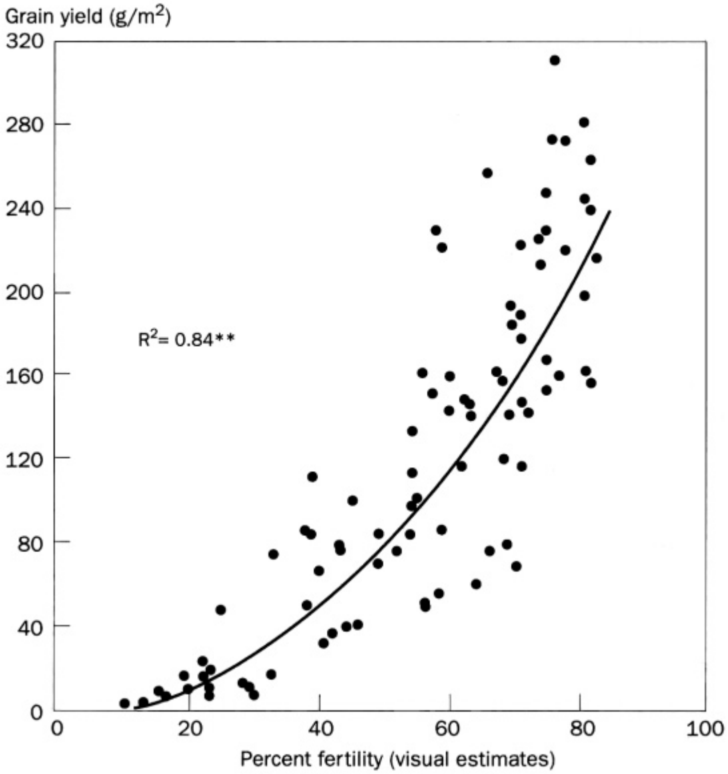
- the date of 50% flowering for each entry,
- a visual estimate of spikelet fertility for each plot after full irrigation is resumed; scoring should follow the *Standard evaluation system for rice* (IRRI 1988d).

Spikelet fertility is related to grain yield in plants that are exposed to drought during flowering (Fig. 5.12); in fact, sterility differences explain 66-84% of yield variation in trials across years. Therefore screening for spikelet fertility can reliably replace direct yield sampling in large tests and may be estimated on plots as small as 1 m^2 (Garrity and O'Toole 1994).

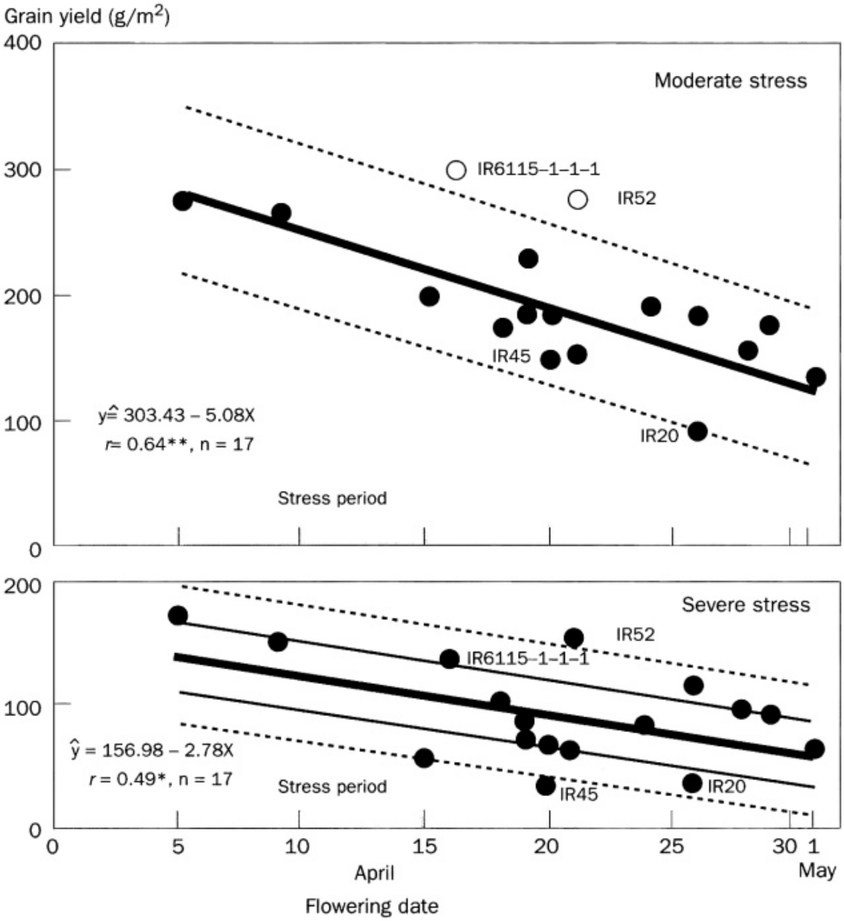
An experienced researcher can estimate spikelet fertility quickly in the field. Ten panicles are randomly selected from a plot in a minute or two; and, after some practice, visual ratings are made that are highly correlated (r = 0.93**) with actual spikelet fertility counts (IRRI 1984a).

Cultivars that flower early in the induced drought period partially escape the most severe stress and, thus, tend to have greater numbers of fertile spikelets than those that flower late in the period. A cultivar's relative performance, therefore, is influenced by the differences that occur among cultivars in the date of flowering in relation to the onset of stress.

Bidinger et al (1982) showed how a drought-stress index can be used to adjust the actual values of spikelet fertility or grain yield for each cultivar and thus remove this source of bias. First, using a best-fit regression model (Fig. 5.13), yield or percentage of spikelet fertility is regressed against flowering date (that is, number of days after the onset of the induced drought on which 50% of the entries flowered). If the regression coefficient is not significantly different from zero, then no adjustment is needed, and the spikelet fertility values are compared directly among genotypes. If the regression coefficient is significantly different from zero, then the index (I) of spikelet fertility (F) for each cultivar is calculated as



5.12. Relationship between spikelet fertility and grain yield, IRRI, dry season, 1982 (Garrity and O'Toole 1994).



5.13. Grain yield of a set of rice cultivars grown under reproductive drought stress plotted against flowering date. The dashed lines are parallel to the regression line and show the entries that have the greatest deviation from the line. IR52 and IR61151-1-1 showed the greatest deviation from regression and were ranked as most tolerant of drought at the reproductive stage.

$$I = \frac{F - \hat{F}}{SE_{\hat{F}}}$$

where $\hat{F}$ is the predicted spikelet fertility for the test genotype, obtained from the regression equation and $SE_{\hat{F}}$ is the standard error of regression for $\hat{F}$. The entries are then ranked according to their index values (see Garrity and O'Toole [1994] for more details).

Because screening at the flowering stage involves a degree of uncertainty, a genotype must perform consistently well in trials over 2 or 3 yr before it can be considered drought resistant during flowering.

Tier three: advanced screening. Advanced screening focuses on 20-30 cultivars that performed well during mass screening. Five planting dates are used to make more detailed evaluation possible. Flowering dates can be predicted more accurately than for mass screening because more information has been accumulated about the entries.

Advanced screening requires the use of at least two irrigation regimes: full irrigation for a control group and artificial drought stress for the trial groups. The control group is managed as a separate experiment. Each experiment is laid out in a blocks-within-reps design, replicated three or four times. The data collected, and the frequency with which they are collected, depend on the objectives and resources of the research team. Records of flowering dates and estimates of spikelet fertility and grain yield, at least, are gathered for each experiment. Where possible, other data are gathered to help explain the mechanisms underlying the genotypes' different responses to drought; these may include

- leaf water potential,
- canopy temperature (Garrity and O'Toole 1995),
- completeness of panicle exsertion,
- flowering delay,
- soil-water extraction, and
- yield components such as number of panicles per m^2, number of spikelets per panicle, percentage of filled grains, and grain weight.

Garrity and O'Toole (1995) assessed the use of canopy temperature as measured with an infrared thermometer as a selection tool for drought avoidance. They found that it classified cultivars similarly to visual drought scoring.

Irrigation management is the same as that in mass screening: a drought is imposed during the flowering stage by partially or completely interrupting irrigation. Plots typically are 10-15 m^2 in size. Data analysis procedures are the same as for mass screening (Fig. 5.13). Superior genotypes are those that have the largest positive deviations from the regression which estimates the expected yield for each date based on the entire dataset. For example, in a test at IRRI, the varieties IR52 and IR6115-1-1-1 had the greatest deviations from regression (Fig. 5.13).They ranked as the cultivars most capable of remaining productive when exposed to drought during flowering.

The three-tiered method has several limitations:

- Staggering planting dates introduces experimental variation because genotypic performance may vary as a function of planting date. This effect makes genotypic comparisons less accurate.
- Staggering planting also increases the complexity of managing the field experiment.
- The method is used in the dry season, so it cannot be used effectively with most photoperiod-sensitive cultivars. Their normal flowering date does not fall during the experimental period, and most fail to flower.

Breeding strategies

In producing rice cultivars with increased drought resistance, breeders must contend with many obstacles:

- The interaction among the plants' resistance mechanisms is complex.
- The inheritance of the mechanisms is complex.
- The relationship between any single plant characteristic and drought resistance often is tenuous.
- While root characteristics are useful indicators of drought resistance in upland rices, they may not be so closely related to drought resistance in lowland rices.
- Because environmental factors, such as weather, are not controllable, it is difficult to apply the same stress to successive field trials.

These obstacles often discourage plant breeders, who are under immediate pressure to develop new rice cultivars for farmers. It is tempting, therefore, to focus on breeding cultivars that are productive when water is available. But drought causes tremendous yield losses; and, recognizing that modern varieties usually are susceptible to drought, many farmers refuse to adopt them.

Thus breeders must be determined to incorporate drought resistance into their programs' objectives, keeping in mind some practical considerations involving choice of parents, selection environments, evaluation of advanced lines, and other approaches.

Choice of parents

The literature reports information about drought-resistant varieties that can be used as parents, and this information can be helpful to breeders as they plan their programs. The best sources of drought resistance, however, are local varieties that have proven their abilities in the field. Thus farmers of the target area are the most reliable source of information about potential parents. Most farmers have evaluated a number of varieties over many years, and many grow local varieties that are known for their performance under drought conditions—Khao Dawk Mali 105, for example, which is grown extensively in northeastern Thailand.

Cultivars that are widely grown in drought-prone areas should be prominently featured in the crossing program. Many of them may be valued by farmers for their ability to escape drought, which involves traits such as photoperiod sensitivity or short duration, tolerance for delayed transplanting, or vigorous vegetative growth or tallness that makes them competitive with weeds. When making crosses, it may be useful to combine these drought-escaping traits with drought-avoiding traits such as deep roots.

While many upland cultivars are drought resistant, they generally should not be incorporated into breeding programs for lowlands because

- few of their drought resistance traits are expressed in lowland environments,

- they tend to combine poorly with lowland cultivars, and
- the progeny of upland-lowland crosses have high sterility rates.

There are exceptions, of course. For example, some Asian upland cultivars belong to isozyme group I (indica) and may give better recombinants than those of group VI (japonica), which includes most upland types. Many upland rices of India and Bangladesh belong to isozyme group II (aus) and thus are more compatible with indica types than the group VI cultivars. Work at IRRI indicates, however, that aus cultivars may not be good sources of drought resistance since many of them have low water use efficiency under stress (Dingkuhn et a1 1989). MGL-2, a lowland cultivar from India that was selected from a traditional red rice, is both drought resistant and adapted to lowlands. Although it belongs to isozyme group I, when it is crossed with improved lowland rices, the progeny tend to have high sterility rates. Finally, the "wide compatibility gene" recently identified in some upland rices of group VI (Ikehashi and Araki 1986) can be useful in making crosses between upland and lowland rices (see Chapter 2). Progeny resulting from crosses between upland japonica rices that have this gene and lowland indica rices have higher fertility rates. Some African upland rices that are drought resistant, such as Moroberekan, have this gene.

Selection environments

Opinions vary on how best to handle early-generation populations when breeding for stress-prone environments. Most commonly, breeders strive to develop varieties that combine drought resistance with superior yields under more favorable conditions. Scientists hope these varieties will be superior to traditional cultivars under both stressed and unstressed conditions. At least, their yields should not be inferior to those of traditional cultivars in more stressful environments.

Heritabilities for yield-associated traits tend to be lower when environmental conditions are stressful than when they are not. Some breeders contend, therefore, that early generations should be selected under optimum conditions. In many field crops, however, selection for grain yield is ineffective in early generations. So if differences in stress resistance can be assessed among individual plants or progeny rows, then it makes sense to grow early generations under stress.

Using drought as a selection pressure during the early generations maximizes the chances of identifying superior plants (Fig. 5.14). Another benefit of applying stress to bulk generations is that the tall plants of the segregating populations—which, due to drought stress, do not achieve their full height—do not compete unduly with shorter neighboring plants, which may be generally more productive than the tall plants. The crops should be planted in well-drained fields that are known to be especially subject to drought, or they should be planted at a time of year when rainfall is scanty. The breeder should use the method of crop establishment that is most often used by farmers of the target area. In later generation pedigree nurseries (F_4 to F_6) more favorable environmental conditions can be applied so lines that perform well when water is available can be identified.

5.14. Growing F_2 or F_3 populations in drought-prone fields makes it possible to identify drought-resistant progeny at an early stage of the breeding process.

While advanced testing under actual rainfed lowland conditions is desirable (see Chapter 13), it is an advantage to be able to control the degree of stress to which early generations are exposed. The strategy of withholding water during early generations and supplying it during later generations presumes that field water can be controlled adequately. In situations where such control is impossible, it is difficult to impose drought consistently and accurately on breeding nurseries. In these cases, special screening nurseries can be used, as described in the preceding sections. When remnant seed from which the pedigree nurseries were planted is sufficient, it can be used to seed a drought screening nursery during the same season as the pedigree nursery is grown. In this case, it is possible to collect drought screening data before the pedigree nursery is harvested. The drought data can then be used in selecting the plants to be harvested and advanced to the next generation.

In most cases, the drought screening is conducted in the off season. It may also require more seed than is available from the harvest of individual plants. In this case, seed from several or all of the plants in a pedigree nursery row can be bulked and this seed can be used for drought screening. This bulking is done after individual plants are harvested within the row to form the next generation in the pedigree nursery. When the drought screening data are available, they can be added to the fieldbook of the subsequent pedigree nursery. For example, suppose three plants are harvested individually from the F_3 pedigree line IR60188-34. These become the F_4 lines IR60188-34-1, IR 60188-34-2, and IR60188-34-3 in the next pedigree nursery. After the three lines are harvested, the remaining plants in the row IR60188-34 are harvested in bulk. This seed is sown in the drought screening nursery in January. The screening results are available in April, and they can be used for selection in the next pedigree nursery. For example, if the line IR60188-34 is susceptible to drought, its progeny (IR60188-34-1, -2, and -3) can be discarded, and selection can be concentrated in the lines with superior drought scores.

Evaluation of advanced lines

When advanced lines already have been bulk harvested from pedigree nurseries, fewer genotypes have to be evaluated and more seed is available per line. Thus more extensive testing for resistance traits is possible. In addition, multilocation observation nurseries can be used to observe the performance of the lines under different stress levels (see Chapter 13).

Other approaches

The method of crop establishment is an important factor in the expression of root characteristics. Dry seeding rice is less labor intensive than transplanting rice, and rice that has been dry seeded is less vulnerable to drought stress because its root system is established earlier and deeper. Thus the use of this practice is likely to increase in rainfed areas. Breeders tor rainfed lowland target areas where farmers commonly transplant rice should consider developing cultivars that are adapted to direct seeding. Genetic differences for drought resistance are greater under direct seeding, and evidence indicates that a genotype may perform differently when dry seeded than when transplanted (IRRI 1988a). Breeders and agronomists should work together to develop improved cultivars for rainfed lowlands that perform well when direct seeded and management practices that are appropriate for those cultivars.

Progress in developing improved drought-resistant types

The new cultivars that have been most successfully introduced into drought-prone areas have been those with reduced growth duration. In areas where photoperiod-sensitive rices predominate, new cultivars that flower at least a week earlier than local varieties are more likely to escape terminal drought. Some shorter duration mutants have been produced from popular photoperiod-sensitive cultivars such as Khao Dawk Mali 105.

Success in developing drought-resistant rainfed lowland cultivars, however, has been limited. IR52 was released in the Philippines for rainfed lowlands because it had high yield potential and performed excellently in drought screening nurseries. Unfortunately, it was susceptible to rice blast and it was not as drought resistant when transplanted as it was when dry seeded under upland conditions (Table 5.4); so it was not widely adopted. Some of IRRI's breeding lines, such as IR13146-45-2-3, have been consistently drought resistant when transplanted and have maintained stable yields in international trials and in drought-prone trials in the Philippines (Mackill et al 1986). The parentage of IR13146-45-2-3, however, does not include any obvious drought-resistant donor, and the line was not purposely selected for drought resistance.

As knowledge accumulated over the past decade, prospects for increased drought resistance have steadily improved. Resources devoted to rainfed lowland rice improvement have been increasing. Knowledge about the traits that are important in conferring drought resistance has expanded; but the tools for genetically manipulating them have remained primitive. This situation is likely to change soon as methods become available for manipulating complicated traits using molecular markers.

The promise of molecular biology

Maps using restriction fragment length polymorphism (RFLP) (McCouch et al 1988) can be used to locate genes that underlie quantitative characteristics (genes known as *quantitative trait loci* or QTL) (Paterson et al 1988). RFLPs are small pieces of DNA (often called *molecular markers*) that can be mapped to specific locations on the rice chromosomes. In crosses, these markers segregate as single genes and can be used to follow the segregation of QTLs. When markers are found that are tightly linked to the QTL, they can be used to screen unambiguously for the presence of the QTL in segregating populations. The markers can be detected much more easily than the actual genes that confer the drought resistance traits.

QTLs for various root characteristics have been identified in a cross between upland and lowland parents (Champoux et al 1995). Progress is being made toward locating QTLs that control other drought-related traits such as root penetration ability and osmotic adjustment. Eventually, it should be possible to use RFLPs or other types of DNA markers to assist in transferring genes that control complicated traits from their sources into modern lines.

Table 5.4. Drought resistance indexes and ranks (in parentheses) for five most drought-resistant and five least drought-resistant rices in a lowland screening nursery (IRRI 1987, Ingram et al 1990).

Cultivar or line	Grain yield Stress (t/ha)	Grain yield Control (t/ha)	Grain yield Ratio	Uprooting force (kg)	Visual score under stress [a]	Canopy air temperature under stress (°C)
Most drought resistant						
IR29723-143-3-2-1	6.0 (1)	7.0	(2)0.85	(5)13.2 (8)	4.0 (6.5)	0.39 (2)
IR48	5.7 (2)	7.2	(1)0.79	(9)12.7 (9)	5.3 (19)	0.89 (5)
IR13146-13-3-3	5.6 (3)5.9	(15)	0.94 (1)	12.4 (11)	5.0 (15)	1.54 (14)
IR13146-45-2-3	5.2 (4)5.7	(20)	0.91 (2)	11.7 (13)	4.0 (6.5)	0.93 (6)
IR29725-109-1-2-1	5.2 (5)6.8	(3)	0.76 (8)	11.1 (15)	2.7 (1)	0.87 (4)
Least drought resistant						
IR12979-24-1	2.7 (25)	4.1 (28)	0.67 (17)	10.7 (17)	6.0 (22)	1.34 (9)
IR11418-15-2	2.7 (26)	5.7 (21)	0.47 (26)	12.0 (12)	6.3 (24.5)	2.81 (25)
IR52	2.2 (27)	6.1 (13)	0.35 (28)	11.1 (16)	6.3 (24.5)	2.32 (20)
KKN7025-39-3-SKN	1.8 (28)	4.9 (27)	0.37 (27)	9.0 (27)	7.3 (27)	2.47 (23)
IR5931-110-1	1.8 (29)	5.4 (24)	0.33 (29)	10.2 (20)	8.0 (29)	2.35 (22)

[a] Based on a score of 1 (most resistant) to 9 (least resistant),.

Chapter 6

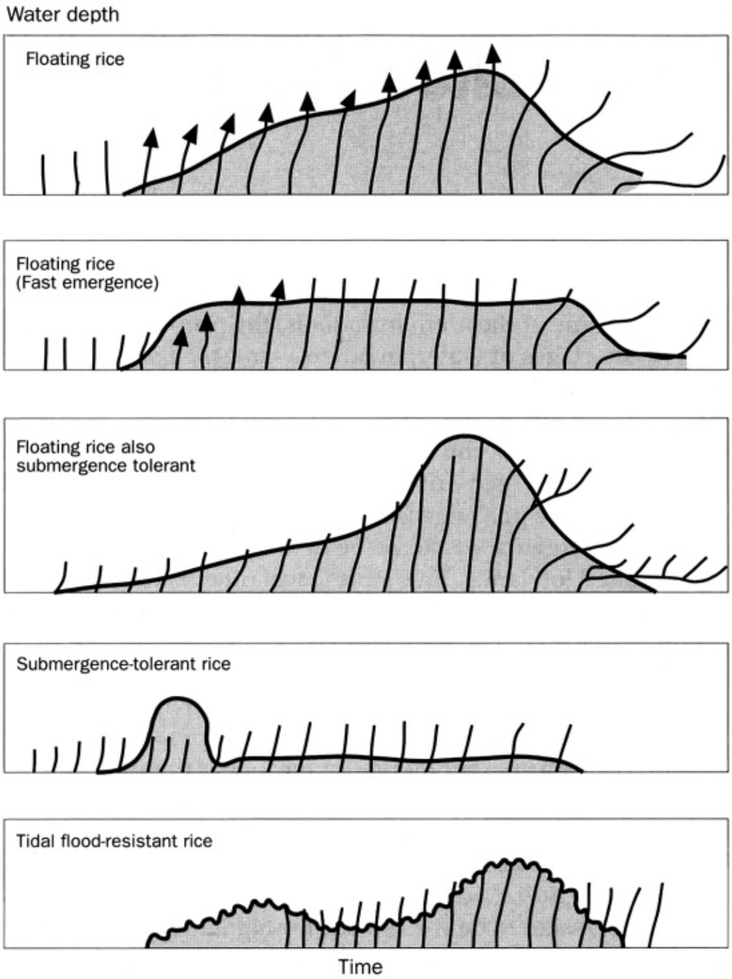
Submergence tolerance

As Chapter 1 explained, rainfed lowland environments are classified by water regime. In some of these environments, the productivity of rice often is constrained by shortages of water; in others—*drough and submergence prone, submergence prone,* and *medium-deep*—the chief constraint is an excess of water.

HilleRisLambers and Seshu (1982) have given several examples of flooding patterns that vary in duration and depth (Fig. 6.1). Rainfed lowlands do not experience prolonged flooding at depths greater than 50 cm. Nevertheless, submergence stress can be damaging in both shallow and medium-deep rainfed lowlands. This stress most often is caused by floods that have an abrupt onset—*flash floods.* Even in areas where the floodwaters usually drain within 10 d, varieties are needed that can tolerate submergence for brief periods. (While 10 d is frequently used as the period that tolerant plants can survive submergence, the level of stress also depends on factors such as water depth and solar radiation. When solar radiation is high, for example, plants can survive submergence for longer than 10 d.)

In general, stagnant flooding at depths greater than 25 cm adversely affects the growth of rainfed lowland rice in *medium-deep* areas, even though the plants are not submerged; in particular, it reduces tillering and increases lodging (Pande et a1 1979, Rao and Murthy 1986, Saha et a1 1993). Some varieties, however, seem to be well suited to stagnant *medium-deep* conditions (Singh and Bhattacharjee 1988), although the mechanism of their tolerance is not known. At present, few data are available that would allow firm conclusions to be made regarding optimum plant type for *medium-deep* areas. Still, in breeding for this type of rainfed lowlands, breeders should develop varieties that have intermediate height; stiff, nonlodging culms; and moderate submergence tolerance. A widely held belief among rice breeders is that cultivars that have large panicles and few tillers (*panicle weight* types) may be especially suitable for *medium-deep* areas because they tend to remain productive under the adverse conditions that prevail in these areas. There is little data available, however, to support this belief.

In rainfed lowlands, rice varieties are needed that can survive submergence without rapidly elongating between nodes. In *deepwater* areas, where floods deeper than 50 cm last longer than 10 d, rapid internodal elongation is necessary for survival: it allows plants to emerge from the water (Thakur and HilleRisLambers 1987). This characteristic, which is conditioned by a reces-



6.1. Flood types and plants' strategies for surviving them (HilleRisLambers and Seshu 1982).

sive gene (Eiguchi et al 1993), is undesirable in rainfed lowlands because flooding seldom is so deep or long lasting; and when the floodwaters recede, elongated plants lodge, impeding harvest and reducing grain quality and yield.

Rapid elongation of the leaves and leaf sheaths is an advantage to rainfed lowland varieties, however, because it lets them avoid submergence stress when moderate flooding occurs during the early vegetative stage (Krishnayya et al 1990). Varieties that lack the capacity for rapid internodal elongation still may have the capacity for leaf and leaf-sheath elongation (Singh et al 1989).

Physiology and genetics of submergence tolerance

The main effect of submergence on plant tissues is carbohydrate depletion. As the rice plant is starved of carbohydrates, its leaves turn yellow and die and, ultimately, the plant dies. Photosynthesis decreases because the supply of carbon dioxide is reduced and light intensity is low during submergence; respiration is reduced because oxygen concentrations are low; and ethylene accumulates in the plants (Setter et al 1988).

Factors that increase the damage caused by submergence include (Palada and Vergara 1972)

- increased water depth,
- increased duration of submergence,
- increased temperature,
- increased turbidity,
- increased rate of nitrogen fertilization, and
- decreased light intensity.

Submergence also causes mud to be deposited on the leaves of the rice plants, which can inhibit photosynthesis; and when the floodwaters are moving rapidly, rice plants may be uprooted. Prolonged submergence stress can damage plant tissues, set back growth, or even reduce the plant population (Fig. 6.2).

6.2. The rice plants in this field have experienced moderate submergence stress. Such stress can reduce leaf area and tillering and, ultimately, can kill plants.

Submergence tolerance is a complex trait; it cannot be attributed just to one or a few physiological or morphological characteristics. Research at IRRI has characterized morphological and physiological differences between submergence-tolerant and -susceptible rice cultivars (Table 6.1).

Submergence-tolerant varieties of rice tend to accumulate more starch in their stem sections than do susceptible varieties, and they experience less carbohydrate depletion after submergence (Karin et al 1982, IRRI 1993, Emes et al 1988). And the decline in photosynthetic ability and chlorophyll content of leaves after submergence progresses more slowly in varieties that are submergence tolerant than in those that are susceptible (Smith et al 1988). Following submergence, tolerant cultivars accumulate smaller amounts of aldehydes, which possibly are toxic end-products of anaerobic metabolism (IRRI 1993). Submergence-tolerant varieties also have been shown to tolerate darkness, and growing plants in the dark has been mentioned as a possible substitute for submergence screening (Table 6.2).

Programs that breed varieties for target areas that are likely to experience submergence stress should seek to incorporate factors that

Table 6.1. Relationship between morphological and physiological characteristics and submergence tolerance of rice plants (adapted from Karin et al 1982 and Mazaredo and Vergara 1982).

Type	Characteristics	Relationship to submergence tolerance
Morphological	Height	Generally greater in tolerant genotypes
	Culm stiffness	Stiffer in tolerant genotypes
	Culm roundness	Rounder in tolerant genotypes
	Leaf blade length	Longer in tolerant genotypes
	Percentage of lacunae per unit area	Lower in tolerant genotypes
	Air spaces within leaf	Fewer in tolerant genotypes
	Overlapping of first leaf sheath	Greater in tolerant genotypes
	Root length	Longer in tolerant genotypes
Physiological	Carbohydrate content	Decreases more slowly in tolerant genotype
	Nitrogen content	Higher, decreases more slowly, and is recovered faster in tolerant genotypes
	Silica content	Higher in tolerant genotypes
	Oxidizing power of roots	Stable in tolerant genotypes; decreases in susceptible genotypes
	Photosynthesis and respiration	Higher rates in tolerant genotypes
	Oxygenrelease	HIgher rates in tolerant genotypes
	Potassium and nitrate content	Higher in tolerant genotypes
	Nitrate reductase activity	Higher in tolerant genotypes
	Chlorophyll synthesis	New synthesis in tolerant genotypes

Table 6.2, **Relationship between submergence tolerance and darkness tolerance in rice cultivars and breeding lines.**[a]

Genotype	Submergence tolerance[b]	Darkness tolerance[c] (% of yellowing)		
		3 d	7 d	10 d
FR13A	1	5	20	35
Thavalu 15314	1	10	25	40
BKNFR76106-16-0-1	3	10	15	35
BKNFR76109-1-2-1	3	10	20	40
IR8234-0T-9-2	5	15	40	65
T442-57	7	20	60	90
RD7	7	20	50	90
Nam Sagui 19	7	25	75	100
Khao Dawk Mali 105	9	30	70	95

Source: Unpublished data of Kupkanchanakul cited in HilleRisLambers et al (1986).
[a] Submergence tolerance is scored from 1 to 9, in accordance with the *Standard evaluation system for rice* (IRRI 1988d). with 1 = highest tolerance. Darkness tolerance is measured as the percentage of plant tissue that turned yellow: lower percentages indicate higher tolerance. High submergence tolerance scores are associated with low percentages of yellowing and low submergence tolerance scores are associated with high percentages of yellowing, [b]Score for recovery from submergence of 30-d-old seedlings. [c]Percentage of plant tissue that turned yellow during darkness treatment of 30-d-old seedlings.

allow the plant to avoid submergence through rapid leaf elongation and emergence, and

enable the plant to tolerate submergence for up to 10 d.

Some other characteristics also should be considered:

Plants that have deeper root systems may resist being uprooted by rapidly moving floodwater more successfully than plants whose roots are more shallow.

Some breeders consider reduced leaf pubescence—that is, less hairiness or roughness—to be desirable because it reduces the deposition of mud on the leaves after submergence. Leaf pubescence may be beneficial, however, because it increases the air layer between the leaf surface and the water, thus increasing gas exchange during submergence.

Plant height may have a pronounced effect on results of submergence screening. Most rice breeders prefer plants of intermediate height, which tend to be more lodging resistant and productive than taller varieties. Tall plants, however, usually perform better in submergence tolerance screening than shorter plants with a similar level of submergence tolerance. While tall plants are submerged, their leaves are closer to the water's surface, and tall plants can more easily escape submergence by emerging from the water if the depth is not sufficiently high.

While some rice workers have reported observing cultivars that can tolerate submergence for a month or more, the experience of most scientists shows that few plants can survive more than 2 wk of submergence. The response of the plants, however, depends on the conditions of submergence.

That is, when the water is clear and cool and the weather is sunny, rice plants are able to tolerate longer periods of submergence than when the water is turbid and the weather is cloudy. Under unfavorable water and weather conditions, complete submergence for 10 d is likely to kill even tolerant cultivars.

The genetics of submergence tolerance has been studied, but the number of genes involved has not yet been determined. It is reasonable to expect the inheritance to be complex, however, since many factors appear to be associated with such tolerance (Table 6.1). The studies that have been done so far indicate that heritability is high and that genes for tolerance are partially to completely dominant (Mohanty et al 1982, Sinha and Saran 1988, Haque et al 1989b).

In the rainfed lowland breeding program at IRRI, it has been relatively easy to obtain progeny with tolerance levels similar to that of the tolerant parent in tolerant × susceptible crosses. These results suggest that one major gene is responsible for most of the tolerance of highly tolerant cultivars. Molecular mapping studies have identified a locus on rice chromosome 9 inherited from FR13A that controls submergence tolerance (Xu and MacKill 1995).

Screening methods

The results of screening for submergence tolerance are influenced by the breeder's choice of

- location of test (greenhouse or field),
- age of seedlings (young or old),
- planting method (transplanted or direct seeded),
- duration of flooding, and
- water condition (clear or turbid).

In comparing results among tests, each choice and its potential influence must be considered.

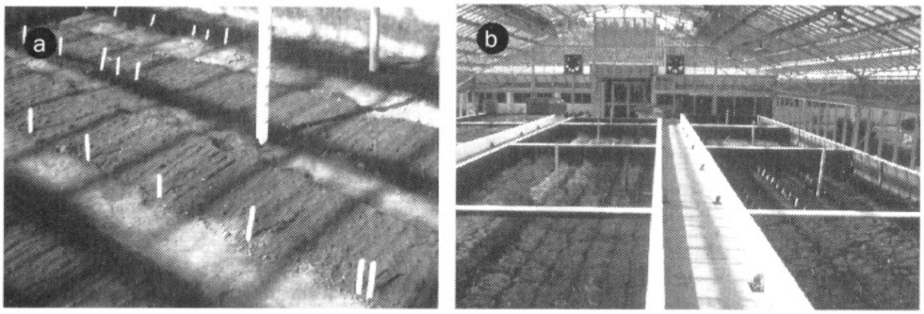
An international collaborative project evaluated various procedures for submergence screening (HilleRisLambers and Vergara 1982). While the tests differed, the most tolerant entries (FR13A, Kurkaruppan, Thavalu accessions 15314 and 15325) performed well in all of them. All entries performed similarly in tests that imposed extremely low or high levels of stress; little discrimination among entries was possible. The tests that were most effective used at least 80 cm of water and seedlings that were at least 21 d old.

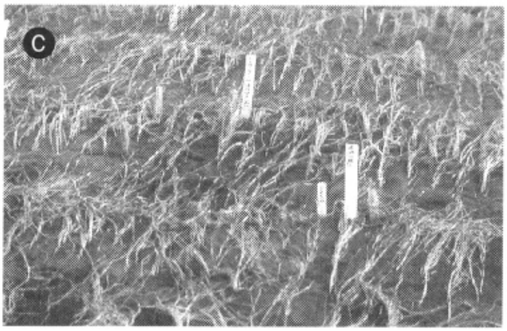
Vergara and Mazaredo (1975) described a screening method using young seedlings that is simple and convenient to use: they direct seeded rice in greenhouse tanks. Then they subjected 10-d-old seedlings to submergence in 30 cm of water for 7 d. They scored the seedlings 5 d after the water was drained. In their first study using this method, they identified 26 cultivars (out of 479 screened) that had survival of 75% or higher (Table 6.3). IRRI scientists have extensively used a slightly modified version of Vergara and Mazaredo's method with repeatable results (described by Figure 6.3).

Table 6.3. Rice cultivars[a] that had survival rates of at least 75% after 10-d-old seedlings were submerged for 7 d (Vegara and Mazaredo 1975).

Cultivar	country of origin	Survival (%)	Height before submergence (cm)	Increase in height during test (%)
Jams Wee	Sri Lanka	100	22	9
Thavalu 15314	Sri Lanka	100	24	8
Thavalu 15325	Sri Lanka	100	18	11
Kaharamana	Sri Lanka	100	23	9
Goda Heenati	Sri Lanka	100	23	9
Madael	Sri Lanka	100	20	25
Weli Handrian	Sri Lanka	100	25	12
Kurkaruppan	Sri Lanka	100	21	10
Padi EwangJanggut	Indonesia	98	22	14
SMLTemerin	Surinam	95	20	55
Lumbini	Sri Lanka	95	21	14
Kalukanda	Sri Lanka	95	20	15
Kanni Murunga	Sri Lanka	95	22	14
Nang Dum To	Vietnam	90	17	18
T442-57	Thailand	90	16	31
Venum Vellai	Sri Lanka	90	17	24
Kaluwee	Sri Lanka	88	19	21
Kottamalli	Sri Lanka	88	18	33
Ratawee	Sri Lanka	88	16	13
Nam Sagui 19	Thailand	85	22	14
Periya Karuppan	Sri Lanka	82	21	10
Kalu Gries	Sri Lanka	82	23	9
BurumaThavalu	Sri Lanka	82	22	9
Madabaru	Sri Lanka	78	21	10
Sudu Gries	Sri Lanka	75	21	14
Pokura Samba 15337	Sri Lanka	75	21	14

[a] 479 cultivars were screened





6.3. At IRRI, breeding lines are screened for submergence tolerance in screenhouse tanks. (a) Each line is planted in a short row (about 50 cm) in the concrete tanks. (b) After 7 d, the tanks are flooded to a depth of at least 50 cm, and the water level is maintained for 7-10 d. (c) One week after the tanks are drained, the lines are scored for survival percentage.

- The method offers rapid turnaround: each test takes about 1 mo.
- Since small, young seedlings are used, a large number of breeding lines can be screened in one tank.
- Where tank space is limited, seeds can be sown in seed boxes, rather than directly in the tank, and the boxes can be submerged in the tank. This practice allows a new set of entries to be submerged every 10 d.

Some rice breeders prefer to test older plants because they believe differences are easier to detect (HilleRisLambers et al 1986). Intermediate levels of tolerance definitely are measured more effectively when the test population is composed of older seedlings. Screening older plants has several disadvantages, however:

- Turnaround is slower than with seedling testing because the plants need time to reach the appropriate growth stage.
- Larger plants occupy more space than smaller plants, so it is seldom cost effective to screen them in the greenhouse.
- The tests must be done in field tanks, where environmental factors are difficult to control and may affect submergence scores. Water control, for example, usually is imperfect in field tanks.

Adkins et al (1988) developed a screening method that minimizes the effects of environmental variation. They grew plants in culture solution rather than soil in an environment where light and temperature were controlled. Under these conditions, it was easy to identify the number of days of submergence at which 50% of the plants died. Fewer entries can be screened with the Adkins et al method than with the Vergara and Mazaredo method because more time and resources are required. The method is useful, however, when submergence tolerance needs to be characterized more precisely.

Allowance can be made for environmental factors by including tolerant and susceptible check varieties in each test and comparing their performance with that of the varieties being tested. Checks are especially important in field screening. After the plants have been completely submerged for about 8 d, the tanks can be drained and plants of the susceptible check can be inspected. If these checks still have many green leaves, the tanks can be reflooded for a few more days to increase the submergence stress.

Most modern cultivars are susceptible and, therefore, can be used as susceptible checks. (The varieties that are moderately tolerant should be avoided.) For the tolerant check, IRRI has extensively used FR13A from Orissa, India, which is one of the most tolerant cultivars available.

One method of scoring for submergence tolerance is based on percentage survival. At IRRI, surviving seedlings are counted 5-7 d after the water is drained, and the percentage of survivors of each variety is divided by the percentage of survivors of FR13A, the tolerant check. For example, if 50% of the seedlings of one test variety and 55% of the seedlings of the tolerant check survived submergence, the test variety's percentage survival would be 50/55 or 91%. The advantage of this system is that scores are consistent from test to test because the same tolerant check variety is used in all tests.

The *Standard evaluation system for rice* (SES) associates single-digit scores for submergence tolerance with percentage survival as follows (IRRI 1988d):

Score	Percentage survival (of check)
1	100% or more
3	95-99%
5	75-94%
7	50-74%
9	0-49%

Using the single-digit score is convenient because most researchers are familiar with interpreting SES scores (that is, 1 is the best and 9 is the worst), and it occupies only a single column in the field book. However, the single-digit score has several disadvantages. The scale is biased against entries with intermediate levels of tolerance, since a variety must have a survival percentage that is 95% of the tolerant check to have a score of 3. Another disadvantage is that lines that are more tolerant than FR13A cannot be identified. In addition, because survival rates vary from test to test, lines that are as tolerant as FR13A may appear to be less tolerant. That is, in some tests, by chance, they will have fewer survivors than FR13A and thus receive scores greater than 1; in others they will have more survivors than FR13A but still will receive a score of 1 because that is the highest possible score; so their mean scores will be greater than 1. To avoid this complication, a breeder could use the survival percentage directly for comparing tolerance levels. Alternatively, a different scale than the SES could be used in which entries with survival similar to FR13A are scored 3.

HilleRisLambers et al (1986) suggested another method of scoring that is based on visual observation:

Score	Symptoms
1	Erect, little or no elongation
3	Erect, green, elongated
5	Elongated and bent at middle
7	Elongated and lodged flat
9	Elongated and apparently dead

They recommended scoring the plants immediately after the tank is drained and again after 7-10 d. Plants that still have green leaves immediately after the tank is drained are the most tolerant lines. Varieties that are near death when the tank is drained may be able to recover and may again have green leaves in 7-10 d. This scale is useful if stress is not sufficient to cause high mortality. The test conditions may produce high survival percentages for all entries, so varietal differences may be most obvious immediately after the stress is relieved.

To produce the most accurate results, observations should be as detailed as possible. Collecting survival percentage data means counting the number of plants per plot before and after submergence. Distinguishing physiological tolerance from avoidance means gathering elongation data—calculating the difference in plant height before and after submergence. Any lines that emerge from the water during the test should be noted, as they will likely escape submergence stress. Water levels should be measured daily, particularly for screening that is conducted in the field. Making such detailed observations, however, requires a lot of time and other resources. For breeding programs that have scanty resources, visual observation of mortality or tissue death may be an acceptable alternative to calculating survival percentage.

Breeding strategies

A breeding program's approach to improving submergence tolerance must come from its overall objectives. If severe, short-term flooding is a serious constraint in the target area, the program should strongly emphasize submergence tolerance. If medium-deep, stagnant flooding is more common in the target area, moderate tolerance may be sufficient. While it might seem that strong tolerance would be desirable under all circumstances, the most highly tolerant varieties are usually not as productive as susceptible varieties when submergence stress does not occur. Since most areas do not have stressful floods each year, the need for submergence tolerance must be balanced against the need for maximum productivity.

In the past, breeders have concentrated on using tall, traditional cultivars such as FR13A and Kurkaruppan to incorporate strong submergence tolerance into modern varieties. This work took time because the traditional donors were poor combiners for agronomic and other traits. While FR13A has been an excellent source of strong submergence tolerance, it has been difficult to use in crosses. It is not a typical indica type but rather belongs to isozyme group II (see Chapter 2).

Recently, a set of advanced lines with strong submergence tolerance and desirable agronomic features has been developed (Table 6.4). Although these breeding lines are shorter than the tall donors, their submergence tolerance is close or equal to that of FR13A. For example, breeding lines from the crosses IR40931 and IR49830 inherit strong submergence tolerance from the breeding line BKNFR76106-16-0-1-0 (Sinha et al 1989, Singh et al 1989). This line was developed in Thailand from FR13A. Other lines, such as IR43522-37-3-3-3, do not have a donor of strong submergence tolerance but appear to survive through rapid leaf elongation. While it may be useful to include a traditional cultivar such as FR13A as a check in screening work, these newer lines are more appropriate donors of submergence tolerance in breeding programs.

Some programs emphasize the testing and adoption of existing varieties over the development of new varieties. These programs should screen a wide range of materials, using traditional and improved cultivars that have strong submergence tolerance as checks. Most programs make their own crosses to incorporate submergence tolerance into adapted lines. These programs may wish to use local traditional or improved cultivars in addition to interna-

Table 6.4. Characteristics of improved breeding lines derived from submergence-tolerant parents.

Improved breeding line	Parentage[a]	Height (cm)	Days to flowering	Submergence tolerance[b]		Grain yield (t/ha)
				GH score	Survival (%)	
IR40931-26-3-3-5	BKNFR76106-16-0-1-0 /IR19661-131-1-2	110	136	1.0	36	4.1
IR43559-25-5-3-2	IR13423-10-2-3/ FR43B//MTU7029/IR19728-9-2-3-3	105	135	2.0	35	3.6
IR40931-33-1-3-2	BKNFR76106-16-0-1-0 /IR19661-131-1-2	105	125	1.3	34	3.4
IR49830-26-1-2-1	IR4568-86-1-3-2/ IR26702-11-1 // IR20992-7-2-2-2-2-3/IR21567-9-2-2-2-1	120	140	3.0	22	4.1
IR43470-7-3-5-1	IR21841-81-3-3-2/ BKNFR76106-13-2 //IR21949-65-3-2	100	130	3.0	20	3.7
IR49830-7-1-2-1	IR4568-86-1-3-2/ IR26702-111-1//IR20992-7-2-2-2-2-3/ IR21567-9-2-2-2-1	110	140	2.3	19	4.9
IR46292-24-2-2-1-2	Chenab 64-117/IR60//CR1009	110	140	1.5	17	3.3
Checks						
IR68 (high-yielding check)		110	95		1	5.0
Pankaj (rainfed lowland check)		125	100		0	4.1
FR13A (submergence tolerant)		165	101	1.0	-	3.0

Source: From Mackill et al 1993 and unpublished data.
[a]The major parental source of submergence tolerance is underlined. The breeding lines from crosses BKNFR76106 and IR26702 inherit their tolerance from the cultivar FR13A.
[b]The GH (greenhouse) scores represent the mean of scores from several tests in which entries were rated on a scale of 1 (survival percentage equals or exceeds that of FR13A) to 9 (no survivors). The survival percentage represents the average survival of a replicated greenhouse and field test conducted at IRRI in 1990-91 (Mackill et al 1993).

6.4. At IRRI, F_2 populations are screened for submergence tolerance in a field that has high levees. After seeding at high density, the field is flooded for 7-12 d. About 2 wk after the field is drained, the surviving F_2 plants are transplanted into the regular F_2 nursery.

tional donors. When donors of strong submergence tolerance are desired, it is not necessary to go back to traditional tolerant cultivars; it is more appropriate to use improved donors such as those listed in Table 6.4.

Once crosses have been made, selection for submergence tolerance must begin in early generations to ensure that susceptible plants are eliminated right away so further selection is concentrated on tolerant lines. The F_2 generation is an excellent place to begin selection, as abundant seed usually is available from the harvest of F_1 plants. Ideally, the F_2 is screened in field tanks, where more space usually is available; but greenhouse tanks also can be used. Sowing the plots densely makes it possible to screen a large number of plants in the tanks (Fig. 6.4). A submergence treatment of 10-14 d usually is sufficient to kill all but the most tolerant plants. (The optimum duration of stress depends on other factors as described in previous sections.) After the stress is applied, the surviving plants are transplanted to the field for further evaluation and selection. Seed from the survivors can be harvested and bulked for another round of selection, or the outstanding plants can be harvested and kept separate as a source of F_3 pedigree lines.

Submergence screening should continue in subsequent generations. Generally, pedigree nurseries should not be subjected directly to submergence screening because, if the entries prove to be susceptible, the entire nursery could be lost. However, if a system is available for large-scale screening of the hundreds or thousands of seedlings that need to be screened (such as the system illustrated in Figure 6.3), remnant seed of the pedigree lines (leftover seed from the same source used to grow the pedigree lines) can be screened, and the scores for submergence tolerance can be incorporated as a selection criterion. Since early-generation lines are segregating and submergence tolerance is influenced by environmental effects, pedigree lines should be screened over several generations. By the time the lines reach the F_5 or F_6 generation, data from three or four tests are available; this accumulation of data makes possible more accurate assessment of submergence tolerance than a single test.

Pedigree lines of the F_5 or later generations that are uniform and combine the most desirable characteristics are harvested in bulk for advanced tests. By this stage, the number of lines being evaluated is reduced since only the exceptional ones are advanced to yield trials. Because the lines are harvested in bulk, sufficient seed is available for replicated tests for submergence tolerance. By conducting replicated screening with various combinations of conditions, a breeder can compile data about the consistency of the entries' performance and use those data in making decisions about which lines to promote to advanced trials (Table 6.5).

A few successes in breeding for submergence tolerance have been reported in the literature. Mohanty and Chaudhary (1986) reviewed the work in India. They noted that, while a number of cultivars had been released for *medium-deep* conditions, Indian breeders in general had neglected to develop rainfed lowland cultivars with adequate submergence tolerance. As mentioned above, breeders in Thailand and IRRI transferred the submer-

Table 6.5. Examples of submergence tests that can be performed on advanced lines.

Test	Application
Greenhouse screening of seedlings	Usually measures strong submergence tolerance. If flooding is too shallow, lines with rapid leaf elongation will emerge from the water and avoid submergence stress.
Field screening, abrupt submergence at early stage	Can measure strong submergence tolerance if flooding exceeds 70 cm and the plants are not more than 30 d old. Some tall entries can emerge from the water and avoid submergence stress. Duration of flooding can be varied to provide different levels of stress.
Field screening, gradual submergence and prolonged flooding	Measures moderate submergence tolerance. Appropriate for medium-deep areas in which flash floods are uncommon.
Field screening, abrupt submergence and prolonged flooding	Measures submergence tolerance and avoidance (through rapid internodal elongation).
Field screening in farmers' fields	Useful for understanding the types of flooding that occur in a target area and the responses of breeding lines under farm conditions. Since water regimes cannot be controlled, detailed records of water depth should be kept to assist in interpreting the results.

gence tolerance of FR13A into semidwarf breeding lines. The improved lines developed at IRRI have desirable agronomic features such as shorter stature (Table 6.4). Yield and submergence tolerance generally are negatively associated. If this association is due to linkage between yield-related and submergence tolerance genes, then repeated backcrossing should break this linkage and produce lines that combine high yields and submergence tolerance. If the submergence tolerance genes are directly responsible for reduced yields, then it may not be possible to combine the high submergence tolerance and high yield potential in one variety. The breeding line IR49830-7-1-2-1 combines high yield with moderately high submergence tolerance (Table 6.4); so it may be possible to combine the two characteristics, even if the resulting cultivar is not as tolerant as lower yielding lines such as IR40931-26-3-3-5.

Chapter 7

Cold tolerance

Low-temperature stress is a major constraint to rice production in many countries, particularly in temperate areas such as China, Japan, Korea, the United States (California), and European countries. In tropical and subtropical areas, low temperatures can be a problem for crops grown at high elevations or for dry-season crops grown at higher latitudes; low temperatures also are a minor source of stress in rainfed lowland environments. Rice breeders surveyed by Mackill (1986) ranked low-temperature stress eighth among nine physical and chemical stresses important to rainfed lowland rice; however, about 15% of the respondents included it as one of the three most important stresses.

In rainfed lowlands, temperatures are naturally favorable during crop establishment; plants are not subjected to cold during the vegetative stage. At higher latitudes, temperatures drop near the end of the growing season and, thus, may adversely affect reproductive growth. The crops most likely to be affected are those that are harvested late: crops grown in *medium-deep* areas, where water remains longer in the field, delaying harvest (Maurya and Mall 1986); and in double-cropped areas where the second crop may be delayed if the first crop is harvested late.

In these areas and circumstances, varieties are needed that tolerate cold during the reproductive stage.

Effects of cold at the reproductive stage

Booting—particularly the young microspore stage of meiosis—is the growth stage that is most sensitive to cold stress (Satake and Hayase 1970). Rice plants subjected to cold during booting often have increased sterility rates. Varieties that have a larger number of viable pollen grains, as measured by staining with potassium iodide, are likely to have higher fertility rates under low-temperature stress (Satake 1986). Since anther length appears to be strongly related to number of pollen grains (Satake 1986), breeders who are seeking to develop cold-tolerant varieties may include anther size among their selection criteria.

Low temperature at booting also reduces the amount of pollen shed on the stigma and the percentage of pollen grains that germinate. Reduced pollen shedding is caused by incomplete anther dehiscence, which results from abnormal development of the tapetum cells in the anther (Ito et al

1970). Low temperature at booting also causes abnormal pollen to be produced, resulting in a lower percentage of germination on the stigma (Koike 1990).

While booting, in general, is the most sensitive growth stage, rainfed lowland rice may be more vulnerable to cold during flowering, merely because low temperatures are more likely to occur during this stage. Rice plants that are exposed to cold during flowering have high sterility rates because less pollen is shed on the stigma (Khan et al 1986) and pollen germination is reduced (Satake and Koike 1983). Low temperature at flowering also inhibits exsertion of the panicle from the flag leaf sheath, which is known to increase sterility (Kaneda and Beachell 1974).

Resistance to cold damage at booting does not appear to be correlated with resistance at flowering (Koike 1990).

For a comprehensive review of the effects of low temperatures on rice plants, see Satake (1976).

Breeding strategies

Inheritance of cold tolerance at the seedling stage is under simple genetic control (Shahi and Khush 1986, Xu and Shen 1988). Inheritance of tolerance at the reproductive stage, however, is polygenic (Acharya and Sharma 1983, Khan et al 1986, Kaw et al 1989). Breeders have reported, however, that selection for tolerance in early generations (F_2 to F_3) is effective (Toriyama and Futsuhara 1960; Futsuhara and Toriyama 1969,1971; Khan et al 1986). Some evidence indicates that inheritance of complete panicle exsertion in cold-tolerant rices is under simple genetic control, with the same gene controlling the trait in different parents (Pandey and Gupta 1993).

At higher latitudes where cold is an occasional problem, breeders do not need to make an unnecessary effort to incorporate tolerant donors into the crossing program. Growing breeding nurseries under the level of stress normally encountered in the target environment should ensure that lines with sufficient tolerance are produced. In areas where cold is a significant constraint, tolerant donors can be included in the crossing program, and segregating generations can be subjected to cold stress to aid in selection.

In screening for cold tolerance, the most reliable results are achieved by growing plants in facilities where the temperature can be controlled. Few such facilities are available, and space in them is limited; thus varieties usually must be screened in the field. In the tropics, varieties can be screened at high-elevation sites for tolerance to less-than-optimum temperatures. At high elevations, however, the temperature may be too low throughout the season to approximate conditions in areas where terminal stress is the main problem. A more practical approach is to plant nurseries later than normal so the plants will flower when temperatures are low.

Spikelet sterility should be estimated for breeding lines as a measurement of cold tolerance. The level of cold stress will depend on the flowering date: lines that flower later usually experience lower temperatures. A check cultivar planted at 1-wk intervals will provide a reference to estimate the degree of stress for different flowering dates. This check should be susceptible and photoperiod insensitive. (Photoperiod-sensitive lines flower on similar dates regardless of planting date.) The sterility rate of each line can be compared with that of the check plot that flowered at a similar date. Or breeding lines that flower on a certain date can be compared only with other lines that flower on a similar date. In most rainfed lowland programs, the target maturity date may be rather narrow (within a 1-2 wk period), so sterility may not be contingent on flowering date.

Majumder et al (1989) advocated a two-tier screening system for cold tolerance based on their observation that tolerance is associated with high germination response to nonanoic acid treatment and presence of the isozyme alleles *Est-2*^{0} or *Est-2*^{2}. In their system, the germplasm is first screened for germination percentage under nonanoic acid (at a concentration of 5-6 m*M*). Cold-tolerant lines have greater than 50% germination. The tolerant lines are assayed for presence of the *Est-2* isozyme allele. (These procedures are described by Glaszmann et al 1988.) Plants with *Est-2*^{0} have high tolerance for cold, those with *Est-2*^{1} have intermediate tolerance, and those with *Est-2*^{2} have low tolerance.

Isolation of genes directly responsible for the response to cold (Bihn and Oono 1992) will open up new screening methods.

Local traditional cultivars, which are adapted to flowering under low temperatures, offer the best source of cold tolerance. These cultivars also contribute other traits that confer adaptation to rainfed lowlands (see Chapter 2). Most rainfed lowland cultivars are indica rices. Japonica cultivars usually are more cold tolerant than indica cultivars at all growth stages (Glaszmann et al 1990). Temperate japonica rices do not grow well in most rainfed lowland environments. They combine poorly when crossed with indica rices and, therefore, are not good donors for rainfed lowland programs. Vergara and Senadhira (1990) suggested using bulu (tropical japonica or javanica) or upland rices as sources of cold tolerance. Although these rices combine poorly with lowland indica varieties, they may also be useful as sources of other traits such as large panicles, thick culms, and drought resistance (see Chapter 2). Improved indica rices that are cold tolerant during the reproductive stage could be useful as donors. The following such varieties have been identified through the International Rice Cold Tolerance Nursery (Seshu and Akbar 1990):

China 1039
HPU5010-PLP21-2-1B
IR1846-296-1
IR19743-46-2-3
IR19746-26-2-3-3
IR24312-R-R-19-3
IR8455-K2

JKAU(K)450-126-10
JKAU(K)450-172-10
K31-163-3 (Khudwani)
K39-96-1-1-1-2

Segregating populations should be planted under conditions that are likely to impose sufficient stress for selection. That is, usually they should be planted late so they will flower when temperatures are low. Results may be confounded by environmental effects and varietal differences in flowering dates; nevertheless, selection repeated over several generations should be effective in improving cold tolerance. Where rapid generation advance facilities are available (see Chapter 12), low-temperature stress can be applied in a room with controlled temperature to select for tolerance (Li and Vergara 1981).

Chapter 8

Adverse soils tolerance

In rice-growing regions, soils often are deficient in nutrients that are essential to the healthy development of rice or contain certain minerals in high concentrations that are toxic to rice. Flooding, however, usually mitigates these adverse conditions by raising the pH of the soil.

Rainfed lowlands are more prone to soil problems than other rice-growing areas because

- drying of the soil adversely affects the availability of nutrients,
- soil amendments that could correct many mineral deficiencies and toxicities usually are either unavailable to rainfed lowland farmers or too expensive for these farmers to buy, and
- rainfed areas with poor soils are not prime targets for irrigation development.

Thus, in rainfed lowlands, farmers' best option for dealing with adverse soils is to choose rice varieties that tolerate the conditions well. In fact, the traditional varieties grown in some areas have been selected for adaptation to adverse soils.

Soil problems in rainfed lowland rice

Rice is susceptible to deficiencies of nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, manganese, zinc, boron, copper, and silicon (Table 8.1). It also is vulnerable to toxicities of iron, manganese, boron, aluminum, and iodine. These stresses usually are associated with adverse soils, such as acid sulfate, peat, and coastal saline. Illustrations of the symptoms of mineral stresses are available in Yoshida (1981) and IRRI (1983b).

According to Ponnamperuma and Ikehashi (1979), rainfed lowland conditions, which usually entail alternate wetting and drying of the soil, are conducive to a range of mineral stresses (Table 8.2). Drying may increase N loss through mineralization of nitrogen in unfertilized fields and denitrification in many lowland soil types. Phosphorus deficiency increases in severity after 2 wk of drying.

The mineral stresses most likely to occur in rainfed lowlands are iron deficiency / toxicity, phosphorus deficiency, aluminum toxicity, manganese toxicity, zinc deficiency, calcium deficiency, and osmotic stress due to salinity. Akbar et al (1986a) found that, in rainfed lowlands, the main deficiencies are of nitrogen, phosphorus, and zinc and the main toxicities involve iron

Table 8.1. Symptoms of mineral deficiencies and toxicities that affect rice growth (adapted from Yoshida 1981).

Type of stress	Element or compound	Symptoms
Deficiency	Nitrogen (N)	Plants are stunted. Tillering is limited. Leaves are narrow, short, erect, yellowish green. Older leaves die when they become light straw colored.
	Phosphorus (P)	Plants are stunted. Tillering is limited. Leaves are narrow, short, erect, and dark. Young leaves are healthy, but older leaves die when they become brown. Some varieties become reddish or purplish.
	Potassium (K)	Plants are stunted. Leaves are short, droopy, and dark green. Interveins of lower leaves turn yellow and dry to light brown, starting from the tip. Brown spots may develop on dark green leaves.
	Sulfur (S)	Same symptoms as nitrogen deficiency.
	Calcium (Ca)	Under acute deficiency, the growing tip of upper leaves becomes white, rolled, and curled.
	Magnesium (Mg)	Leaves become wavy and droopy due to expansion of angle between leaf blade and sheath. Interveinal chlorosis of lower leaves is orangish yellow.
	Iron (Fe)	Entire leaf becomes chlorotic and then whitish.
	Manganese (Mn)	Plants are stunted. Interveinal chlorotic streaks spread downward from leaf tip to base, later becoming dark brown and necrotic. Newly emerging leaves become short, narrow, and light green.
	Zinc (Zn)	Midribs of younger leaves become chlorotic, especially at the base. Brown blotches and streaks appear on lower leaves, followed by stunting. Leaf blade size is reduced. Growth is uneven, and maturity in the field is delayed.
	Boron (B)	Plants are shorter than normal. Tips of newly emerging leaves become white and rolled. In severe cases, the growing point may die.
	Copper (Cu)	Leaves become bluish green, then chlorotic near the tips. Chlorosis spreads downward on both sides of the midrib. Dark brown necrosis of the tips follows. The upper parts of leaves or entire leaves do not unroll as they emerge.
	Silicon (Sı)	Leaves are soft and droopy.

Table 8.1. continued

Type of stress	Element or compound	Symptoms
Toxicity	Iron (Fe)	Tiny brown spots appear on lower leaves *(bronzing)* starting from the tips and combining at the interveins. In severe cases, the entire leaf becomes purplish brown.
	Manganese (Mn)	Plants are stunted. Tillering is limited. Brown spots appear on the veins of leaf blade and sheath, especially of lower leaves.
	Boron (B)	Chlorosis occurs at the tips of older leaves, especially along margins; then large, dark brown, elliptical spots appear. Leaves ultimately turn brown and dry up.
	Aluminum (Al)	Orange interveinal chlorosis develops. Chlorotic portions may become necrotic in severe cases.
	Iodine (I)	Small brown spots appear on the tips of lower leaves and spread over the entire leaf, resulting in yellowish- brown or brown discoloration. Affected leaves eventually die.
	Sodium chloride (NaCl) (salt; salinity)	Plants are stunted. Tillering is limited. Leaf tips are whitish, and parts of leaves frequently become chlorotic.

Table 8.2. Mineral stresses associated with alternate wetting and drying of lowland soils (after Ponnamperuma and Ikehashi 1979).

Soil type	Time of season at which stress occurs	Stress	
		Drying after flooding	After reflooding
Neutral	Early	Iron and phosphorus deficiencies	Nitrogen deficiency
	Late	Iron deficiency	
Strongly acid	Early	Phosphorus deficiency	Iron toxicity
	Late	Manganese toxicity	
Acid sulfate	Early	Aluminum toxicity and phosphorus deficiency	Iron toxicity
	Late	Aluminum toxicity	
Calcareous	Early	Iron deficiency	Zinc and nitrogen deficiencies
	Late	Iron deficiency	
Alkaline	Early	Iron and calcium deficiencies	Zinc and nitrogen deficiencies
	Late	Iron deficiency	
Saline	Early	Severe osmotic stress	Osmotic stress
	Late	Osmotic stress	Osmotic stress

and coastal-saline and acid-sulfate soils. Most of the breeders of rice for rainfed lowlands surveyed by Mackill (1986) said phosphorus deficiency was the most common soil stress, followed by salinity; zinc deficiency, acidity, and stresses associated with peat soils were lesser problems.

Boje-Klein (1986) mapped the extent and distribution of various problem soils in South and Southeast Asia. Much of these problem soil areas are not currently cropped. Some of these areas have little potential for growing tolerant rice cultivars; they must be put to more economically or environmentally desirable uses. Still, Boje-Klein estimated that 9.5 million ha were suitable for the production of rices that tolerate saline and sodic soils, 3.0 million ha for rices that tolerate acid-sulfate soils, and 10.6 million ha for rices that tolerate peat soils.

The major stresses are discussed below. A summary of screening methods that have been used at IRRI is given in Table 8.3.

Salinity

Many breeding programs have focused on developing salt-tolerant rices for saline soils, which commonly are classified as either *coastal* or *inland* (Akbar et al 1986a). Coastal saline soils may be affected by additional stresses, in particular submergence stress caused by tidal flooding.

The level of salinity determines the degree to which plant growth is impaired. Rice plants are damaged by salinity when the soil's electrical conductivity exceeds 4 dS/m (decisiemens per meter). Electrical conductivity greater than 10 dS/m drastically affects rice growth (Akbar and Senadhira 1985). Soil salinity is reduced during the middle of the wet season as salt is leached from the soil and diluted by rainfall, but it increases as the rains cease and the rice begins to mature.

Rice varieties differ widely in salt tolerance, but tall plants often tolerate saline soils well (Flowers and Yeo 1990). Salt damage is related to the level of positive sodium ions in the plant tissue. In tolerant cultivars, Na^+ ions are excluded from the roots (Maegawa et al 1987, Akita and Cabuslay 1990). Yeo and Flowers (1986) found several mechanisms to be important in salt tolerance, including reduced transport of sodium chloride from the roots, localization of excess sodium chloride in older leaves, and high tissue tolerance. A cultivar may not have all of these mechanisms, however; so Yeo and Flowers advocated intercrossing among cultivars that have different mechanisms to increase the overall level of salt tolerance.

Genetic studies indicate that salt tolerance is a polygenic trait. Some workers have observed fairly high heritabilities (Akbar et al 1986b, Jones 1986). Others have reported low heritability caused by strong environmental effects (Gregorio and Senadhira 1993); they recommended screening nurseries in later generations (F_5 to F_7) under controlled conditions rather than in the field.

Ideally, plants should be screened for salt tolerance at all growth stages because tolerance may not be the same throughout the life cycle (Akbar et al 1986a). For example, the cultivar Nona Bokra of West Bengal, India, is very

Table 8.3. Screening procedures for adverse soils (Neue et al 1990).[a]

Stress	Soil/medium	Fertilizer	Method of establishment	Layout	Check varieties	Rating time[b]
Salinity	Maahas clay treated with NaCl to EC of 8 dS/m	N as urea at 25 mg/kg	Transplant 2-wk-old seedlings grown in culture solution	Greenhouse trays, 35 x 27 x 11 cm; 3 seedlings per variety; 3 varieties per tray	T = IR9764-45-2-2 S = MI-48 T and S check in each tray	4 WAT
	Maahas clay treated with NaCl to EC of 8 dS/m	N as urea at 100 kg/ha; P as solophos at 20 kg/ha	Transplant 1-mo-old seedlings grown on wet seedbed	Block L5, IRRI Farm; 2.1-m rows, 20 x 25 cm	R = IR9764-45-2-2 S = IR5929-12-3 T and S check after every 18 entries	4 and 8 WAT
	Maahas clay treated with NaCl to EC of 8 dS/m	N as urea at 100 kg/ha	Transplant 1-mo-old seedlings grown on wet seedbed	Block 428, IRRI Farm; three 5-m rows, 20 x 20 cm; 3 replications	T = IR9764-45-2-2 or IR9884-54-3 S = IR5929-12-3 T and S check after every 10 entries	4 and 8 WAT
Alkalinity	Maahas clay treated with Na_2CO_3 to pH 8.6, SAR: 35	N as urea at 25 mg/kg: 4% zinc oxide dip	Transplant 2-wk-old seedlings grown in culture solution	Greenhouse trays, 35 x 26 x 11 cm; 3 seedlings per variety; 3 varieties per tray	T = IR46 S = IR5931-110-1 T and S check in each tray	4 WAT
	Maahas clay treated with Na_2CO_3 to pH 8.6	N as urea at 100 kg/ha: P as solophos at 20 kg/ha; 4% zinc oxide dip	Transplant 1-mo-old seedlings raised on wet seedbed	Block L5, IRRI Farm; 3.1-m rows, 20 x 15 cm	T = IR46 S = IR5931-110-1 T and S check after every 10 entries	4 WAT
	Maahas clay treated with Na_2CO_3 to pH 8.6	N as urea at 100 kg/ha; 4% zinc oxide dip	Transplant 1-mo-old seedlings raised on wet seedbed	Block 429, IRRI Farm; three 5-m rows, 0.6 x 5 m per entry; 20 x 20 cm: 3 replications	T = IR46 S = IR5931-110-1 T and S check after every 10 entries	4 WAT

Table 8.3. continued

Stress	Soil/medium	Fertilizer	Method of establishment	Layout	Check varieties	Rating time[a]
Peat soil problems	Calauan; pH 5.8; organic C 25.6%	N as urea at 50 kg/ha; P as single superphosphate at 25 kg/ha; K as muriate of potash at 50 kg/ha	Transplant 3-wk-old seedlings raised on same soil	Three 5-m rows, 20 x 20 cm; 3 replications	T = IR8192-31-2-2 S = IR5931-110-1 T and S check after every 20 entries	4 and 8 WAT
Acid-sulfate conditions/ iron toxicity	Balza; Malinao; Albay: pH 3.7; organic C 0.6%; active Fe 2.3%; active Mn 0.003%	N as urea at 50 kg/ha; P as solophos at 25 kg/ha; K as muriate of potash at 25 kg/ha	Transplant 3-wk-old seedlings raised on same soil	Three 5-m rows, 20 x 20 cm; 3 replications	T = IR36 S = IR21015-136-1-2-31 T and S check after every 10 entries	4 and 8 WAT
Zinc deficiency	Bay; pH 7.2; organic C 3.9%; available Zn 0.19 ppm	No fertilizer	Transplant Swk-old seedlings grown in trays in greenhouse	Three 5-m rows, 20 x 20 cm; 2 replications	T = IR34 S = IR26 and IR6115-1-1 T and S check after every 10 entries	4 WAT
Phosphorus deficiency	Culture solution	P levels 0.5 ppm and 10 ppm	Direct seed	Greenhouse 3-L pots; 4 seedlings per variety; 1 variety per pot; 2 replications	T = IR54 S = IR6115-1-1 T and S check after every 50 entries	4 WAT
Boron toxicity	Maahas clay treated with B as borax at 10 mg/kg	N as urea at 50 mg/kg; P as single superphos-phate at 25 mg/kg	Transplant 2-wk-old seedlings grown in culture solution	Greenhouse 16-L pots; 4 seedlings per variety; 1 variety per pot; 2 replications	T = IR9129-209-2-2-3 S = IR29723-143-3-2-1 T and SW check after every 20 entries	8 WAT and maturity

[a] Notes: EC = electrical conductivity; SAR = sodium absorption rate; T = tolerant; S = susceptible; WAT = weeks after transplanting.
[b] From *Standard evaluation system of rice* (IRRI 1988d).

tolerant at the vegetative stage but its sterility rate increases when it is exposed to salinity at the reproductive stage (Akbar and Senadhira 1985). Other cultivars are known to be susceptible at germination but tolerant several weeks later.

Screening under field conditions can produce unreliable results since the level of salt stress can vary widely within a season and even within a field. To screen plants under controlled conditions, seedlings usually must be grown in culture solution or pots. Aslam and Qureshi (1989) found that the tolerance of 14-d-old seedlings grown in salinized nutrient solution correlated well with that of plants grown in soil-filled pots or fields; thus they suggested that the use of nutrient solution as a growing medium would simplify the screening of large amounts of breeding material.

At IRRI, seedlings are grown in nutrient solution for 2 wk and then transplanted to soil salinized to an electrical conductivity of 8 dS/m (Table 8.3). Guo and Chen (1988) modified this method by sowing seeds directly in soil and screening at the three-leaf stage. They believed this method would be easier and less costly than solution-culture screening. In their method, seedlings grown in soil are transplanted at the three-leaf stage into trays (41 × 27 × 13 cm filled with 7 kg clay loam soil) to which 5.6 liters of 0.5% sodium chloride is added. This concentration of salt results in electrical conductivity of 8-10 dS/m. Plants are scored for leaf injury 4 wk after transplanting.

Akita and Cabuslay (1990) observed that salt-tolerant cultivars have low leaf area ratios (leaf area per total dry weight), thicker leaves, and higher rates of photosynthesis than intolerant varieties. They recommended screening first for low leaf area ratio and then screening the few remaining entries for exclusion of Na^+ from the roots.

The research programs of IRRI and other organizations have extensively screened rice varieties for salt tolerance. Two of the most widely used donors are the Indian cultivars Nona Bokra and Pokkali (from Kerala). Tolerance from these donors has been incorporated into improved breeding lines as follows:

Donor	**Improvedlines**
Nona Bokra	IR10198-66-2
	IR9884-54-3
Pokkali	IR4630-22-2-5-1-3
	IR4630-22-2-1-17
	IR4595-4-1-13

Some traditional varieties are not only salt tolerant but also adapted to other features of their environment (for examples, see IRRI 1984b). These varieties would be excellent donors for the development of improved cultivars adapted to their regions. Because maternal effects have been noted for salinity tolerance, it is advisable to use the tolerant donor as a female parent in crosses (Gregorio and Senadhira 1993). (See Chapter 11 for more information about choosing parents for hybridization.)

Iron toxicity

About 7 million ha of rainfed lowland ricelands are affected by iron toxicity, which is associated with soil pH of less than 5.0 (Akbar et a1 1986a). Tolerance for iron toxicity—a major factor in adaptation to acid-sulfate soils—differs greatly between varieties. The widely grown variety Mahsuri and the Sri Lankan H4 both have some tolerance (Ponnamperuma and Ikehashi 1979). The genetics of tolerance for iron toxicity is not well understood. It is clear, however, that tolerance can be transmitted to modern varieties.

Phosphorus and zinc deficiencies

Of the rainfed lowland ricelands in Asia, phosphorus deficiency affects 12 million ha and zinc deficiency affects 3 million ha (Akbar et al 1986a). Phosphorus deficiency is generally associated with acid soils, while zinc deficiency is more often associated with alkaline, calcareous, or neutral soils. Either of these deficiencies can be eliminated by applying the nutrient to the soil; however, supplies of phosphorus and zinc are limited in some areas, and many soils fix high levels of applied phosphorus.

Varieties clearly differ in their tolerance for both of these stresses. Mahsuri, for example, is noted for its tolerance for phosphorus deficiency. Tolerance for deficiencies of phosphorus and zinc appear to be widespread in rice germplasm. It often is possible to identify tolerant lines that have not been bred for the traits. If these stresses cannot be imposed in the breeding nurseries, advanced lines from the breeding program can be evaluated in farmers' fields that have the stress.

Acid-sulfate soils

Acid-sulfate soils are those derived from marine sediments that are rich in pyrite (Ponnamperuma 1981). They are extremely acid when drained but can support rice production if kept submerged.

The primary stresses created by acid-sulfate soils are phosphorus deficiency and aluminum and iron toxicities. Dao and Nguyen (1982) found that, in the germplasm they screened, tolerance for phosphorus deficiency and aluminum toxicity were correlated; tolerance for aluminum and iron toxicities were not. Acid-sulfate soils also may be saline.

When tolerant cultivars are grown under acid-sulfate conditions, their yields exceed those of intolerant cultivars by about 2 t/ha. Many modern varieties—such as IR36, IR42, IR46, and IR52—can produce excellent yields in acid-sulfate soils (Ponnamperuma 1981). Breeding lines such as IR4422-480-2 tolerate more extreme conditions. The widely grown Thai variety Khao Dawk Mali 105 is noted for its tolerance for acid-sulfate soils (IRRI 1984b). Varieties such as Khao Seta of Thailand tolerate both acid-sulfate and saline soils.

A breeding program for acid-sulfate areas should emphasize the use of tolerant parents in the crossing program and the growth of early-generation breeding nurseries at target sites where the stress is known to occur.

Peat soils

Peat soils (also called *Histosols)* have high proportions of organic matter. These soils commonly are deficient in nitrogen, phosphorus, potassium, copper, and zinc. They also tend to have high concentrations of salt, hydrogen sulfide, and various toxic organic compounds.

Most of the 30 million ha of peat soils in the humid tropics are uncultivated. Boje-Klein (1986) estimated that 10.6 million ha of peat soils in South and Southeast Asia could be brought into production with tolerant varieties of crops. A soil scientist working with the breeding program can greatly facilitate the identification of appropriate selection conditions.

Symptoms of intolerance for peat soils include leaf discoloration (purple, reddish brown, orange, yellow), drying, and death (Akbar et al 1986a).

Marked varietal differences in tolerance for peat soils have been observed. While all IRRI varieties and most breeding lines do not perform optimally in peat soils, several IRRI breeding lines that were not bred for adaptation to peat soils perform as well as traditional cultivars from peat soil areas (IRRI 1978). Developing improved rices for such areas, therefore, should be successful.

Breeding strategies

In developing varieties adapted to adverse soils, a breeder first must consider what priority to place on tolerance for mineral stresses. In most rainfed lowlands, the first priority must be to deal with water-related stresses: drought and flooding. Mineral stresses are usually a lower priority concern.

Thus, for most rainfed lowland rice breeding programs, the breeder should focus on developing cultivars that tolerate water-related stresses but should incorporate into the crossing program cultivars that are adapted to the locally encountered mineral stresses. Further, the breeder should be sure that the soils of the nurseries and field-test sites adequately represent the soil types of the target areas.

In some cases, a mineral stress may not be present in breeding nurseries but still may be problematic in the target area. When adverse soils do not occur naturally in breeding nurseries, artificial screening conditions can be created (Table 8.3). Creating these artificial conditions, however, often is too expensive and laborious to be undertaken by rainfed lowland breeding programs. Further, it may not be possible to recreate the combination of stresses that is likely to be encountered in the natural environment.

When it is too expensive to grow breeding nurseries at sites that have the mineral stress, it may be sufficient to ensure that tolerant donors are included in the crossing program; in early generations, selection can focus on other important traits. Screening the advanced lines under mineral stress should allow tolerant lines to be identified, and they then can be further evaluated for release (Ponnamperuma and Ikehashi 1979).

While in situ selection for tolerance has many advantages, it has one great disadvantage: the level of stress can vary greatly within small areas.

Even within the same plot, plants can experience different levels of stress. Several breeding program practices can compensate for this problem, at least to some extent:

- Tolerant and intolerant check varieties can be included in the nursery to be used for comparison during selection. (The use of check varieties is common in screening pedigree and advanced lines—see Chapters 12 and 13.) If soil stress conditions are highly heterogeneous and space permits, alternate rows can be used as check rows. More commonly, a check row is included as every fifth or tenth row.
- In early-generation bulk populations, selection should be based on comparisons of immediately adjacent plants. Many breeders are tempted to select the healthiest looking plants from only the healthiest looking plots. These plots, however, probably have experienced less stress than plots that appear less healthy overall. The best performing plants from the high-stress plots are likely to have superior tolerance.
- Modifications can be made to experimental designs that take into account higher-than-usual variability within plots. These include reducing the plot size and increasing the number of replications, using smaller block size or incomplete block designs, and employing moving mean or check comparisons (see Chapter 13).

Once appropriate tolerant donors have been identified, standard breeding methods should be sufficient for developing improved cultivars (see Chapter 12). Some special approaches, however, may be useful for programs that seek to breed cultivars for tolerance for adverse soils.

Anther and tissue culture (see Chapter 12) have been used to develop rices with superior salt tolerance (Mori and Kinoshita 1987, Zapata et al 1989). Salt stress easily can be applied via culture media, and this technique seems to allow selection for physiological tolerance (Mori and Kinoshita 1987). Many tolerance mechanisms, however, such as exclusion of ions from the roots and localization of ions to older leaves, probably are not expressed in cultured cells (Yan et al 1992).

Induced mutation (see Chapter 12) may be an excellent means of improving the plant types of traditional cultivars that are adapted to adverse soils. Reduced-height mutants are easily obtained and could be expected to maintain their adaptation to problem soils. Mutants of photoperiod-sensitive tidal-wetland cultivars with intermediate plant height (130 cm vs 160 cm of the parents) have been obtained through induced mutation (Mahadevappa et al 1981).

Rapid generation advance (RGA) (see Chapter 12) also may be suitable, especially where photoperiod sensitivity is desired. A soil stress such as salinity can be applied to the small RGA pots to aid in selection during the early generations (Jones 1989).

Chapter 9

Disease and insect resistance

One of the outstanding successes of programs that breed rice for the tropics has been the development of modern varieties that resist damage from diseases and insects. Some varieties, such as IR36, resist several pests and, as a result, are widely grown throughout the Asian tropics. Some are known for their resistance to one particularly devastating pest, such as the varieties that have controlled gall midge damage to crops in India.

Some scientists maintain that, while breeding programs' success in improving varieties resulted in the green revolution, it also created pest problems. That is, they argue that intensive cropping of modern rice varieties under high inputs provided a favorable environment for many pests: as a limited number of modern varieties began to be widely cultivated, the populations and economic importance of their associated pests increased, and new pathogen strains and insect biotypes developed. Misuse of broad-spectrum insecticides also may have boosted the proliferation of some pests.

Nevertheless, the use of resistant semidwarf varieties (along with other management strategies) has proven to be consistently and significantly more productive than traditional rice culture. High-input cultivation of modern varieties does not necessarily result in increased pest pressure. Since IR8 and other blast-resistant modern varieties have become widely used, the incidence of rice blast has declined, and many lowland breeding programs were able to reduce their emphasis on this disease. The brown planthopper, once a major threat to rice production in Asia, has been controlled in areas where pest-resistant varieties are being cultivated. Modern semidwarf varieties also are thought to be more resistant to stem borers than tall traditional varieties (Pathak 1972).

Rainfed lowlands do not seem to provide an ideal environment for fostering diseases and insect pests because

- Rainfed lowland farmers tend to cultivate a diverse array of cultivars. This environment is less conducive to rapid buildup of diseases and insects than an environment in which a single modern variety is cultivated extensively.
- Rainfed lowland farmers seldom use large amounts of inputs.
- Rainfed lowlands almost always have a distinct fallow period, which prevents a continual buildup of pests.

In fact, the participants of the 1978 International Rice Research Conference, which focused on rainfed lowland rice, suggested that disease and insect pests will not become serious constraints in rainfed lowlands (IRRI 1979).

Results of a survey conducted by Mackill (1986), however, showed that breeders of rainfed lowland rice disagreed with this assessment. They considered the lack of disease and insect resistance to be the major defect of currently grown rice cultivars. They also pointed out that long-duration cultivars are commonly used in rainfed lowlands; and because such cultivars are in the field longer, disease organisms and insects have more time to multiply to damaging levels.

Other characteristics of rainfed lowland rice may differ substantially from those of irrigated rice, but disease and insect problems are quite similar for both environments. Therefore, since the factors that must be considered in breeding for resistance also are similar, this chapter examines the subject only briefly.

Jennings et al (1979), Pathak and Saxena (1980), and Bonman et al (1992) offer general discussions of the applied aspects of breeding for resistance. Khush (1984a) and Khush and Virmani (1985) provide more detailed information. And Heinrichs et al (1985) have published an excellent monograph on breeding rice for insect resistance. These publications are useful resources for breeders who need more detail than this chapter provides.

Types of resistance

Plants generally show two types of resistance to diseases or insects. These are usually referred to as *vertical* and *horizontal* (Van der Plank 1968). While other terms sometimes are used, these two types of disease resistance have been widely observed.

Vertical resistance (also known as *specific, complete, true,* or *qualitative*) usually is inherited simply and often consists of a gene-for-gene relationship between resistance in the host and virulence in the pathogen. Horizontal resistance (also known as *nonspecific, partial, general, field,* or *quantitative*) often is complex in inheritance and usually is not race specific; that is, the level of resistance does not vary greatly with different pathogen races or insect biotypes.

Fry (1982) defined resistance more comprehensively, dividing it into eight classes based on

- magnitude of effect,
- number of genes governing inheritance, and
- presence or absence of differential effects (Fig. 9.1).

In his classification system, vertical and horizontal resistance are two specific cases among all possibilities.

A major objective in breeding for resistance is durability. A cultivar's resistance is durable if it is effective for a prolonged period under widescale cultivation (Johnson 1981). Vertical resistance generally is easier to transfer than horizontal resistance because it usually depends on major genes, which are easily transferred. In most cases, however, vertical resistance genes are not durable: new races develop that can overcome the resistance. Horizontal resistance is more likely to be durable, but it is not simply inherited and,

Small effect Monogenic Differential	Large effect Monogenic Differential 'Vertical'
Small effect Monogenic Nondifferential	Large effect Monogenic Nondifferential
Small effect Polygenic Differential	Large effect Polygenic Differential
Small effect Polygenic Nondifferential 'Horizontal'	Large effect Polygenic Nondifferential

9.1. Types of resistance based on magnitude of effect, number of genes governing inheritance, and presence or absence of differential effects (Fry 1982).

thus, not simply transferred. Horizontal resistance genes usually confer partial or moderate resistance.

While these generalizations have many exceptions, they illustrate the difficulties inherent in achieving durable resistance. In developing varieties for rainfed lowlands, breeders must seek to incorporate a large number of traits simultaneously. Thus, where resistance is concerned, they are likely to follow the easier path of transferring vertical resistance, hoping that (as has happened in some cases) the major resistance genes will remain effective for many years.

A cultivar is *partially* (or *quantitatively*) resistant when it has limited symptoms or damage. Because partial resistance is not always sufficient to control a pest, several approaches have been proposed for attempting to convey the complete resistance conferred by major genes while increasing durability. The most popular strategies—gene rotation (also called sequential release), gene deployment, gene pyramiding, and multilines—are discussed in detail by Jennings et al (1979). While these strategies may be useful in situations where several resistance genes can be transferred easily into new varieties and where the occurrence of new pathogen races can be monitored accurately, they probably are not practical for rainfed lowland rice breeding programs, which must deal with a complex array of traits.

In describing plants' responses to disease, the terms *resistance* and *susceptibility* are relative (Nelson 1973). In a disease-resistant variety, the spread of the pathogen and, consequently, damage to the host plant is limited. *Immune* varieties—those that remain completely free of a pathogen—are rare among crop species. Many vertical resistance genes result in a *hypersensitive* response to the pathogen. Plant tissue immediately adjacent to the infection site dies, thus preventing spread of the pathogen. In rice, for instance, small necrotic spots are sometimes produced by incompatible races of the blast pathogen. *Tolerance* for a disease refers to the situation in which a cultivar is technically susceptible; however, the plant is still able to produce an economic yield despite the presence of the disease.

The discussion of vertical vs horizontal resistance above could apply equally well to insect pests. In describing plants' resistance to insect pests, entomologists often use the following terms (Painter 1951):

- *nonpreference* The plant is not preferred by the insect pest for feeding or as a host for oviposition.
- *antibiosis* The plant has an adverse effect on the biology of the insect pest.
- *tolerance* The host plant produces an adequate yield even when the population of the insect pest is high.

Nonpreference is a common type of resistance to rice pests such as green leafhopper. During screening, nonpreferred varieties may escape damage because alternate genotypes are available to the insect; however, the insects will feed on the variety if no choice is available. Many breeders consider tolerance to be a more durable resistance mechanism than nonpreference or antibiosis because it does not usually lead to the development or selection of new insect biotypes.

Varieties that are moderately resistant to insects fit well with integrated pest management systems by allowing pest populations to be maintained at levels that do not result in significant damage (Heinrichs et al 1985). Decimation of pest populations by strong resistance also reduces the populations of natural enemies that feed on the pest and could ultimately lead to resurgence of the pest.

Resistance often is strongly related to a plant's growth stage; for instance, some plants are resistant only in the later stages of growth. Breeding programs tend to screen for resistance during the early growth stage because a larger number of plants can be accommodated in the test, and turnover is more rapid when several tests are being performed sequentially. Care must be taken, however, that varietal differences in the screening tests also reflect differences exhibited under field conditions at the growth stage most likely to be affected—that is, cultivars should not be screened for resistance at the seedling stage if the problem occurs during flowering unless resistance is correlated at the two stages.

Interdisciplinary approach

Serious pest problems can be overcome only through the unified efforts of plant breeders, pathologists, and entomologists. Commonly, however, breeders select for agronomic traits in early generations and then ask for assistance in determining which of the relatively few advanced lines are resistant. Breeders must encourage active participation by pathologists and entomologists earlier in the breeding process.

For instance, Heinrichs et al (1985) suggested that entomologists should be involved in

- developing efficient screening methods,
- identifying resistant donors,
- screening breeding lines developed by the breeder,
- determining the nature and causes of resistance,
- selecting biotypes to be used in screening,
- determining the rate of biotype selection, and
- identifying resistance genes.

These activities are equally appropriate for plant pathologists who work with crop improvement programs.

Screening methods

In most cases, resistance should be selected for in breeding nurseries with natural or slightly augmented pest populations. This procedure requires few resources and little time while exposing the rice plants to the pests that are most likely to be prevalent in the target area.

Resistance is difficult to assess accurately in breeding nurseries, however, because the host-pathogen interaction is so complex. A disease or insect population develops differently in segregating ricefields than in a uniform variety in a farmer's field. Heterozygosity, heterogeneity among plants, and changes in the pest population over time all affect the degree to which plants or plant families are damaged (Buddenhagen 1983). The effects of differences between the test environment and the growing environment can be overcome somewhat by designing experiments appropriately and by not relying too heavily on data from a single test. Repeating estimates of resistance over time and over generations provides the most sound basis for selection.

In many cases, important pests are not present in breeding nurseries, so screening must be done in hot spots or special facilities. Data gathered from this screening can be incorporated easily into the selection program. Regardless of the screening method used, the program's pathologist or entomologist should be actively involved in the testing.

Several questions must be answered in deciding whether special screening nurseries or tests are needed:

- Can the screening be effective using natural pest populations in field nurseries?
- Can populations be augmented in breeding nurseries to detect differences in resistance?
- If separate screening tests must be performed, are the necessary supplies and facilities available?

For most breeding programs, special screening nurseries are justifiable only for the most damaging pests and for cases where natural disease or insect pressure is not sufficient in breeding nurseries to select for resistance.

Donors of resistance

A full discussion of the available donors of resistance to the most prominent diseases and insect pests is beyond the scope of this book. Some donors have been sources of broad-based resistance for many breeding programs; but in many cases, differences in pathogen races or insect biotypes require the use of donors with resistance genes that are specific to the location. Furthermore, new donors are being identified continually, and previously used donors often become susceptible to new pest strains. One of the responsibilities of the plant breeder is identifying the best possible donors in relation to the breeding program's target area.

In most rainfed lowland breeding programs, improved plant type, tolerance for environmental stress, and responsiveness to inputs are more important objectives than pest resistance. In programs that focus on irrigated conditions, however, resistance to disease and insects often is the first-priority breeding objective; so many of these programs are transferring resistance genes from traditional cultivars or wild species into improved lines. Breeders of rainfed lowland varieties can conserve time and resources by using the improved sources of resistance that are available from irrigated programs.

However, rainfed lowland programs may have to resort to using unimproved sources when

- the only effective sources of resistance are not being used by other resistance breeding programs,
- a disease or insect pest limits yields in the target area, and improved sources have not yet been developed, or
- the source of resistance is itself adapted to rainfed lowland conditions or has other traits needed in the target environment.

Some prominent sources of resistance are mentioned in the sections that follow, and references that list additional sources are cited. Information about new sources is reported in various publications such as IRRI program reports, INGER (IRTP) reports, and the *International rice research notes.* Seeds of prospective donors usually are available from national agricultural research centers or from IRRI.

More effort is needed to make available to the international rice research community the seed of valuable donors that have been identified by national or local research programs. And more information should be compiled about the most likely sources of durable resistance since they would be breeders' first choice for use as parents.

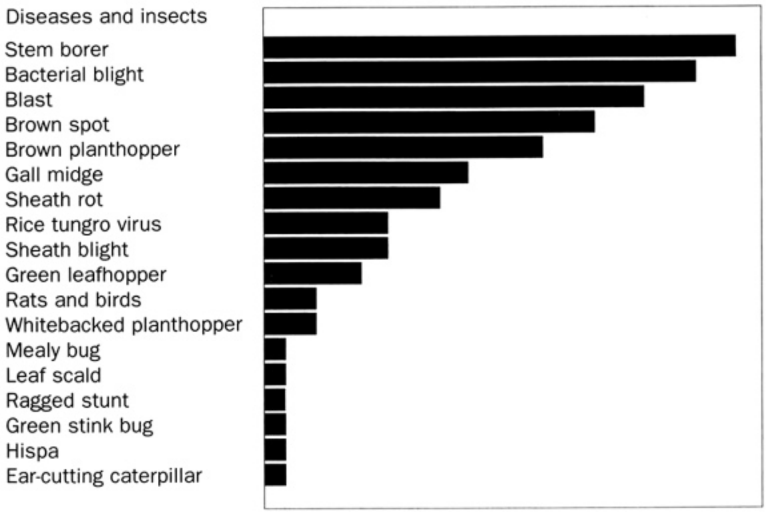
Pest problems in rainfed lowland rice

According to results of a survey of breeders of rainfed lowland rice for South and Southeast Asia (Mackill 1986), the predominant disease and insect pests of rainfed lowlands are not strikingly different from those of irrigated areas (Fig. 9.2).

The distribution and concentration of any particular pest changes over time. When deciding which resistances to include as objectives of a breeding program, the breeder must consider not only the extent of damage caused by the pest but also the level of resistance available in the germplasm and how it is inherited. As more traits are added to the list of breeding objectives, it becomes increasingly difficult to recombine all the desired genes into a single line. In incorporating genes for low-priority traits, the breeder risks sacrificing more important objectives. Physicochemical stresses are overriding considerations in rainfed lowland programs, so only a limited number of disease and insect resistances can be included. Furthermore, pest populations are dynamic; new races or biotypes can evolve during the course of a breeding program, negating its efforts to incorporate resistance. Ultimately, when resistance cannot be bred into a variety, other forms of disease or insect management must be used.

Before they can set priorities for their programs, breeders must know the amount of economic loss associated with each pest; then lower priority can be assigned to breeding for resistance to pests for which other, low-cost control methods are available (Heinrichs et al 1985). Jennings et al (1979) provided some guidelines for setting priorities for resistance breeding:

- Give high priority to breeding for resistance to pests that cause the greatest annual losses to farmers.



9.2. Disease and insect pests as ranked in order of importance by rice breeders for South and Southeast Asia (Mackill 1986).

- Focus on the best prospects for identifying and transferring durable resistance into breeding material. While the development of resistant material may be hastened by using simple screening procedures and donors with simple inheritance of resistance, the durability of the resulting resistance may be poor. Therefore, wherever possible, multigenic resistance should be sought.
- Work on problems for which resources—scientific staff, fields, greenhouses, screenhouses—and environmental conditions are favorable. If resources are not currently available to screen for resistance to major pests, consider setting up screening tests in epiphytotic areas, building new screenhouses, or having material screened cooperatively by other programs or through INGER.

The discussion that follows covers only the pests that are most likely to be of concern to breeding programs. Other pests may be important locally or may become important in time. Information about these less-prominent pests, and more detailed information about genetics and screening methods, is available from the sources mentioned earlier.

Disease resistance

The rice diseases that most frequently and severely affect rainfed lowlands are (Reddy et al 1986)

- bacterial blight,
- tungro,
- blast,
- sheath blight,
- brown spot, and
- sheath rot.

Bacterial blight

The most widespread disease affecting rainfed lowland rice is bacterial blight, which is caused by the pathogen *Xanthomonas oryzae.* This disease is particularly severe when rainfall is heavy. Traditional cultivars may escape serious damage if rainfall declines and, thus, the incidence of the disease declines before they ripen. Improved photoperiod-insensitive varieties that flower early, when rainfall is abundant, are affected more than are traditional varieties.

At least 15 genes have been identified that are associated with resistance to bacterial blight (Table 9.1), and breeding for resistance has been effective in many irrigated areas (Khush et al 1989). The *Xa-4* gene, used widely by IRRI and other programs, provided effective resistance for many years and appears to offer some residual, partial resistance against virulent races of bacterial blight (Koch and Parlevliet 1991b). Elite lines have been developed that incorporate other resistance genes such as *xa-5* and *Xa-7;* some use the source of resistance found in the wild species *Oryza longistaminata* and

Table 9.1. Genes conferring resistance to bacterial blight of rice (Ogawa and Khush 1989).

Gene symbol	Original designation	Representative cultivars
Xa-1	Xa-l	Kogyoku, Java 14
Xa-1^h(t)	Xa-1^h	IR28, IR29. IR30
Xa-2(t)	Xa$_2$	Rentai Emas 2, Tetep
Xa-3	Xa-w	Wase Aikoku 3, Chugoku 45, Java 14
	Xa-4	Semora Mangga
	Xa-6^b	Zenith
	xa-9	Sateng
Xa-4	Xa-4	TKMG, IR20, IR22
	Xa-4^a	
xa-5		DZ192, IR1545–339
Xa-7		DV85
xa-8		PI 231129
Xa-10		Cas 209
xa-11		Elwee, IR8, RP9-3
Xa-12(t)	Xa-kg	Kogyoku, Java 14
Xa-12^h(t)	Xa-kg^h	IR28, IR29, IR30
Xa-13		BJ1, Chinsurah Boro II
Xa-14		TN1
Xa-21		*Oryza longistaminata*

O. minuta (Amante-Bordeos et a1 1992). Some breeding lines (RP633-76-1, IR54, DV85, IR4442-46-3-3-3) developed from diverse sources of resistance are resistant at a wide range of test sites (Seshu 1989).

Quantitative resistance to bacterial blight also can be exploited. In addition to the major genes that govern resistance to bacterial blight, polygenic sources of resistance have been observed (Yoshimura 1989, Koch and Parlevliet 1991a). The resulting resistance is partial but appears to be more durable than that conveyed by major genes because it is not race specific.

Early generations and breeding lines that become naturally infected can be evaluated for their resistance to bacterial blight. However, since the presence of the disease depends on climatic conditions and the flowering dates of the genotypes, artificial inoculation using the clipping method (Kauffman et a1 1973, Ou 1985) allows much more effective assessment of both qualitative and quantitative resistance (Koch 1989). Large nurseries can be inoculated and scored by the pathologist, and the resulting data can be used in selection before the nursery is harvested. It is best to use both major-gene and polygenic sources of resistance as parents.

Tungro

Tungro is the most widespread and destructive virus of rice in the Asian tropics. It is most damaging in irrigated areas, where conditions favor the multiplication of the vector, the green leafhopper.

Tungro actually is a complex of two viruses: rice tungro spherical virus and rice tungro bacilliform virus (Hibino et a1 1978). Green leafhoppers must ingest the spherical virus before they can transmit tungro. Typically, plant symptoms are caused by infection with the bacilliform virus or the bacilliform plus the spherical virus. Plants infected only with the spherical virus show no symptoms.

Rather than addressing the tungro viruses directly, most breeders have focused on developing plants' resistance to the green leafhopper. Such resistance is controlled by major genes and is not durable. New biotypes of green leafhopper can develop rapidly (Dahal et al 1988), and the new biotypes can transfer tungro to formerly resistant varieties.

Sources of resistance to the virus complex have been identified (Table 9.2). Some sources show no symptoms when infected (Hasanuddin et al 1987); others are adequately productive even when damaged by tungro. Most varieties that are resistant to tungro viruses also are resistant to the green leafhopper.

Resistance to the bacilliform virus appears to be under polygenic control in cultivars such as Utri Merah, Kataribhog, and Pankhari 203 (Shahjahan et al 1990). Levels of resistance to the bacilliform virus found in some wild species such as *O. rufipogon* are much higher than those found in cultivated rices (Kobayashi et al 1993).

Several varieties developed by IRRI inherited resistance to the spherical virus from the cultivar TKM6 (Cabunagan et al 1989). These varieties show tungro symptoms when infected with the bacilliform virus by green leafhoppers carrying both viruses; however, they help reduce the spread of the disease because they do not support the spherical virus, which is required for transmission of tungro to other plants.

Tungro usually is not a serious problem in rainfed lowlands, where only one rice crop is produced each growing season. Because rice plants are not continuously available as a food source, the green leafhopper population does not have the opportunity to build up enough to allow a tungro outbreak. Even in rainfed lowlands, however, when conditions are favorable, tungro will occur, sometimes spreading from adjacent irrigated areas.

Breeders who are developing varieties for rainfed lowland target areas in which tungro is a problem should try to select resistant varieties. Breeding for resistance to the vector may be more effective for rainfed lowlands than for irrigated areas because the insect is under less pressure to develop new biotypes in rainfed lowlands: because these areas have a rice-free period, insect populations do not build up as they do in areas that are continuously

Table 9.2 Sources of resistance to tungro identified at IRRI.

Type of resistance	Source variety
Resistant to tungro	Habiganj DW8, Utri Merah, Utri Rajapan
Tolerant of tungro	Balimau Putih, Kataribhog
Moderately resistant to tungro and resistant to green leafhopper	ARC11554, Pahkhari 203, Latisail, Gam Pai 30-12-15, Sigadis
Resistant to rice tungro spherical virus	TKM6, IR20, IR26, IR30, IR40

Sources: Hibino 1987, Tiongco et al 1987, IRRI 1988a, Cabunagan et al 1989.

cropped. Nevertheless, breeding for resistance to the viruses themselves is likely to produce more durable results and does not stimulate the development of new biotypes of green leafhoppers.

So far, breeders have found it difficult to transfer tungro resistance into improved breeding lines due to the polygenic nature of the resistance and the poor combining ability of the donor parents. Resistance to the spherical virus, however, as demonstrated by TKM6 and its progeny (including IR20), appears to be easier to transmit and is likely to be effective in rainfed lowland conditions.

Most programs can rely on the F_2 and pedigree nurseries to become infected naturally. If necessary, the incidence of tungro can be increased by planting rows of infected seedlings of a highly susceptible variety such as TN1 in the nurseries. If the green leafhopper population is sparse, however, the infection may fail to spread enough to make selection feasible, even when infected rows are planted. Late-seeded nurseries usually have higher rates of infection because green leafhopper populations have built up throughout the season.

Blast

Rice blast, caused by the fungus *Pyricularia grisea,* occurs erratically in most rainfed lowland environments, being severe in some seasons and absent in others. It is most severe where plants have been subjected to drought stress and where soils are adverse. Blast pressure is highest in temperate rice-growing regions and tropical uplands. Even in tropical lowlands, however, damage to susceptible varieties can be severe. In rainfed lowlands, leaf blast can devastate seedbeds or dry seeded fields; however, even a moderate level of resistance provides effective protection (Bonman and Mackill 1988).

Most research has focused on leaf blast, but neck blast is even more destructive. While the relationship between leaf and neck blast resistances is controversial, it is clear that, with some exceptions, the two are strongly related (Bonman et al 1989).

The interaction between the blast pathogen and rice appears to follow the classical gene-for-gene system, in which virulence genes in the pathogen are matched by resistance genes in the host (Silué et al 1992). A large number of genes are available that convey resistance to tropical races of *P. grisea* (Mackill et al 1985). Major genes provide strong resistance to specific races, but this resistance can be overcome easily by the pathogen. It might be possible to use major gene resistance effectively in rainfed lowlands, especially where the disease occurs sporadically. In areas where the incidence of blast is high, however, more durable resistance is needed.

Many rice cultivars appear to have durable resistance to blast (Bonman and Mackill l988); for example, IR20 and IR36 have been grown for many years over large areas of tropical Asia with no breakdown of blast resistance. Varieties that have durable resistance may be susceptible when exposed to high disease pressure in upland conditions, but their partial resistance to the fungus is effective under most field conditions. The primary effect of partial resistance is that lesions are fewer and smaller, thus the diseased leaf area is

Table 9.3. Strategy for achieving durable blast resistance (Bonman and Mackill 1988).

Breeding phase	Steps to follow
Parental selection	If possible, include a parent that has durable resistance.
	Avoid highly susceptible parents.
Screening	Use appropriate checks, such as IR50 as a susceptible check and IR36 as a resistant check.
	Screen early generations in an upland nursery. Screen F_2 populations as single plants and F_3-F_6 populations as single rows.
	Avoid highly susceptible and highly resistant lines.
	Select lines with susceptible-type lesions but with resistance similar to or greater than IR36.
Evaluation	Evaluate elite lines for leaf blast in three-row replicated plots.
	Compare disease progress curves with those of IR50 and IR36.
	Evaluate elite lines for neck blast in lowland field trials.

reduced (Yeh and Bonman 1986). This type of resistance has low heritability because environment has a strong influence on the expression of the resistance genes (Wang et a1 1989). Nevertheless, partial resistance has been identified in many rice cultivars of diverse origin.

Using natural infection to select for blast resistance in lowland breeding nurseries usually is unreliable because the incidence of blast is not high and it varies from year to year. Disease pressure also is different for short- and long-duration cultivars. Upland nurseries usually are used instead, screening many lines simultaneously (Jennings et al 1979). Intense selection for high levels of resistance should be avoided, however (Table 9.3). The plants that are most resistant may share a major gene that protects them effectively from the predominant race(s) of blast but that masks the expression of genes that confer more durable partial resistance. In screening varieties targeted for rainfed lowlands, it is more effective to select against susceptibility rather than to select for a high level of resistance.

It is much easier to screen for resistance to leaf blast than for resistance to neck blast, Leaf blast resistance can be screened for in seedbed nurseries, where thousands of lines can be grown in a small area. The lines usually are planted in single 50-cm-long rows with 10 cm between rows. The test can be completed in about 1 mo. In screening for neck blast resistance, however, the plants must be grown at normal field densities and evaluated near maturity. Varieties flowering at different times may be subjected to different levels or races of blast.

Sheath blight

The use of modern varieties and increased inputs has raised the incidence of sheath blight, which is caused by the pathogen *Rhizoctonia solani.* This disease is favored by high humidity, which is likely to be associated with increased tillering (Ou 1985).

Screening at the seedling stage is ineffective because seedlings are not much affected by sheath blight. If measurements of resistance are to be accurate, they must be made at the booting stage or later.

If breeding nurseries are to be screened for resistance to sheath blight, sclerotia from fungi grown in rice hulls can be applied to the leaf whorl to increase the level of infection (Jennings et al 1979). When plants are screened under upland conditions, differences in resistance are more obvious (IRRI 1988a). Scoring for resistance is based on relative lesion length (Table 9.4).

So far, no varieties that are highly resistant to sheath blight have been identified. Several cultivars with moderate resistance, including Tetep, have been reported (Premalatha Dath 1985, Wasano et al 1985, Sha and Zhu 1989). Reddy et al (1986) reported that the widely grown cultivar Pankaj also has moderate resistance.

The inheritance of sheath blight resistance is not well understood but appears to be complex. Heritability is low (Wasano et al 1985, Sha and Zhu 1989), indicating that selection in early generations will not be effective in developing resistant lines.

Most rice breeding programs for rainfed lowlands will not be able to put high priority on selection for resistance to sheath blight in early generations. They have other, higher priorities and the likelihood of success is low. If the disease occurs naturally in nurseries, particularly susceptible entries can be eliminated. If sheath blight is considered to be an important constraint in the target area, advanced lines should be artificially inoculated and screened, and highly susceptible types should be discarded.

Brown spot

Brown spot, caused by the pathogen *Helminthosporium oryzae,* was reputed to be the cause of the famous Bengal famine of 1947. Its occurrence is associated closely with various soil problems, particularly potassium and nitrogen deficiencies (Ou 1985).

Several cultivars, including Tetep, have been reported to be resistant to brown spot (Ou 1985, Baloch and Bonman 1985, Singh 1988a). Only limited efforts have been made to develop resistant varieties. Brown spot resistance is likely to be a low priority; therefore, the most practical breeding approach would be to eliminate highly susceptible lines when the disease occurs in breeding nurseries.

Sheath rot

A common disease in rainfed lowlands, sheath rot is caused by the pathogen *Sarocladium oryzae.* Factors such as drought or floods, other diseases such as tungro, wounding, and insect damage predispose plants to infection with sheath rot (Purkayastha and Ghosal 1982, Ou 1985, Singh 1988b).

Purkayastha and Ghosal (1982) identified resistant varieties, and Misra and Mathur (1983) found the widely grown variety Pankaj to be resistant. Little information is available about the genetics of resistance to sheath rot, however, because such resistance is difficult and time consuming to evaluate accurately.

Selecting for vigorous, stress-resistant plants and eliminating highly susceptible plants or lines should limit damage from the disease.

Table 9.4. Scoring system for evaluating resistance to sheath blight (Ahn et al 1986).

Score	Relative lesion height (%)[a]	Sheath position[b]	Relative intensity of disease	Yield reduction (%)[c]	Classsification
1	<20	<4	1	1	Resistant
3	20-30	3-4	5	1-5	Moderately resistant
5	31-45	2	20	6-15	Moderately susceptible
7	46-65	1	50	16-30	Susceptible
9	>65	>1	100	>30	Highly susceptible

[a] Lesion height/plant height x 100. [b] 1 = uppermost sheath (with flag leaf). [c] Estimated reduction in yield of milled rice due to disease.

Insect resistance

Kalode et al (1986) listed the major insect pests of rainfed lowlands as

- stem borers,
- gall midge,
- green leafhopper,
- rice hispa,
- brown planthopper,
- rice bug,
- ear-cutting caterpillars,
- caseworm,
- leaffolder, and
- rice thrip.

The most widespread pests, and the ones for which breeding for resistance appears most feasible, are stem borers, gall midge, and planthoppers and leafhoppers.

Stem borers

Of the many species of stem borers that attack rice, two are most important in Asia and have been the subject of most resistance work: the striped stem borer *(Chilo suppressalis)* and the yellow stem borer *(Scirpophaga incertulas).* Stem borers damage rice both at the vegetative stage (causing deadheart) and, more commonly, at the reproductive stage (causing *whitehead*). So far, no rice varieties have been identified that are highly resistant to these stem borers, but many are known to be moderately resistant. (For lists of donors of moderate resistance, see Chaudhary et al 1984 and Heinrichs et al 1985).

Several morphological characteristics appear to be associated with resistance, such as tight leaf sheaths (Pathak 1972). Chemical factors within the plant also play a role in resistance (Saxena 1986).

Resistance to one species of stem borer usually — but not always — implies resistance to other species (Pathak 1972, Chaudhary et al 1984). In some cases, resistance at the deadheart stage is not correlated with resistance at the whitehead stage (Chaudhary et al 1984).

Resistance appears to be inherited polygenically and, therefore, is difficult to transfer; however, breeders have been successful in transferring moderate resistance into improved varieties. This resistance seems to be durable: resistant varieties such as IR20 have been grown for many years with no breakdown of resistance (Kalode et al 1986). Recurrent selection, using the diallel mating system and male-sterile-facilitated intermating, has been used at IRRI to increase levels of resistance to yellow stem borers (Chaudhary et al 1984).

Many breeders rank the yellow stem borer as the most serious insect pest of rainfed lowland rice (Mackill l986); that is, it is the pest that causes the greatest economic losses. Screening lines for resistance to this pest is not an easy task, however. Because mass rearing of the insect is difficult, greenhouse screening is not likely to be practical for breeding programs. Field screening in the presence of natural or, where necessary, augmented populations of stem borers is both practical and effective (Heinrichs et al 1985). One successful screening strategy is to grow segregating populations in hot spots (areas known to have heavy infestations of stem borers). In most breeding nurseries, stem borer infestation is sporadic, so selection may be limited to eliminating highly susceptible entries.

Gall midge

The rice gall midge, *Orseolia oryzae,* extensively damages rice crops in many Asian countries. When infestations are extreme, susceptible varieties can be completely destroyed. Varietal resistance is successful, however, in controlling the pest (Heinrichs and Pathak 1981).

An international collaborative program identified eight biotypes of gall midge in several countries (IRRI 1981) (Table 9.5). India has at least three major biotypes (Kalode and Bentur 1989), but a possible fourth biotype has been identified in Andhra Pradesh (Kalode and Bentur 1988). Several donors of resistance to this biotype have been identified. It appears that, although resistant varieties of rice have been grown in India for many years, this fourth biotype is the only damaging new biotype of gall midge to emerge on a large scale.

Resistance to the gall midge is inherited simply. At least four resistance genes have been named: *Gm-1, Gm-2, Gm-3,* and *gm-4* (Chaudhary et al 1986, Tomar and Prasad 1992), and many resistance donors have been identified (see Heinrichs and Pathak 1981, Heinrichs et al 1985, Kalode and Bentur 1988). In choosing a donor of resistance, it is important to be sure that the resistance applies to the prevailing biotype. Most major gene sources of resistance give complete protection. Some sources of moderate resistance may be available but, so far, are not well documented. If the development of new biotypes becomes a problem, however, more effort will have to be applied to locating sources of horizontal resistance. The cultivar CR1014 has been reported to be tolerant of gall midge (Prakasa Rao 1989); that is, it will produce an economic yield even when infested.

Plants can be screened in the greenhouse or in the field for resistance to the gall midge. Either approach has advantages and disadvantages

(Heinrichs et al 1985). When breeding nurseries are screened in the field, lights may be used to attract the insects to the plants to lay eggs.

Planthoppers and leafhoppers

As mentioned earlier, infestations of brown planthoppers and green leafhoppers are likely to be more serious in irrigated environments than in rainfed lowlands because rainfed lowlands are not as favorable to the buildup of pest populations. That is, the planting and harvesting of large areas of rainfed lowlands often are synchronized, and there is a long break in cropping during the dry season. Hoppers also are not favored by the low fertility, drought, and floods that are common to rainfed lowlands. Nevertheless, hoppers can sometimes damage rainfed lowland crops, particularly when nearby irrigated fields are infested.

The brown planthopper *(Nilaparvata lugens)* damages plants directly and also transmits grassy stunt and ragged stunt viruses. The green leafhopper (most commonly, *Nephotettix virescens)* can cause direct damage by feeding on the plants but is more dreaded as the vector of tungro.

Resistance to both pests is conferred by a series of major genes, most of which are dominant. Each gene conveys resistance to specific biotypes; some appear to convey resistance to many biotypes. Of the resistance genes for brown planthoppers, *Bph1* and *bph2* are not effective in India, but *Bph3* and later genes are (Valusamy and Saxena 1989). At least eight genes have been identified for resistance to green leafhopper (Ghani and Khush 1988). Some genes that confer resistance in the Philippines *(Glh1, Glh2, Glh3, Glh5)* are not effective in Bangladesh (Rezaul Karim and Pathak 1982).

Resistance usually is determined through seedbox screening using 7-d-old seedlings infested with second- or third-instar nymphs (Heinrichs et a1 1985). A modified method uses 10-d-old seedlings and slightly lower hopper populations. For brown planthoppers, this test appears to be appropriate for detecting field resistance; for example, IR46 is susceptible to brown planthopper biotype 2 in the conventional seedling test, but it is resistant in

Table 9.5. Reaction patterns[a] of rice cultivars to biotypes of gall midge in Asia (IRRI 1981).

Varietal group	Variety	China	Indonesia	Thailand	India				Sri
					Raipur	Hyderabad	Cuttack	Ranchi	Lanka
Leuang 152	Leuang 152 CR95-JR-46-1	R	R	S	R	R	R	S	R
Ptb	Ptb 18 Ptb 21 IR36	S	S	S	S	R	R	S	R
Eswarakora	W1263 Kakatiyan	R	S	R	R	R	S	MR	S
Siam 29	Siam 29 IET2911	MR	R	S	R	R	R	S	R
Muey Nahng 62M		S	R	MR	S	S	MR	S	S
Ob 677		R	R	S	R	R	R	S	R

[a] R = resistant, MR = moderately resistant, S = susceptible.

the modified test and in the field. Other examples include the cultivars Utri Rajapan and Triveni (Medrano et al 1987)—each has two recessive genes that confer field resistance (Valusamy et al 1987). Field resistance also can be evaluated in the field using resurgence techniques or other methods (Heinrichs et al 1985).

Some entomologists have maintained that hopper resistance conferred by major genes can be effective and durable when crops receive proper management (planting synchronously, allowing rice-free periods, and using minimal amounts of insecticides). The widespread use of year-round cropping and the tendency of hoppers to migrate, however, usually limit the effectiveness of resistance genes to 5 yr or less. New genes need to be incorporated continually into the breeding program. Currently, sufficient sources of new genes are available and wild species are beginning to be exploited. But the cost—in resources and time—of continually incorporating new resistance genes is high, especially when other breeding objectives compete for the breeder's attention.

In rainfed lowlands in which hoppers or tungro are not frequent problems, resistance probably is not essential; promising but susceptible breeding lines should not be rejected. Where some resistance is needed, field-resistant varieties should be developed through modified seedling screening.

Progress in developing disease- and insect-resistant types

In addition to the conventional approaches used to develop more resistant cultivars, biotechnology is opening up new possibilities for rice improvement. Techniques that could be applied to resistance breeding include mapping and tagging resistance genes with molecular markers, characterizing pathogen populations, and introducing novel genes into rice (*transformation*).

The use of DNA-marker technology is revolutionizing plant breeding and genetics. Restriction fragment length polymorphism (RFLP) markers are currently the most widely used markers, but others are rapidly being developed. The first RFLP map of rice was published in 1988 by McCouch et al. RFLP markers are small pieces of DNA that can be mapped to specific locations on the chromosome and used to follow the segregation of genes to which they are linked. When markers are found that are tightly linked to the gene of interest, the marker can be used to select for that gene. The ideal is to identify two markers that closely flank the resistance gene.

This technique can be used to determine the relationships between resistance genes that are newly identified and those that already are known. It also can be used for selection when expression of the gene is difficult to measure. And it is particularly useful when several genes are being combined into one line or cultivar—when two or more genes are present in a single line, it becomes difficult to select for them because almost all progeny are resistant to the races or biotypes available for screening.

One of the most exciting applications of RFLP mapping of disease resistance genes has been the isolation of the genes responsible for the resistance. Knowledge has been increasing about the array of genes expressed during a plant's response to disease attack (Lamb et al 1992). Ultimately, this information will be useful in devising strategies for obtaining durable resistance. The genes responsible for gene-for-gene interactions in disease resistance are now being isolated (Martin et al 1993). An exciting observation is that genes conferring resistance to a diverse array of pathogens in different crops are often similar (Bent et al 1994, Jones et al 1994). These genes appear to be responsible for pathogen recognition and initiation of the disease response (Lamb 1994).

Results of tagging resistance genes with molecular markers are accumulating rapidly, so a comprehensive survey would soon be out of date. Perhaps the most progress has been made with blast resistance, where a number of major genes have been tagged with molecular markers (Yu et al 1991, Wang et al 1994). Recently, thanks to RFLP analysis, *quantitative trait loci* that control blast resistance have been located in the upland cultivar Moroberekan (Wang et al 1994). The resistance of this cultivar has proved to be durable in Africa, and scientists are now transferring the newly identified genes into improved varieties. Similar approaches are being followed in seeking resistance to other diseases and insects; as a result, genes have been tagged that confer resistance to bacterial blight (IRRI 1992) and the gall midge (Mohan et al 1994).

Another type of marker, the *MGR probe,* has been used to better characterize blast populations. These *moderately repetitive sequences* are present in multiple copies in most organisms. They make it possible to detect genetic relationships between different strains of organisms. The use of MGR probes has been used to characterize pathogen lineages (Levy et al 1991). Blast isolates assigned to the same lineage as identified with MGR probes usually have virulence against the same resistance genes. Because it appears to be difficult for an isolate of one lineage to acquire the virulence pattern of other lineages, combining resistance genes that are effective against as many lineages as possible may provide broader, more durable blast resistance.

The technology that allows DNA to be introduced directly into rice has developed rapidly since 1987. Techniques for introducing new genes into rice are now straightforward, usually consisting of transforming rice *protoplasts* (rice cells lacking cell walls) or particle bombardment. One of the primary objectives of current research into transformation is the introduction into rice of a gene that allows the bacteria *Bacillus thuringiensis* (BT) to produce a toxin against stem borers. The gene for BT toxin already has been introduced into rice and has been shown to be effective against striped stem borer (Fujimoto et al 1993). These genes are expected to be available for breeding soon, but they must be exploited carefully. Widespread deployment of the BT toxin gene potentially could lead to rapid increase of stem borer populations that are unaffected by the toxin.

While these developments in resistance breeding offer new opportunities to programs that are developing rice varieties for the tropics, conventional plant breeding approaches are unlikely to be replaced. The most common application of molecular markers such as RFLPs is to assist in selecting for specific genes in breeding programs. Likewise, introducing DNA into rice through transformation is not the final step in producing a new variety: considerable work is required to put the novel gene into the proper breeding line. And lines that are developed using these technologies still must be evaluated through the methods outlined in this book.

Chapter 10

Grain quality

Because rainfed lowland farmers are among the most impoverished of rice producers, some breeders of rice for rainfed lowlands assign low priority to the objective of improving grain quality, assuming that these farmers are more interested in quantity than quality. Breeders need to bear in mind, however, that rainfed lowland farmers have rejected otherwise superior varieties because they considered the grain quality to be unacceptable. In fact, many of the rices that are most highly prized for their grain quality are grown in rainfed lowlands (see Chapter 2), and the extra income generated by these crops helps to compensate for their low yields. New varieties that are introduced into rainfed lowland regions must compete with traditional cultivars that may have been selected over centuries for desirable grain quality characteristics.

Quality factors that can be assessed visually grain size, shape, and chalkiness—are most easily measured. Chemical characteristics—amylose content, gel consistency, gelatinization temperature—are more difficult to measure but are just as important to plant breeding programs. And a new variety must pass the ultimate measure—the taste test—before it is ready to be released to farmers.

Grain length and shape

The length of rice grains is determined after the grains are hulled. Grains are classified as follows (IRRI 1988d):

Classification	**Length**
Extra long	Greater than 7.50 mm
Long	6.61-7.50 mm
Medium	5.51-6.60 mm
Short	Less than 5.51 mm

Grain length preferences vary enormously from region to region. In the rainfed lowlands of Asia, most farmers prefer medium- to long-grained rices; some extra-long types are preferred in Thailand.

Grain shape is the ratio of length to width of brown rice grains. The major classifications are

Classification	**Ratio**
Slender	Greater than 3.0
Medium	2.1-3.0
Bold	1.1-2.0
Round	Less than 1.1

Grain shape is less variable than grain length, and it is less important to consumers; the highest paying markets, however, usually demand slender to medium grains.

Grain length and shape are closely related to head rice yield—the percentage of unbroken grains after milling. Short to medium grains usually break less than do long grains during milling. It is probably wise to give more emphasis to improving head rice yield than total rice yield because head rice yield is more important commercially, varies more, and is easier to improve. (See the discussion of milling quality that follows.)

Grain length and shape are inherited independently and can be combined as desired (Jennings et al 1979). Further, no barriers have been discovered to recombining grain length and shape with other quality traits or with dormancy period, growth duration, or plant type.

Association of specific grain types with cooking behavior may be the result of prolonged selection; that is, farmers probably have selected rices repeatedly over the centuries to meet their eating preferences and, thus, fluffiness (high amylose content) came to be associated with long grains and stickiness (low amylose content) came to be associated with short grains. The rainfed lowland cultivar Khao Dawk Mali 105 of Thailand (see Chapter 2) is a notable exception in that it has both extra-long grains and low amylose.

The breeder needs to know what grain types are considered desirable in the target area of the breeding program. All segregants that do not have such grains should be rejected. It is not worthwhile to spend years developing high-yielding, drought- and disease-resistant lines for rainfed lowlands only to find that farmers, millers, or consumers discriminate against them because the quality of the grain is unacceptable to them.

Grain length and shape are quantitatively inherited. The F_1 generation typically is intermediate between its parents in length; in the F_2, plants are frequently observed whose length or shape falls outside of the range of either parent (a phenomenon known as *transgressive segregation*). If extra-long grains are desired, however, at least one parent with extra-long grains must be included in the cross. Grain length is highly heritable, being little influenced by environment; therefore, it can be selected for effectively in off-season nurseries or greenhouses.

Despite their complex inheritance, grain length and shape appear to be fixed in early segregating generations. Thus, where a certain type of grain is strongly preferred, selection should be strict in the F_2 generation (or the F_1 of multiple crosses). If the desired quality is not expressed in the F_2, the chances of finding better types in the F_3 are extremely limited.

How completely the seed is enclosed by the lemma and palea is a minor grain trait; however, it is particularly important in rainfed lowlands. The grains of some plants have a gap between the glumes. These gaps are undesirable because pathogens may enter through them and spoil the grain, especially when conditions are humid in the field or the storehouse.

In pedigree nurseries, visual inspection is sufficient for selecting plants with the desired characteristics. It usually is not necessary to measure grain length or width except in advanced breeding lines.

Chalkiness

Grain appearance is an important consideration for most rice consumers (Jennings et al 1979, Juliano 1985, Ikehashi and Khush 1979). In most regions, rice that has clear endosperm is preferred over rice that has opaque endosperm, even though all grains are equally translucent after cooking and clarity of endosperm does not affect the rice's taste or texture.

Grain opacity or chalkiness is caused by loose packing of starch and protein particles. Chalky grains have lower market value than clear grains. Opaque areas are called *white belly, white center,* or *white back,* depending on the location of the chalky spot. Breeding programs usually group all opaque grains together—chalkiness is undesirable, regardless of its location.

Waxy or glutinous endosperm and immature grain harvested at high moisture content sometimes may be mistaken for chalky grain. Waxy grains, however, generally are uniformly white and opaque, whereas chalky grains usually have translucent areas. Lines that have no waxy parent do not have waxy grains. If only mature, well-dried grains are evaluated, confusion between immaturity and chalkiness can be avoided.

Chalkiness is influenced by both genetics and environment. The most influential environmental factor immediately after flowering is temperature: high temperature increases chalkiness; low temperature decreases or eliminates it (Resurreccion et al 1977). Other factors such as soil fertility and water management—both of which tend to be problematic in rainfed lowlands—are suspected to affect the degree of chalkiness.

While chalkiness is under genetic control, the exact mode of inheritance probably depends on parental and environmental influences. Most breeders' experience shows that chalkiness is fixed in early generations, so strict selection against chalkiness should be begun as early as possible. If chalkiness is unacceptable in the target area and, thus, would prevent a new variety from being adopted by farmers, F_3 grain from F_2 plants should be evaluated. That is, the breeder should record the average score of 5 or 10 grains per plant or panicle, using a scale of 1 (clear) to 9 (opaque).

Translucency can be combined with any desired grain length or shape, amylose content (except waxy), or gelatinization temperature and is inherited independently of agronomic traits such as plant height, growth duration, and yield (Jennings et al 1979).

Amylose content

Starch, a polymer of glucose, constitutes about 90% of the dry weight of the rice grain (Juliano 1979). It consists of amylose, which is the linear fraction, and amylopectin, which is the branched fraction. Amylose content strongly affects rice's cooking and eating quality—its cohesiveness, tenderness, color, and gloss.

The terms most often used to describe amylose content are

Term	Amylose content
Waxy	0-2% amylose
Low amylose	8-20% amylose
Intermediate amylose	21-25% amylose
High amylose	More than 25% amylose

Waxy rice—also known as *glutinous* rice—is the staple food of the rainfed lowlands of Laos and much of northern and northeastern Thailand. In other parts of Southeast Asia, it is used to prepare rice cakes, desserts, sweets, puffed rice, and parboiled rice flakes. Cooking quality varies considerably among waxy varieties, but all absorb little water during cooking and thus have low volume expansion.

Low-amylose rices are moist, sticky, and glossy when cooked; they split and disintegrate when overcooked. Most japonica rices have low amylose content. Rices with low and intermediate amylose content are used in making fermented rice cakes because they retain gas better and are softer than rices with higher amylose content (Perdon and Juliano 1975).

High-amylose rices, which are widely grown in Asia, cook dry and fluffy but become hard when cool. They are the staple food in Sri Lanka, Pakistan, and India, although Basmati rices (which have intermediate amylose content) also are popular. High-amylose rices are used in making noodles because they resist disintegration during boiling.

Rices with intermediate amylose content approach the ideal for many consumers: they are fluffy when cooked and remain soft when cool. Intermediate amylose is preferred in most of the rainfed lowlands of Asia, particularly in Indonesia, Malaysia, the Philippines, Thailand, and Vietnam.

Different alleles at the *wx* locus confer very low, low, intermediate, and high amylose content (Kumar et al 1987). The amylose content of the heterozygote is intermediate between the parents but cannot be stabilized. Therefore, if the progeny are to have intermediate amylose content, one of the parents must have intermediate amylose.

Amylose content of a variety can vary by as much as 6% between seasons, depending on environmental conditions. High temperatures during ripening lower amylose content (Resurreccion et al 1977).

Breeding for a specific amylose content is not difficult because the trait is simply inherited. Directly determining amylose content is difficult, however, because the procedure is expensive, slow, and delicate (see Jennings et al 1979)—many programs lack the resources to support this procedure. It often is practical, therefore, to substitute simpler alkali tests for gelatinization temperature: where low-amylose types are undesirable, varieties that have high gelatinization temperatures can be rejected because these types always have low amylose content. Rices that have intermediate gelatinization temperatures rarely have low amylose content and can be retained. However, gelatinization temperature cannot distinguish high amylose content from intermediate. Many programs have recently been switching to the use of NIR (near infrared) reflectance to determine amylose content (Villareal et al l994). While this technique is more convenient, the cost of the NIR machinery is still too expensive for most programs.

Gel consistency

The gel consistency test (see Jennings et al 1979) differentiates rices with high amylose content into three types

Type	Gel consistency
Very flaky	Hard
Flaky	Medium
soft	soft

Among high-amylose rices, soft gel consistency generally is preferred by consumers (Juliano 1979). Rices that have less than 24% amylose usually have soft gel consistency. According to Tang et al (1991), gel consistency is controlled by one gene with different alleles for hard, medium, and soft consistency.

Gelatinization temperature

Cooking quality can be tested by determining a rice's gelatinization temperature—the temperature at which water is absorbed and the starch granules swell irreversibly, resulting in loss of crystallinity. Such temperatures range from 55 °C to 79 °C, with rices classified as follows:

Classification	Gelatinization temperature
Low	Below 70 °C
Intermediate	70-74°C
High	Above 74 °C

As mentioned in the preceding section on amylose content, gelatinization temperature can indicate whether a variety has low amylose content (though it cannot distinguish between intermediate and high amylose content). Sometimes, therefore, the gelatinization temperature test can substitute for the more complicated and expensive amylose content test.

Gelatinization temperature is important in determining the physical cooking properties of rice. Rices that gelatinize at high temperatures become excessively soft and disintegrate when overcooked. They generally require more water and time for cooking than do rices that have low or intermediate gelatinization temperatures. Such rices are undesirable in all rice markets.

Gelatinization temperature may reflect the hardness of a rice's endosperm and starch granules. Most tropical indica rices have intermediate or low gelatinization temperatures; most japonica rices have low gelatinization temperatures. Both seem to be acceptable to most consumers.

The inheritance of gelatinization temperature is not entirely clear, but it appears to be simple, involving one or two major genes (Shen et al 1987). Although the heritability is high, gelatinization temperature may vary by as much as 10 °C within a variety, depending on environmental factors. High air temperature after flowering raises gelatinization temperature; low air temperature lowers it.

Crosses using a high-gelatinizing parent always produce many high-gelatinizing F_2 plants. Crosses between japonicas (which have low gelatinization temperatures) and indicas also often produce high-gelatinizing segregants. Because high gelatinization temperature is associated with low amylose, the high lines can be discarded by rainfed lowland breeding programs that consider low amylose undesirable.

The gelatinization temperature test is simple and rapid (see Jennings et al 1979). Milled rice is treated with 1.7%) potassium hydroxide solution for 23 h at 30 °C. Grains with low gelatinization temperature dissolve completely; those in the intermediate class spread partially; and high-gelatinizing rices are unaffected by the alkali.

Milling quality

The term *milling quality* refers to the ability of rice grains to resist breaking while being mechanically hulled. The price of rice generally is based on the percentage of whole grains. Evaluation of milling quality, particularly head rice percentage, is critical to all breeding programs, even if the harvest is largely parboiled to reduce grain breakage (Jennings et al 1979). Currently, no simple, accurate techniques are available that allow the milling recovery of a bulk harvest to be measured from individual plants in segregating generations. Breeders should be aware, however, that traits such as long or extra-long grain, excessively slender or bold shape, partially flattened grain, and chalkiness may contribute to increased breakage; and they should select against these traits in the nursery.

Direct measurement of milling quality begins when elite lines are bulked for preliminary yield trials. A 1-kg sample of grain dried to 14% moisture content is dehulled and milled with laboratory equipment. The results produced by a 1-kg laboratory mill generally correlate to those produced by large commercial mills; smaller laboratory mills produce less reliable results. After milling, the whole and broken grains are separated by a sizing device. The head rice percentage is determined by dividing the amount of unbroken grain by 1 kg. The total yield of milled rice (the combined amount of whole and broken grains divided by 1 kg) varies less between varieties than does head rice yield and, thus, is of less concern to breeders.

Milling quality tests should be performed through successive cycles of yield testing and multiplication of a line. Standard check cultivars also should be tested. Lines with unusually low head rice yield should be rechecked, and all lines with unsatisfactory milling recovery should be discarded. Head rice percentage varies widely between cultivars and also is influenced by environmental factors. Values of up to 68% are possible (McKenzie et al 1987), but greater than 50% is considered good for most programs.

Most breeding programs need to be able to mill small samples. Jennings et al (1979) describe the construction of a satisfactory mill using a one-cylinder engine: a hard piece of wood is shaped to fit precisely into the cylinder and is bolted to the top of the piston, leaving a few centimeters' clearance above the cylinder when the piston is completely depressed. A wooden block, with holes bored to hold 27 test tubes, is attached to the top. The engine is then connected with a belt to an electric motor. Samples of 1-2 g can then be milled.

Juliano et al (1993) related head rice yields to the results of a "stress test" in which dried rough rice was soaked in 30 °C water for 1-3 h, then air dried and micromilled. They found that varieties whose grains had a low degree of cracking when tested also had high head rice yields.

Cooking quality

Grain size and appearance as well as tests for amylose content, gel consistency, and gelatinization temperature are useful for classifying lines into broad groups; but cooking quality still varies between lines within a group. It is essential, therefore, for breeders to cook and taste samples of hot and cold rice of the most promising breeding lines. (See Jennings et al 1979 for details of testing procedures.)

Field workers should be recruited to serve on taste-test panels because their quality preferences often differ from those of persons who have higher incomes. Samples of milled rice also can be distributed to families in the area, along with a questionnaire, for evaluation of cooking quality.

Rough rice should be stored for at least 4 mo after harvest before taste tests are conducted. Storage helps the rice to absorb more water and expand more during cooking, resulting in more flaky cooked rice.

One important aspect of cooking quality is volume expansion. The volume of a rice grain expands 300-400% during cooking. Most varieties produce grains that expand evenly; but some, particularly those in isozyme group V (see Chapter 2), lengthen by as much as 100%. Prominent examples of such varieties are the Basmati rices of the Punjab and Sadri rices of Iran. Some rainfed lowland cultivars, such as Nga Kywe (D25-4) of Myanmar, also have this characteristic. These varieties generally have intermediate amylose content (20-25%), medium gel consistency, and low to intermediate gelatinization temperatures (Juliano 1979).

Protein content

Breeders have used both natural and induced variability to try to increase the protein content of rice. Neither approach has been very successful. Experience at IRRI indicates that it may be possible to combine higher protein content and normal amino acid balance with higher yields (Coffman and Juliano 1976,1979; Nanda and Coffman 1979b). Nevertheless, breeding for increased protein content entails many problems and, thus, probably is an unwise investment for programs that have limited resources.

Aroma

The scent or aroma of rice is a minor quality characteristic. Still, aromatic rice is preferred in some parts of Asia and draws a premium price in certain specialty markets. Pakistan and Thailand are the best sources of strongly aromatic varieties such as Basmati 370 and Khao Dawk Mali.

In some areas, however, aromatic rice is considered undesirable. As breeders develop varieties for these areas, they must be cautious in using as parents improved lines or established varieties from countries where aroma is prized. Aroma is conditioned by at least one gene of major effect (Tsuzuki and Shimokawa 1990, Ahn et al 1992), which can be transferred easily into productive rice genotypes.

Procedures for evaluating aroma are outlined in the *Standard evaluation system for rice* (IRRI 1988d).

Dormancy

Grain *dormancy* —the ability of rice seeds to resist the imbibition of water that leads to germination—is an advantageous trait for rainfed lowland rice, preventing grains from germinating prematurely when the panicles are wet from heavy rainfall or submersion in floodwater. Lack of grain dormancy can cause excessive yield losses when weather is wet during ripening and at the time of harvest.

Many japonica varieties have no dormancy. Traditional indica varieties have adequate dormancy; but the dormancy of many modern indica cultivars has been reduced through selection in irrigated breeding programs that produce more than one crop per year.

The widely grown cultivar Mahsuri is the most famous example of a rainfed lowland variety that lacks adequate grain dormancy. One of its parents is a nondormant japonica cultivar. Because of this lack of dormancy, crop losses have been disastrous in some regions, leading farmers to abandon Mahsuri despite its many other desirable qualities.

While long-duration cultivars tend to have greater dormancy and short-duration cultivars to have less, the association does not appear to be genetic; that is, in crosses, this association has not been observed (Chang and Tagumpay 1973). In some cases, dormancy appears to be controlled by a major gene (Seshu and Sorrells 1986). Genetic studies of dormancy can be complicated by environmental effects: weather during ripening and harvest can affect the expression of dormancy.

Dormancy normally is not selected for in early generations, except that plants whose seeds are germinating in the panicle are eliminated. Later generations or advanced lines can be screened by seeding 1-2 wk after harvest: those that germinate are nondormant and can be discarded.

Chapter 11

Selecting parents and making crosses

Regardless of the breeding objectives or the breeding systems used, rice improvement programs should be organized in the same basic way. Successful plant breeding programs are systematic. The best approach is to set up and follow a system that specifies procedures for each operation, nursery, and trial to be conducted and that permits maximum efficiency in crossing, screening, and generation advance.

This chapter summarizes such procedures, drawing heavily on methodology outlined by Jennings et al (1979).

How parents are selected

High-volume crossing is essential to an effective rice improvement program. As a breeder, you must have clear objectives and priorities, and you must be familiar with the characteristics of important varieties and breeding lines—comparing and choosing parents is easier if you have memorized as much information as possible about these characteristics. Until you have used the potential parents, however, you still will not be able to predict their behavior in crosses because closely related and morphologically similar lines may differ in combining ability.

If you have no experience with the parents, increase the number of crosses, and reject inferior crosses in the F_2 generation (or even in the F_1). Take care, however, when a particularly important trait is available only in one or a few donors. If one parent of a single cross has poor combining ability, a topcross, backcross, or double cross involving better adapted parents gives better results. Such multiple crossing also helps speed up the combining of several characters into one line.

Jennings et al (l979) described the types of crosses as follows:

- **Single crosses:** One parent is hybridized with another. Choose parents from diverse genetic backgrounds, if available. Select as many female parents as possible for each objective, using plants of exotic or unimproved strains as females to help diversify cytoplasm.
- **Backcrosses:** An F_1 is crossed with one of its parents. Backcrosses are particularly suitable if one parent is highly adapted and has many desirable characteristics.
- **Topcrosses** (or three-way crosses): An F_1 is crossed to a variety or line.
- **Double crosses:** Two F_1 hybrids are crossed.

Before making back-, top-, and double crosses, take notes on plant type, growth duration, and other characteristics of the potential parents. Familiarize yourself thoroughly with the parents of the F_1 and of the varieties being considered for topcrossing so you can decide, as you observe the F_1 generation in the field, which parents to use for the next cross.

Topcrosses and double crosses increase the number of desirable segregants from "difficult" or poor-combining parents. In these crosses, the genetic contribution of the poorest parent can be limited by crossing it to a good-combining parent and then crossing the F_1 to another good-combining parent or F_1. They also let you combine traits from more than two parents—a useful procedure for rainfed lowland programs, in which the number of traits being considered often is large. Parents in top- or double crosses should be chosen for complementary characteristics to facilitate combining as many desirable traits as possible.

In backcrossing, a donor parent is selected to introduce a desirable trait into an adapted recurrent parent. The F_1 is backcrossed to the recurrent parent, and the processes can be repeated several times until progeny resemble the recurrent parent except for the trait being introduced. While backcrossing up to six times is common, making only one backcross can allow more genes to be incorporated into the recurrent parent while reducing the undesirable characteristics contributed by the donor parent. Backcrossing is appropriate when the recurrent parent of the single cross is superior to other potential parents for topcrossing. It also is useful when an essential parent, which is excellent for several characteristics, is a poor combiner. Parents such as Khao Dawk Mali 105 and Mahsuri (see Chapter 2), which are adapted to rainfed lowlands, are good candidates for backcrossing.

Using the F_1 as a male in topcrossing makes it easier to detect self-fertilized plants. (The selfs are identical to the female parent.) When the F_1 is used as a female, the selfs are F_2 plants and are difficult to distinguish from the multiple-cross F_1. However, pollen usually is more plentiful in the parent variety or line, so it is frequently more practical to use the F_1 as a female. The F_1 plants that flower on a given day can be emasculated, then crossed the following day with a suitable male parent. Thus, if the pollen shed is plentiful, one or two single-cross F_1 plants can produce a large number of multiple-cross F_1 seeds.

A double cross can be used to combine a large number of desirable traits in one cross. It also may be useful for increasing genetic variability where major differences in traits of all four parents are minimal. Many breeders favor topcrosses over double crosses. It usually is more convenient to use a variety or breeding line as a parent because seed is more plentiful, so pollen plants will be abundant. It also may be difficult to synchronize flowering of two F_1s because seed limitations will prevent staggered plantings. Finally, there is often no need to use two F_1s as parents because topcross parents with sufficient desirable features complementary to the single-cross F_1 usually are available. Jennings et al (1979) provided the following rules of thumb for making crosses:

- If one parent of the single cross is a poor combiner, use a backcross.
- If both parents of the single cross combine well but lack one or more important traits, use a topcross.
- If both parents of the single cross combine well but lack important traits, and no topcross parent is available with all the needed traits, use a double cross.

Plant the parents in flooded pots that are large enough to hold three to five normally developed plants. Three plants will produce enough crossed seed for most purposes. Three plantings of parents at 10- to 14-d intervals should assure simultaneous flowering of both parents of the cross.

In large crossing programs such as IRRI's, it is inconvenient to grow the parents in pots because screenhouse space is limited. These programs resort to growing the parents in the field. The parents are maintained in the field in a hybridization block. The entire set of parents is planted at 2-wk intervals. On the morning of the day before pollination, the female parents are transplanted to pots; in the afternoon, they are emasculated. Male panicles are collected the following morning and used to pollinate the females. Transplanting into pots is labor intensive, but this method saves greenhouse space and lets breeders evaluate parents under field conditions before crossing. It also allows parents to be chosen from other field-grown samples—for example, plants grown in pedigree nurseries or observation trials—as well as hybridization blocks.

Take care with photoperiod-sensitive parents; if they are seeded from January to June, they flower in October or later, depending on the daylength that triggers flowering (see Chapter 4). Thus crosses made in the dry season (January to May) will not flower with the insensitive parents. If crosses are made in the wet season, it is difficult to synchronize flowering of two photoperiod-sensitive parents with different flowering dates (that is, critical daylengths). To synchronize flowering dates for photoperiod-sensitive parents, use seeding dates at 2-wk intervals from August to December. In the tropics, hybridization blocks can be used to cross photoperiod-sensitive parents in the off season, so long as the blocks are seeded before January. In higher latitudes, where low temperatures preclude the use of off-season nurseries, photoperiod-sensitive parents can be synchronized by giving short-day treatments in a greenhouse, if adequate space is available.

Maintaining the purity of the parents for succeeding seasons is essential. Select a few panicles and thresh them by hand for future use as seed sources. If you do not anticipate using a specific parent again in the next season, it can be removed from the nursery. Even a sizeable breeding program for rainfed lowland conditions limits the number of parents used in a season to 50 or fewer (Jennings et al 1979) because most programs lack the resources needed to maintain large numbers of potential parents for future use. They can, however, request seed of specific parental material from IRRI or elsewhere whenever it is needed.

How crosses are made

For a thorough review of crossing procedures for rice, see Coffman and Herrera (1980). The following is a summary.

Rice is easy to cross if certain basic procedures are followed. Crossing in the field usually is impractical because

- It is difficult to take pollen to the emasculated panicles. A panicle that is ready to release pollen is delicate. As it is transported, all its pollen may be shed before it reaches the female.
- Footing is poor in the flooded ricefields, and tools often are lost in the water.
- Since it is difficult to control the field environment, plants may be damaged by diseases, insects, rodents, and weather.

Greenhouses are ideal for crossing, but they are essential only where the climate limits year-round plant culture. A screenhouse is adequate in the tropics. Screens at the sides and top of the facility keep out rodents and birds. The screenhouse base should be gravel or concrete, and a source of water should be available.

You will need the following tools to emasculate and pollinate rice plants:

stool,

- apron with pockets or a small box for carrying tools,
- scissors (small, sharp, pointed),
- fine forceps (not sharp),
- vacuum emasculator (optional),
- glassine bags, about 5 × 15 cm,
- paper clips,
- pot labels,
- tags, and
- marking pencil.

Emasculation

Emasculation is the process of disabling or removing the anthers of the florets. The emasculated plant, which is incapable of self-fertilization, then serves as the female parent.

Rice is ready for emasculation when the panicle has emerged about half way from the boot. (Some dwarf types may not attain 50% emergence before anthesis.) Flowers can be emasculated any time after emergence and before anthesis. In tropical areas, emasculation should be started after anthesis has ceased for the day. Determine the optimal times for emasculation at each location through observation and experience.

Select plants for emasculation that are representative of the cultivar and that have the maximum number of panicles in the optimum stage. Jennings et al (1979) recommended using one or two emasculated panicles for a single cross, seven for a backcross or topcross, and eleven for a double cross.

Several techniques are used to emasculate spikelets. One technique kills pollen by subjecting it to hot air or water in a thermos bottle. The advantage of this method is that, since the spikelets remain open for several minutes after the panicle is withdrawn from the thermos bottle, they can be pollinated before they close. The disadvantages are

- The method is slow.
- Seed set is low due to damage to the spikelets.
- The culm can easily break when the panicle is inserted into the —thermos.
- Pollen must be immediately available for pollination and must be introduced manually into the spikelets before the glumes close.
- If pollen is not readily available, the spikelets must later be clipped or forcibly reopened for pollination.

A simpler and more efficient emasculation technique is to clip the spikelet and remove the anthers with tweezers or a vacuum. A simple-to-build vacuum emasculator speeds the process and makes it less tedious (Herrera and Coffman 1974).

Carefully remove the flag leaf of the panicle to be emasculated; avoid breaking the stem. Use scissors to cut off all florets that have already undergone anthesis. (These appear translucent and usually have the anthers clinging to the outside.) Cut off the young florets at the bottom of the panicle—those in which the top of the anthers are below the midpoint of the floret. Obliquely cut away one-third to one-half of the tissue of the remaining florets to expose the anthers; then remove the anthers with forceps or, preferably, with a vacuum emasculator. Cover the emasculated panicle with a glassine bag you have dated and initialed. Close the bag by folding the open edge diagonally and fastening it with a paper clip.

Pollination

Pollination techniques vary according to breeders' preferences, local conditions, and the facilities available.

If the male parents are grown in the field, collect the panicles just before anther dehiscence. Take care to select representative plants. Remove the flag leaves, and take the panicles to the location where pollination will occur. If several crosses are to be made at the same time, be sure to keep the parents separated and clearly labeled to avoid mixing their pollen, thereby contaminating the crosses. You may find it convenient to place the panicles in small pots of water.

The optimum time to pollinate is when the maximum number of anthers are extruded and they shed pollen when gently touched with the finger. To apply the pollen, remove the glassine bag from the female; then gently remove the pollinator panicles from the water and shake them over the female panicle. Replace the glassine bag over the female, note the parents of the cross on a tag, and attach the tag to the female panicle.

The stigmas of the emasculated spikelets remain receptive to pollination for at least 5 d; so, if necessary, female plants may be repollinated on subsequent mornings. If the pollination is good, seed set should be 50% or higher.

The International Center for Tropical Agriculture (CIAT) has recently described a crossing method, modified from techniques developed by French and Brazilian scientists, that allows many crossed seeds to be produced efficiently (Sarkarung 1991). In this method, female tillers are removed from field-grown plants when panicles are emerging from the boot. All leaves are removed from the tillers; then they are placed in pots filled with tap water. About 50-100 spikelets are emasculated per panicle. These panicles are bagged and kept in the shade. The female plants that develop from these panicles are pollinated as described above, except that panicles of male parents do not have to be removed from the plant. For pollination, the pots containing the female plants can be brought to the male parents in the field. When the pollen is ready to shed, the male panicles are shaken over the female panicles. Pollinated female panicles are kept in pots or buckets in the greenhouse or in an office near a window until the seed is ready for harvest. (The water in the containers is changed every 2-3 d.)

Processing F_1 seed

The seed is mature when it loses its green color, about 25 d after pollination.

Harvest, thresh, and bag the seed from each female panicle separately. (Coin envelopes make convenient containers.) Then assign a number to each cross.

Several procedures are used to number crosses and the resulting segregating lines. Most rice breeders number crosses consecutively, adding a prefix of one to three letters to identify where the cross was made. Under this system, no two crosses carry the same number, and the year and season of each cross can be determined from records of cross numbers assigned each season. New cross numbers are given to all backcrosses and multiple crosses.

Record crosses by listing the pistillate parent (female) followed by the staminate parent (male). While several consecutive-numbering systems are in use, the following two are common (Jennings et a1 1979):

Type of cross	First system	Second system
Single cross	A x B	A/B
Backcross	A/2 x B	A^2/B
Three-way cross	(A x B) x C	A/B//C
Four-way cross	(A x B) x (C x D)	A/B//C/D
Compound cross	(([(A x B) x C] x D) x E) x F	A/B//C///D/4/E/5/F

In the second system, which is simpler, the symbol "×" is replaced with the symbol "/" and the crosses are ordered chronologically:

Chronologicalorder	Symbol
1	/
2	//
3	///
4	/4/
5	/5/
backcross	exponent

When keeping records on a computer, an asterisk (*) can be used instead of an exponent to designate backcrosses. (Software limitations often make the use of exponents inconvenient or impossible.) Thus, a backcross to the female parent is indicated by A*2 /B (instead of A^2/ B); a backcross to the male parent is A/2*B (instead of A /B^2).

Prepare several copies of crossing records so they can be stored at several locations, avoiding loss of data and making access easier. Ideally, the records should be maintained on a computer. If you store the data in a simple database on a personal computer, it will be easy for you to trace the use of any particular parent from the beginning of the breeding program.

Include the following information in the crossing records:

- cross number,
- names and pedigrees of both parents,
- pot identification numbers of both parents, and
- number of crossed seeds obtained.

Dormancy often is stronger in seeds from clipped spikelets. Break dormancy by placing the seeds in a dry-air oven for 7 d at 50-55 °C.

Then lightly treat the seeds with a nonmercuric fungicide and germinate them on moist filter paper in petri dishes. Never sow naked seeds directly in soil. Keep the petri dishes in a 30 °C germinator or at room temperature on a laboratory bench. Transfer the seedlings to puddled-soil pots at the one-leaf stage (7-10 d).

Inspect the F_1 plants before and after flowering and destroy any that have self-fertilized. Then harvest the grain from the F_1 plants,

Plants of single-cross F_1s can be bulked for producing the next-generation (F_2) seed. While some breeders reject undesirable crosses in the F_1 generation, it probably is difficult to predict the nature of the F_2 population based on the appearance of the single-cross F_1 plants. In wide crosses involving a particularly unadapted parent, it is advisable to use the F_1 plants only for further crossing. As the F_1 of multiple crosses segregates, it usually is wise to select the most promising plants and harvest only their seed to be used in producing the F_2 generation. Plants can be bulk harvested within a multiple-cross F_1; but if there is considerable segregation for growth duration or plant height, you may wish to maintain the F_2 seed from each F_1 plant separately.

Chapter 12

Managing segregrating generations

Breeding programs for different types of rice culture rely on the basic breeding methods that have been successful for other self-pollinated crops. The choice of method depends more on the resources available than on the cultural type being addressed. Breeders of rainfed lowland rice, however, may need to adjust the standard methods somewhat to meet their breeding objectives. Alternatives to the pedigree method are likely to be attractive for some objectives.

Procedures that have proven useful in rainfed lowland breeding programs at IRRI and other locations are discussed here.

Managing breeding nurseries

Conditions at experiment stations usually are more favorable than conditions in farmers' fields. If a new variety's potential for success is to be assessed realistically, conditions in the nursery must simulate those under which the variety is expected to be grown. That is, field and growing conditions and planting methods should match or approximate those of the target area.

Field and growing conditions

Varieties that are classified as rainfed lowland rice are grown in fields that range from drought prone to flood prone. Thus, in breeding for rainfed lowland conditions, it is an advantage to be able to adjust the depth of water in the nursery to match the depth expected in the areas for which the variety is targeted. When developing varieties for drought-prone areas, use well-drained fields to stress early generations. When developing varieties that will be grown in medium deep water, use low-lying fields where water can be impounded up to 50 cm deep. (Achieving this depth may mean excavating existing fields and increasing the height of the bunds.)

Often, it is simpler and more cost effective to grow early generations in farmers' fields that are typical of the target growing area, rather than to modify the experiment station environment to simulate on-farm conditions. Under this approach, farming operations and growing seasons can be matched to those followed by the farmers, and early generations can be selected under conditions that are likely to be encountered on farms but not on experiment station plots. For example, soil conditions in farmers' fields may be quite different from those at the station: unforeseen soil-related stresses such as nutrient deficiencies and toxicities and problems of soil texture may become apparent in on-farm nurseries.

This approach has considerable disadvantages, however. If fields are not selected carefully to represent the most commonly encountered environments, breeding lines may be produced that are adapted only to limited situations. Further, managing an off-station nursery may be difficult if the fields are so distant or transportation is such a problem that the breeder can spend only a limited amount of time at the site.

Representative growing conditions must be maintained throughout the life cycle of the crop if superior plants and lines are to be identified and selected with confidence. Plot management that is ideal for developing rice varieties to be grown in irrigated fields is unsatisfactory for developing varieties to be grown under less favorable conditions, as in rainfed lowlands. In these areas, the potential for plant stress is high; thus, varieties developed for these areas should be sufficiently vigorous and well adapted to produce moderate yields when farming practices are less than ideal, and they should respond to improved practices with increased grain yield.

In general, highly favorable conditions favor short plants over tall and intermediate types, which tend to lodge. Under stresses such as drought, plant height is reduced, so shorter plants appear stunted and unproductive. At IRRI, early generations often are grown under mild to severe drought stress to avoid intensive competition from taller plants, particularly in F_2 populations. This practice emphasizes plants with stress tolerance and vegetative vigor. Later generations (in pedigree rows) can be grown under more favorable conditions to eliminate types that are susceptible to lodging.

Soil-related problems such as nutritional deficiency or toxicity are common in rainfed lowlands. While deficiencies can sometimes be alleviated by applying the essential element to the soil before planting, this is often not practical. Some toxicity problems can also be controlled by management, but tolerance for toxicities may need to be incorporated as breeding objectives (see Chapter 8).

If infections and infestations are significant farm problems, they should be simulated or enhanced during breeding so resistant plants can be selected. Selecting of resistance under field conditions is almost always preferable to screening nurseries artificially (see Chapter 9).

Planting methods

If the practice of farmers in the target area is to transplant seedlings, then breeding materials should be transplanted as opposed to seeding it directly. If farmers seed directly, follow their practice. Otherwise, the varieties that are produced may not be appropriate to farm conditions; for example, direct seeding tends to favor selection of plants with low tillering ability (Jennings et al 1979), an undesirable characteristic for varieties that farmers will transplant.

Transplanting a breeding nursery has a number of advantages (Jennings et al 1979):

- Transplanting at uniform spacing reduces interplant competition and encourages uniform growth.

- During early-generation selection, it is easier to separate single plants in transplanted fields (where single-plant hills are typical) than in direct seeded fields (which often are machine-planted).
- Transplanting requires less seed than direct seeding.
- Plants that are transplanted into rows produce more seed than direct seeded plants.
- Weeds and volunteer seedlings are more easily controlled in transplanted fields than in direct seeded fields.

The primary disadvantages of transplanting are (Jennings et al 1979):

- It requires more time and labor than direct seeding.
- Transplanted fields have softer soil than direct seeded fields and, therefore, are more difficult to walk through.

The space between transplanted rows should be 30 cm (Jennings et al 1979). Closer spacing makes it difficult to walk within plots and make selections. Within rows for segregating lines (early-generation families grown in rows), plants can be spaced at 25 cm. Number each row with a wired tag; then, during pulling, use the tag wire to bundle the seedlings and attach them to a stake in the field to which the line will be transplanted.

Jennings et al (1979) described the dry and wet seedbed methods used in rice breeding programs. The wet-seedbed method is modified from conventional Asian rice culture: after the field is puddled, the mud is thrown up in beds about 1 m wide. The top is smoothed off and, after 1 or 2 d, rows are made at 10-cm intervals with a wooden template. The seed is dibbled in the rows and covered with fine, dry soil; then the depressions between the beds are flooded. Dry seedbeds can be grown on a fairly light upland soil where facilities for flood irrigation are available. The seedbeds can be made manually or with a tractor, and rows can be made with a wooden template. When the depressions are flooded, water is splashed on the beds with a shovel. The emerging seedlings must be protected from rodents and birds.

In irrigated areas of the tropics, seedlings commonly are transplanted at 21 d. In rainfed lowlands, however, transplanting frequently is delayed due to lack of water. In general, long-duration cultivars are more tolerant of delayed transplanting than short-duration cultivars; however, tolerance varies within maturity groups. Using older seedlings to transplant segregating populations can help to select for seedling age insensitivity. The older the seedlings used, the greater the selection pressure that can be exerted. Seedling ages of 30-40 d are sufficient for selection; ages beyond 50 d are impractical for large nurseries because such seedlings are difficult to pull from the seedbed. It is not necessary to select for seedling age insensitivity in each generation.

Jennings et al (1979) suggested that even breeding nurseries of varieties developed for direct seeding can be transplanted without concern for natural selection against desired traits. However, while transplanting may be appropriate for F_2 populations—in which single-plant hills are desirable for selection—continued selection under transplanting may produce plants with excessive tillering or shallow root systems. These traits may be undesirable in plants that will be direct seeded. If most farmers in the target area direct seed ricefields, then the pedigree nurseries also should be direct seeded, even if doing so makes crop management more difficult.

Dry seeding is practiced in many rainfed lowland areas. Selection under dry seeded conditions emphasizes early seedling vigor for weed competition, deep root system development, and drought resistance. Dry seeding also probably results in more blast disease, which allows selection for resistance. Thus, in breeding for areas in which dry seeding is common practice, pedigree nurseries should be dry seeded.

A field that is to be direct seeded should be mechanically rowed out immediately before planting (Jennings et al 1979). Standard row spacing is 30 cm. This spacing is wider than that usually found in farmers' fields, but it makes it easier for plant breeders to walk through the field to select plants and allows higher tillering types to be identified easily. Divide the field, using twine to mark the blocks and leaving 1-m alleys between blocks. Apply basal fertilizer uniformly over the field. Stake every fifth row soon after germination, so rows can be identified easily and seedling characters can be recorded in the field book.

F_2 generation

The F_1 generation (single cross) has little variation. The F_2 has maximum genetic variability and thus is the most critical generation in rice breeding. Success in selecting superior F_2 plants depends on using large populations, spacing the plantings properly, strictly adhering to selection criteria, applying heavy selection pressure, ruthlessly discarding poor or dubious material, and differentiating between the effects of competition and inherently undesirable morphology (Jennings et al 1979).

One reason F_2 selection is so important is that many characters are fixed early in the breeding cycle. If F_2 segregates do not have all the necessary traits, it is unlikely that superior plants will be obtained in later generations. In crosses of diverse parentage, the F_2 will contain a "bewildering array of undesirable segregates, with a sprinkling of good ones" (Jennings et al 1979). The breeder's ability to identify the desirable F_2 plants determines the quality of lines in the subsequent pedigree nurseries.

Seed from each single-cross F_1 hybrid are bulked to form the F_2 population (see Chapter 11). Plants from segregating (multiple-cross) F_1s can be harvested individually; but it is convenient to bulk seed within a cross after the most undesirable plants are removed.

When nurseries are transplanted rather than direct seeded, it may be possible to select seedlings before they are transplanted (Jennings et al 1979). Selection is easier if the seedlings are first exposed to a particular stress such as disease and insect pressure or submergence for 7-10 d. The surviving seedlings can be transplanted to the field where the nursery is to be grown.

In rainfed lowland breeding programs, many of the best donors of various traits may not combine well with the improved indica breeding lines that form the basis of most tropical rice improvement programs. Some widely grown farmers' varieties also are known to be poor combiners. Nevertheless, a breeding program may have to rely on these cultivars as sources of important traits. If you are using particularly important or interesting parents but the frequency of desirable F_2 plants is low, consider using a larger population. If you identify progeny that seem to incorporate some desirable traits from the "difficult" parent but are inferior in other respects, use them as parents in additional crosses to improve the inferior agronomic traits.

F_2 populations that are segregating for tall and semidwarf plants are extremely difficult to select without *roguing* (removing undesirable plants), especially if they are direct seeded or grown in highly fertile fields. One advantage of using multiple crosses—especially when the F_1 between a tall and intermediate or short parent is crossed to a topcross semidwarf (or intermediate) parent—is that tall F_1 plants can be rejected, ensuring that competition from tall plants will not be severe in the resulting F_2 population. If tall plants are desired, the tall F_1 plants can be harvested separately, and the resulting F_2 populations can be grown separately from those of the shorter progeny.

The number of plants selected from the F_2 generation varies greatly. If the parents combine well, 400-500 plants may be selected from an F_2 population of 8,000 (Jennings et al 1979). In most cases, however, the number of outstanding plants will be much lower.

Pedigree nurseries

The pedigree method, which is the most widely used breeding method for rice improvement, has many advantages in breeding self-pollinated crops. Breeders can eliminate undesirable genotypes rapidly and concentrate their efforts on the most favorable material. They also can maintain extensive records of breeding lines, accumulating data over several generations of selection; so by the time pedigree rows are bulked for yield testing, considerable information is available about the breeding lines. While an unreplicated test conducted only in one season may be strongly affected by environmental factors, repeated testing over generations is likely to produce accurate data.

The pedigree method also has disadvantages:

- It is labor and resource intensive.
- It may be ineffective in selecting for certain traits in early generations because heterozygosity and heterogeneity may prevent breeders from assessing the lines accurately; thus the results achieved may not justify the resources required.

In the pedigree method, seed from individual F_2 plants are sown in single-row plots to form the F_3 generation. The seed of the best plants in superior F_3 rows are harvested individually to form the F_4 lines. The process is continued until the lines are uniform (usually F_5 to F_7), when superior lines are harvested for testing in larger plots.

Frequency of planting

If climate permits and water is available year round, several smaller nurseries can be planted at 1-2 mo intervals rather than a large nursery. This spreads labor requirements more evenly throughout the season. There is a risk, however, of subjecting plants to conditions not commonly encountered during the normal cropping season. For rainfed lowland rice improvement programs, it is essential to follow a realistic, seasonal planting schedule if plants are to be selected that have appropriate harvest dates, particularly if photoperiod sensitivity is required. Still, it is possible to grow two generations a year if temperatures are not too low and adequate water is available during the dry season.

Using dry-season nurseries to advance generations can minimize the time required by the segregating populations to reach homozygosity. Many characters, such as plant type and growth duration, cannot be evaluated accurately during the dry season. Others, such as grain quality, can be. Special dry-season nurseries can be established to aid in selecting for drought and submergence tolerance and disease and insect resistance.

It often is difficult to select for characteristics of plant appearance in dry-season nurseries because the plants' appearance is affected by the environment, which in this case is not representative of the target environment. One approach is to bulk panicles harvested from several plants within each row. If you maintain the same distribution of rows in the subsequent nursery, the generation can be advanced and genetic diversity within families will be preserved for detailed selection during the following wet season.

Preparing seed for planting

Jennings et a1 (1979) outlined detailed seed preparation procedures that are appropriate for rainfed lowlands, as well as other target environments. In brief: dry recently harvested panicles for 1 d at a maximum temperature of 40 °C. Thresh the panicles by hand, and clean the grain by blowing lightly to remove the unfilled hulls. (A small thresher can be used instead; be careful to clean the machine after each plant is threshed to avoid mixing seed.) Package the seed of each plant in a coin envelope labeled with the number of the row from which it was harvested. Transfer seed for the next-generation pedigree and screening nurseries to new coin envelopes, appropriately labeled.

Row planting and labeling

Pedigree lines from the F_3 to F_6 or F_7 generations should be grown in single rows 5 m long and 30 cm apart (Jennings et al 1979). Within a row, plants should be no less than 20 cm apart; thus, a row can contain 26 plants. About 2-3 g of seed is sufficient to plant one row.

For direct-seeded pedigree nurseries, use about 5 g of seed for each 5-m row. The higher seeding rate is necessary because normal densities and vigorous growth are important beginning in the F_3(Jennings et al 1979).

Place a bamboo or wooden stake at the end of every fifth row. Cut wooden pot labels into 5-cm lengths. Write the row number on both sides of a pot label, dip the label in melted paraffin to prevent the label from being erased by rain, and attach the label to the stake with wire.

Check rows

Plant check varieties at fixed intervals, usually one check row to 20 pedigree rows. Plants in the check rows should be of varieties that exemplify the major breeding objectives. For nurseries of photoperiod-sensitive varieties, use standard varieties with known flowering behavior as checks. If you include typical short-, medium-, and long-duration cultivars of the area as checks, you can accurately assess the flowering dates of the photoperiod-sensitive breeding lines.

Recording data

When considering a field book in which to record pedigree data, remember that you will carry the pedigree book into the field. A small book will fit in your pocket and leave your hands free for other tasks. Large books are preferred at IRRI, however, because they accommodate computer-generated pages, and larger pages are easier to photocopy and distribute to all of the scientists on a team.

Since 1979, advances in computer technology have simplified and improved the accuracy of data collection. If a computer is available, opt for computer-generated and -maintained pedigree records over manual records.

The principles of data collection established by Jennings et al in 1979 still are appropriate. It is essential to record frequent field observations to aid in the selection process. Entries from the pedigree nursery are screened in duplicate nurseries if resources are available. Data from duplicate screening nurseries (such as those that screen for submergence tolerance, disease and insect resistance, and grain quality) should be added to the field book as they become available. The ability to identify the best plants (especially in early generations) is directly related to the completeness and accuracy of the data and observations recorded in the field book. Early-generation pedigree lines are segregating for many important characters, so it is convenient to use codes in recording data since codes occupy less space than written descriptions. The scoring system described by IRRI (1988d), which ranks traits from 1 (desirable) to 9 (undesirable), is appropriate for recording most data and observations.

For rainfed lowland programs, it is important to collect data on

- grain quality (grain length and shape, gelatinization temperature, amylose content);
- tolerance for environmental stresses (drought, submergence, adverse soils); and

resistance to important pests.

The stage of the breeding program at which selection for these characters begins depends on the availability of resources and the relative importance of the traits to the breeding program's objectives.

Most programs also should keep records of seedling vigor and number of days to 50% flowering

Selecting pedigree lines

Selection pressure in the pedigree nursery is generally more strict than in the F_2 generation because more information is available about line behavior. The more complete and accurate the data recorded in the field book, the easier and more accurate is selection.

Many lines can be rejected because of their performance in screening nurseries. Such shortcomings in quality or tolerance / resistance often cannot be determined in the pedigree nursery. For example, submergence tolerance may be a critical selection criterion, but it usually is too risky or difficult to submerge the entire pedigree nursery. Hence, a screening nursery is required to assess this trait accurately (see Chapter 6).

To make selections in the pedigree nursery, first evaluate families of related lines. If you grow three or more lines originating from different plants of the same line in the previous generation, you can better assess genotypic worth. Concentrate selection in the most outstanding families. Harvest the best plants from the superior row of each outstanding family. At IRRI, breeders usually harvest three plants per row but may harvest six from particularly excellent rows.

Jennings et al (1979) gave the following selection philosophy:

> 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.

The Jennings team cited the example of grain length: when a breeding program is seeking to produce only long-grained varieties, early-generation lines that have medium or short grains must be discarded. They will not produce long-grain segregates in later generations.

In general, rainfed lowland rice improvement programs should be guided by the advice of Jennings et al: unacceptable lines should be rejected. It may be worthwhile to select plants from lines that are not ideal, however, under certain exceptional circumstances—for example, when a line is likely to perform well in a different environment, or when a line definitely excels the parents but still lacks a few necessary characters.

Closely examine the plants in pedigree nurseries to identify superior families. Then use a sickle to harvest those that have the desired grain and plant type. Place each harvested plant in a labeled envelope or bag—one plant to a bag. Note the number of plants selected from each row in the field book.

Selection usually begins when the first lines in the nursery reach maturity. In most nurseries, heading dates differ substantially among the lines. If a range of heading dates is desired, make selections at regular intervals (usually weekly) until the latest acceptable maturity date is reached. If you need more seed for screening tests, bulk the seed from the row in which panicles were selected. (Bulking is more appropriate in later than in earlier generations because in later generations the plants within a row are more uniform.)

Most rice breeders continue pedigree selection up to the F_5 or F_6 generation; then they bulk-harvest uniform rows for yield testing. Experience with crosses that involve genetically distant parents, which are common in rainfed lowland programs, shows that segregation can continue into the F_6 or F_7 generation. If the seed of an F_5 or F_6 line is bulk–harvested to be used in observational yield plots, it may be desirable to take some panicles for continued pedigree selection. These pedigree lines can serve as a seed source for lines that perform well in the observation plots.

Bulk breeding

A common alternative to the pedigree method for self-pollinated crops is the bulk method. *Bulk breeding* avoids the disadvantages of pedigree breeding—labor and resource intensity, and heterozygosity and heterogeneity in early generations—because it postpones detailed selection until after the generations have been advanced, when the plants are largely homozygous.

Under the standard bulk-breeding method, each generation beginning with the F_2 is harvested in bulk until homozygosity is attained (in the F_5 to F_7). Natural selection is allowed to take its course, which favors plants that produce more seed. In the final bulk generation, the best plants are selected and their seed is sown in pedigree rows or observation plots. Uniform lines are entered immediately into yield trials.

For irrigated rice improvement programs, when adequate resources are available to support the pedigree method, the bulk method usually is avoided because many breeders believe bulk populations offer too much competition against plants that are most productive in a pure stand. The competition is especially pronounced in populations that are segregating for plant height (cf. Jennings and Herrera 1968) because taller plants crowd out the shorter plants, which generally are more productive.

For rainfed lowland programs, this disadvantage may not be significant. Interplant competition may be useful in rainfed lowland populations since taller, more vigorous plant types often are desirable. When interplant competition is undesirable, it can be reduced or eliminated by applying stress to the bulk generations.

Bulk breeding is most appropriate for populations having parents that are similar in plant height. For such populations, bulk breeding offers savings in labor and other resources, such as field space, over the pedigree method. Bulk breeding can be used for crosses that are segregating for height if tall plants are rogued in the F_2 generation.

A modified form of bulk breeding has been used at IRRI for rainfed lowland rice: the F_2 population is subjected to drought stress. Because this stress is severe, the resulting plants are stunted, and many do not produce panicles or have high sterility rates. All panicles are harvested and bulked; thus, selection favors types that are more productive under stress.

If the population is subjected only to mild stress, most of the plants survive and produce seed; so panicles can be harvested and bulked from only the most productive plants. Usually, because the soil is heterogeneous, the level of stress varies in different areas of the field; so a plant should be rated in comparison only to other plants in the immediate surroundings.

Bulking and drought selection continue for two or three generations. Then individual plants are harvested and entered into a pedigree nursery grown under more favorable conditions, and more data are collected. The pedigree method is then followed until lines are uniform.

The modified bulk method is also useful in selecting for submergence tolerance. Early generations (F_2 to F_4) are grown under artificial flooding, and seed from surviving plants is bulked to form the next generation. Bulk populations can be planted at high density because many susceptible plants are eliminated by the flooding stress; thus many F_2 populations can be grown in a small area. IRRI has used this strategy effectively to increase the submergence tolerance of lines in pedigree nurseries.

Single seed descent and rapid generation advance

As was mentioned earlier, selecting for a complex trait such as yield in early generations usually is ineffective because heterozygosity and masking of recessive genes are high in these generations. The *single-seed descent* (SSD) procedure seeks to advance crosses to homozygosity as rapidly as possible while maintaining maximum genetic diversity for future selection (Brim 1966).

Under the SSD method, plants are selected from the F_2 population, and the resulting progeny are planted in short, single-row plots. In each successive generation, one plant is selected from each family, and its seed is harvested; thus, each line can be traced to a different F_2 plant. Because the F_2 generation has maximum genetic variability, the resulting inbred lines should differ from each other markedly, facilitating selection for desirable characteristics.

SSD is often combined with methods that shorten the growth cycle, reducing the time necessary to achieve homozygosity. One such method, *rapid generation advance* (RGA), combines close plant spacing in small pots, nitrogen deficiency, and artificially short days to minimize growth duration. RGA is particularly suitable for situations in which photoperiod sensitivity is desired (Ikehashi and HilleRisLambers 1979).

RGA cultural methods were described in detail by Vergara et al (1982). Briefly, seeds are pregerminated for 2 d, then planted in wooden boxes at 3 × 3 cm spacing. Fertilizer is applied: 1 g ammonium sulfate, 0.5 g solophos, and 0.5 g muriate of potash per liter of soil. Leaves are pruned if vegetative growth is excessive. At 40-50 d after sowing, ammonium sulfate can be dissolved in water and applied at the rate of 10 g/m^2.

In the RGA screenhouse at IRRI, pots are maintained on carts, each holding more than 400 plants (Fig. 12.1). Breeders harvest two seeds per plant to ensure that each will contribute a progeny plant to the next generation. Both seeds are planted in the same pot in the next cycle; later the plants are thinned to one per pot. Beginning at 20 d after sowing, the plants are subjected to artificial short days (that is, the carts are moved into a darkroom at 1700 h and removed the following day at 0700 h) until 50% of the plants have flowered (Vergara et al 1982). Using this method, crosses even of photoperiod-sensitive varieties can be advanced from the F_2 generation to the F_6 in as little as 2 yr (Ikehashi and Nieto 1980). The F_5 or F_6 generation is grown in the field, and the best plants are harvested to produce pedigree rows.

A disadvantage to RGA is that, since selection is omitted in early generations, useless material may be carried through to advanced generations. To avoid this disadvantage, the F_2 populations can be grown in the field and selected rigorously for important traits such as plant height, growth duration, and grain type. Then equal amounts of F_3 seed from the selected plants can be bulked and entered into RGA.

The major advantage of the RGA method is that it hastens the breeding process. The expected benefits depend on the number of generations that can be grown each year in conventional field nurseries. When only wet-season nurseries can be grown in the field, the RGA method can produce advanced lines for yield testing at least 3 yr earlier than the pedigree method (Table 12.1). If two generations per year can be grown in the field, the RGA method is not appreciably shorter than the pedigree method, especially if the F_2 generation is grown in the field before the population is entered into RGA. If the F_2 is grown in the RGA greenhouse, then the RGA method can save 1 yr over the pedigree method (Table 12.1).

Some traits can be selected for in the RGA facility if space is sufficient (Vergara et al 1982, Murayama 1989). RGA facilities usually are small due to their expense, however, so they tend to be used only for high-priority crosses. Any large, well-funded breeding program that has photoperiod sensitivity as an objective should consider building an RGA facility.

Anther culture

Another method of rapidly obtaining fixed lines from a cross is *anther culture,* which produces doubled haploid plants. These plants are completely homozygous, so it is unnecessary to grow segregating generations.

12.1. Trolley used in the RGA facility at IRRI. The seed can be sown directly in trays that are placed on the trolley or can be sown in small pots if they need to be handled individually. The trolleys are wheeled into a dark room at the end of the day (usually 1600 or 1700 h) to provide the short-day treatment that induces flowering.

In anther culture, the anthers of F_1 plants are placed on an appropriate medium, where the haploid pollen cells produce callus tissue. When appropriate hormones are added, these calli are regenerated into plants. Many of the resulting plants may be haploid, having the genome of the pollen gamete. Many, however, will spontaneously double their chromosome number, giving rise to normal diploid plants. Doubled haploids from a cross are similar to inbreds produced through SSD; but the process of producing them is shorter than inbreeding because only one generation of recombination is required (the F_1), and homozygosity is achieved in that generation.

Anther culture would be particularly useful for breeding improved photoperiod-sensitive rices since developing homozygous lines of these rices after a cross otherwise takes such a long time (Table 12.1). Unfortunately, however, most rainfed lowland rice is indica, and indica rices respond poorly to anther culture. Anther culture currently is used successfully only with japonica rices.

Breeders at CIAT have produced useful breeding lines from upland (group VI or japonica) x lowland crosses using anther culture (Martinez 1990). Anther culture has been advocated as a means of overcoming the sterility observed in early generations of indica X japonica crosses (Narasimman and Rangasamy 1993), but high sterility rates have been observed in some doubled haploid lines produced from indica X japonica hybrids (Guiderdoni et al 1992).

Table 12.1. Comparison of time required to obtain advanced lines from the pedigree method, rapid generation advance (RGA), and anther culture.[a]

Year[b]	Season	Pedigree method		RGA[c]		Anther culture
		One generation per year	Two generations per year	Condition A	Condition B	
1	DS	Cross	Cross	Cross	Cross	Cross
	WS	F_1	F_1	F_1	F_1	F_1
2	DS				F_2-F_5 Greenhouse	Tissue culture
	WS	F_2	F_2	F_2		
3	DS		F_3	F_3-F_6 Greenhouse		DH lines
	WS	F_3	F_4		F_6	Yield
4	DS		F_5		F_7	
	WS	F_4	F_6	F_7	Yield	
5	DS		F_7			
	WS	F_5	Yield	Yield		
6	DS					
	WS	F_6				
7	DS					
	WS	F_7				
8	DS					
	WS					

[a]The generation grown in each season in each year after making the cross is shown. For the pedigree and RGA methods, it is assumed that F_7 lines are grown in the pedigree nursery before lines are selected for yield trials. For this example, it is assumed that the cross is made in the dry season and the F_2 is grown only in the wet season. [b]DS = dry season, WS = wet season. [c]Condition A = F_2 generation grown in the field and only WS nurseries can be grown in the field. Condition B = F_2 generation grown in the RGA greenhouse and two generations per year can be grown in the field.

Backcross breeding

Backcross breeding is useful for introducing one or a few characters into a highly adapted cultivar or breeding line, termed the *recurrent parent.* The donor variety usually has one or two genes that markedly affect the phenotype (conveying, for example, disease resistance, semidwarfism, or improved amylose content). The F_1 of the initial cross is backcrossed to the recurrent parent, and subsequent F_1 plants that have the desired gene(s) are again backcrossed to the recurrent parent. This backcrossing is repeated up to six or seven times until the phenotype of the recurrent parent is restored except for the trait being introduced.

While backcross breeding has been used extensively for many other crop species, it has not been widely used for tropical rices because

- Many breeding programs lack sufficient funding and labor to make the large number of crosses required.
- Among tropical rice varieties, few parents have only a single weakness.
- Most crosses of tropical rice varieties address several traits.
- Many of the traits that are of interest in tropical rices, such as yield and drought resistance, are not controlled by major genes.

Backcrossing could be an excellent approach to improving widely grown rainfed lowland cultivars that are difficult to replace, such as Mahsuri and Khao Dawk Mali 105. Overreliance on this method using one or two recurrent parents, however, would perpetuate the use of a narrow germplasm base over large areas. This could lead to genetic vulnerability should a new race or biotype of a disease or insect pest become established in an area. And, since repeated backcrossing produces lines that are genetically similar to the recurrent parent, it may not provide the genetic variability required for making major advances over currently grown cultivars.

A compromise between single crosses and repeated backcrossing would be to make just one or two backcrosses to the recurrent parent. If the donor parent is a poor combiner, a backcross increases the frequency of desirable genes; thus it is easier to recover agronomically desirable lines than with a single cross. Limiting the number of backcrosses to one or two increases the genetic diversity of the segregating populations, making it easier to recover novel combinations of favorable genes than with repeated backcrossing.

Population improvement

Most breeding programs rely on single, top, or double crosses to develop populations from which to select superior new recombinants. Only two to four parents can thus contribute genes to the segregating population. Furthermore, segregating genes rapidly become fixed (that is, homozygous) due to self-pollination. By chance, many of the undesirable alleles are fixed during selfing before the desirable alleles can be selected for.

In long-term breeding programs, as superior recombinants are isolated, they are recycled into the crossing program to develop lines with even higher levels of the desired traits or to incorporate additional traits. *Population improvement* is a more efficient method of systematically recombining many genes.

In this technique, a population is developed by intercrossing a group of parents in all combinations in a diallel crossing scheme. The F_1 plants are again intercrossed in as many combinations as possible. Intercrossing is repeated for at least three cycles to ensure sufficient recombination before selection.

For self-pollinated crops such as rice, introducing a male sterility gene greatly facilitates intercrossing. Most male sterility genes are recessive and are designated *ms.* The homozygous dominant (*MsMs*) or heterozygous (*Msms*) genotypes are fully fertile. The homozygous recessive plants (*msms*) are male sterile, but they can be pollinated by fertile pollen of surrounding plants. Most male steriles set 10-20% of crossed seed under normal conditions.

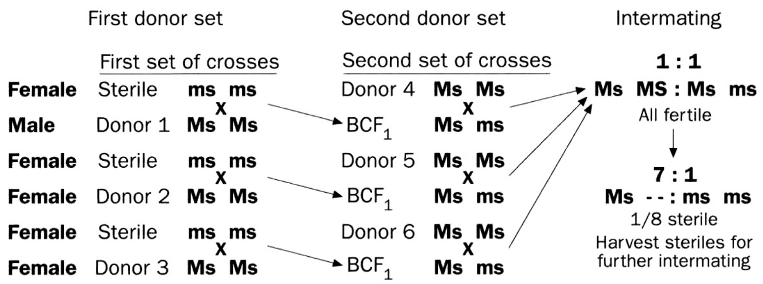
To develop a population, donor plants are crossed as males to a source of genetic male sterility (such as IR36 *ms* used at IRRI). The resulting F_1 plants, which are *Msms* (fertile), can be crossed as males to an additional set of donor plants (Fig. 12.2). Using the *Msms* plants as males in an additional cross reduces the contribution of the donor of male sterility and assures that the cytoplasm is diversified.

Seeds are harvested from male sterile plants in successive cycles. (Male sterile plants are easy to recognize: they produce few seeds, their panicles remain erect at maturity, and they may have poor panicle exsertion.) Since the male sterile plants have infertile pollen, the seeds are the result of crosses with surrounding plants that have fertile pollen. Intercrossing can be continued for three cycles before selection must begin.

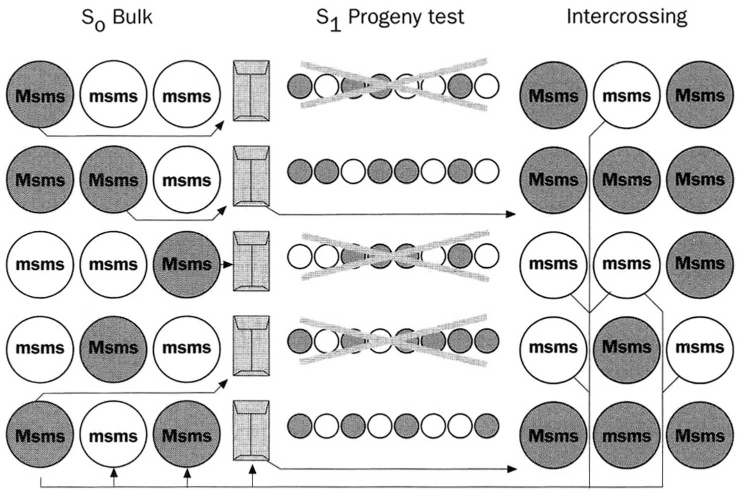
The populations developed through this method can be pedigree– or bulk–bred; but some type of recurrent selection scheme usually is used (Fujimaki 1979), such as the S_1 selection method, which is the most commonly used method for self-pollinated crops. In S_1 selection, fertile plants are harvested from the bulk population (S_0) to produce S_1 families (Fig. 12.3). At least 200 S_1 families are evaluated for the target traits. The S_1 generation has about three fertile plants for each sterile plant. It is important to maintain at least 5 g of remnant seed of each S_1 family.

The best S_1 lines (about 10% of the total) are used to reconstitute the next cycle of the population. Remnant seed from these S_1 lines is bulked to form the intermating generation. From the resulting bulk population intermating is affected by harvesting sterile plants. Seed is bulked to produce the S_0 population of the next cycle, from which fertile plants are harvested. In any cycle, fertile plants from superior S_1 lines can be harvested and entered into a pedigree nursery for further selection and evaluation.

Recurrent selection methods, such as the S_1 method, can be used not only to recombine traits from many parents but also to improve a specific trait within a population while maintaining genetic diversity for unselected characters. Despite these advantages, recurrent selection has not been widely used for rice or other self-pollinated crops because the method is slow. Thus,



12.2. Population development using genetic male sterility. The first set of crosses is made between the male sterile plants (designated msms) and the rainfed lowland donor varieties. The second set of crosses is made to an additional set of donor cultivars with the backcross F_1 plants, which are fertile, as the male parents. All progeny of these crosses are fertile, so all plants are harvested and planted again. One-eighth of the plants in the next cycle should be sterile; these are harvested and planted for continued intermating.



12.3. The S_1 population improvement scheme. In the S_0, which follows intermating, male fertile plants are harvested. At least 5 g seed of each harvested plant is maintained as remnant seed. All the resulting S_1 plants are grown in a progeny test. Remnant seed of the superior S_1 lines is bulked and sown for the intercrossing. All male sterile plants are harvested and bulked, and this seed is planted as the S_0 of the next cycle.

it is generally regarded as a long-term complement to more common breeding methods.

Alternatives to hybridization

The basis of the breeding methods described above is the production of genetic variability by crossing parents with complementary characteristics. This hybridization allows selection of new recombinants that have more desirable characteristics than were available in either of the parents. Two common alternatives to hybridization are mutation, where genetic variability is produced by a mutaginizing agent, and pure line selection, where variability in traditional varieties is exploited to produce pure lines superior to the original population.

Mutation breeding

As an alternative to backcrossing, *mutation breeding* produces improved variants of a widely adapted cultivar through the use of agents that increase the chances of gene mutations. Mutation breeding can be a successful alternative to backcrossing when the donor parent's desirable gene is linked to undesirable genes. Induced mutations also can help to isolate new genes that are not available in the germplasm. So far, mutation has been most useful for inducing semidwarfism in tall cultivars and shortening the duration of long-duration varieties.

Gamma rays (from ^{60}Co) and chemicals such as ethyl methane sulfonate are commonly used to induce mutations. After the seeds are treated, the M_1 generation is grown in the field and seed from promising plants is harvested. This M_2 seed is sown—one row per M_1 plant—and the resulting plants are examined carefully for useful mutations. Recessive mutants usually breed true by the M_3 generation; lines can be bulked for more advanced testing.

Successful applications of mutation breeding in rainfed lowland rice include the release of a waxy mutant (RD6) and a short-duration mutant (RD15) from the widely grown Thai rice variety Khao Dawk Mali 105.

Pure line selection

Pure line selection is the improvement of a crop species through selection among traditional varieties or land races. This method was popular for use with self-pollinated crops when traditional varieties still were widely grown. As it approaches the limits of its utility, however, further crop improvement requires hybridization.

During the early decades of efforts to improve tropical rice, pure line selection was responsible for the development of many widely grown cultivars. Traditional rainfed lowland varieties had considerable genetic variability, and in many cases pure lines isolated from these cultivars were superior to the original varieties. Since these traditional varieties are still grown in unfavorable rainfed lowlands, some breeders have continued to use pure line selection. For irrigated rice, pure line selection is not used because traditional plant types are seldom productive under irrigation.

Pure line selection involves

- selection from diverse traditional varieties to identify homozygous lines that are more productive than the population as a whole, and
- identification of highly adapted or productive strains that can be multiplied and distributed to farmers for widescale cultivation.

Pure line selection probably is most useful in situations where little breeding has yet been done or it is difficult to develop new lines that outperform traditional varieties (such as for deepwater rice). Except where resources are extremely limited, it probably is not an appropriate method by which to improve rainfed lowland rice.

Chapter 13

Evaluating advanced breeding lines

As the segregating early generations are advanced, the number of genotypes decreases and the frequency of promising selections increases. Thus, in later generations the breeding lines are ready for more intensive evaluation than was possible with the large number of lines and heterogeneity of the earlier generations.

Procedures for rainfed lowland rice are most different from those for irrigated rice at this stage of the breeding program. Both types of programs have similar stages of evaluation: observational yield trials, replicated yield trials, and multilocation yield trials (Jennings et al 1979). But in other aspects—how the trials are set up, how the experiments are designed, what sites are used, and most importantly how the results are interpreted—they differ markedly.

When lines in the pedigree nursery become uniform (usually in the F_5 to F_7 generation), all the plants in each line can be harvested in bulk. The increased amount of seed available allows wider evaluation. Accurate yield testing requires larger plot sizes of at least 5 m^2 and replication. Many breeders prefer to grow an initial unreplicated yield trial, often termed an *observational yield trial* (OYT). This trial lets the breeder see how the lines look in larger plots (four to six 5-m rows) but does not require as much space and seed as replicated trials. The lines also are grown in special screening nurseries (which test, for example, the lines' tolerance for drought or submergence or their resistance to diseases and insects) and they are evaluated for grain quality traits. The most promising entries are advanced to a *replicated yield trial* (RYT) for more accurate assessment of yield. Ultimately, the lines must be evaluated at several locations representing the target environment before the most promising lines can be nominated for release.

Rice improvement programs routinely use farmers' filed trials to screen cultivars at the end of the breeding process prior to official release. But for rainfed rice, this is often too late. Practical methods are needed to incorporated agroecological variation into the breeding program. Testing needs to begin as early as possible in as wide a range of rainfed conditions as possible. This necessarily requires more resources and teamwork than for irrigated rice.

The agronomist is a crucial partner to the plant breeder in advanced generation screening. He should bring to the team a farming systems perspective. He works with the breeder to select sites for on-farm testing, and may manage this network of trials on behalf of the team. He may integrate other agronomic studies with the screening program at the same sites. He focuses special attention to local farmer reactions to the test materials to provide the breeder with key feedback.

Observational yield trial

By the time the most promising breeding lines from the pedigree nursery are bulked, they have been evaluated repeatedly for resistances, grain characters, maturity, plant type, and other essential traits. During observational trials, breeders can confirm previous screening results and conduct evaluations that were infeasible during earlier generations; that is, they can assess yield components (spikelets per panicle, tiller number, grain weight, sterility), resistance to shattering, milling quality, and adaptability to environmental stresses, in addition to grain yield.

OYTs ordinarily include only one plot of each entry at each site—the large number of lines under evaluation does not permit replication. Thus within a site some entries yield more than others because they happen to be located in portions of the field that have more favorable conditions: higher soil fertility, more water, or lower concentration of a toxic compound, for example. Breeders commonly plant a check cultivar at frequent intervals so the yields of the lines being tested can be compared with those of the variety in the nearest check plot. For instance, yields of the lines being tested can be expressed as percentages of the yields of adjacent checks by dividing the line's yield by the mean yield of the nearest check plot on either side of the entry and multiplying by 100.

A disadvantage of this approach is that the number of check plots is large, taking up valuable space in the nursery. To avoid this problem, a moving mean can be used for comparison (Mak et a1 1978). That is, the yield of each line can be compared with the means of the yields of adjacent lines—commonly three to five plots on either side of the entry.

Another useful procedure is the augmented design proposed by Federer (1956), which includes unreplicated breeding lines or cultivars within blocks of replicated check cultivars. It is beyond the scope of this book to present the analysis associated with this procedure; however, Scott and Miliken (1993) have developed a computer program for the augmented design that is based on the popular SAS program (SAS 1990).

When space and funds are too limited to allow the OYT to be replicated, data are lacking that would allow traits to be analyzed statistically; however, the main objectives of the trial—rapidly screening many breeding lines, eliminating the inferior ones, and identifying the most promising ones for more intensive evaluation—can be achieved. If the breeding program prefers to keep the total number of advanced lines constant, the discard rate must equal the rate of production of new advanced lines from the early-generation nurseries.

In the typical irrigated breeding program, one OYT is conducted at the experiment station; then the most promising lines from that trial are advanced to an RYT, also conducted at the station (Jennings et a1 1979). This

13.1. On-farm observational and yield trials allow farmers to provide valuable feedback to breeders in addition to providing information on adaptation of experimental lines to actual rainfed lowland conditions.

approach is appropriate for irrigated programs since the growing conditions at the experiment station are similar to those on irrigated farms.

For rainfed lowland breeding programs, one OYT usually is not sufficient. Growing conditions for rainfed rice are much more variable than those for irrigated rice. An experiment station cannot offer the range of environmental conditions under which the lines must be grown if they are to be evaluated accurately. The most useful approach for rainfed lowland rice is to conduct OYTs at several sites that have differing growing conditions. While these *multilocation trials* can be expensive in comparison to on-station trials, they are the most efficient means of identifying the most promising breeding lines. Further, when trials are conducted on working farms, the farmers have an opportunity to offer input and feedback at an early stage of the breeding process (Fig. 13.1). If financial or other constraints make it impossible to conduct OYTs in the fields for which the lines are intended, use several locations near the experiment station that have different growing conditions.

An OYT plot usually consists of four to six rows that are 5-10 m long. Since the OYT is the major source of seed for future trials, spacing between rows and hills should be wide enough to facilitate roguing of off types (30 × 15 cm or 20 × 20 cm); density should be one plant per hill. (For direct-seeded plots, use 30-cm row spacing.) At least every twenty-fifth plot should be of a check variety. This placement of check varieties makes it possible to recognize when plants are not doing well due to environmental problems such as soil heterogeneity rather than due to inherent weakness in the plants.

For the OYT, use seed from the most uniform plants of the F_5 to F_8 lines from the pedigree nursery. A minimum of 20 g of seed is needed to plant a transplanted four-row plot. Use more seed at remote farm sites because seedbed conditions probably will be less favorable and germination rates may be lower than at the experiment station. It is best to have 50 g of seed of each OYT entry for each location to ensure that adequate seed is available for screening nurseries and grain quality evaluation. Thus, if OYTs are conducted at four locations, 200 g of seed is sufficient—an amount that can easily be obtained from a single pedigree row.

Management of the OYT plots should represent a compromise between farmers' practices and optimum practices. That is, strictly following the practices of resource-poor farmers may not allow the entries to express their genetic potential fully; but using inputs (such as fertilizer and pesticides) at levels that farmers can never hope to afford will produce results that cannot be duplicated on the farm. Nevertheless, take any necessary steps to eliminate pests for which no genetic resistance is likely to be found and that may so devastate the stand that you cannot accurately judge varietal differences.

Conduct one OYT at the experiment station in irrigated plots to assess potential yield under optimum conditions and to assure that sufficient seed is available for future trials. In this irrigated trial, rogue off types frequently, particularly around the flowering stage. Record both numerical rankings of and descriptive notes about important characters. Unless some entries are obviously inferior or still segregating, harvest all plots of the irrigated OYT.

Collect data from OYTs at other sites as often as possible, and measure yields at those sites. Field trials are more difficult to supervise and thus assure the purity of the seed. It is therefore usually not desirable to use seed harvested at farmers' field sites for future trials. Since the seed will not be used, it is not necessary to rogue off types.

Jennings et al (1979) recommended the following procedure for evaluating yield: harvest the central rows of each plot, leaving one border row at each side. Dry, clean, and weigh the harvested seed; convert the yield to kg/ha; and enter the result in the field book. In general, yield values should be corrected to 14% moisture; but uncorrected value can be used without much error if the samples have been dried for 1-2 d in the sun or in a seed dryer. Select about 100 panicles from border rows of uniform plots to provide seed for the RYT.

Phenotypic acceptability

The International Network for Genetic Evaluation of Rice (INGER) relies extensively on phenotypic acceptability (PA) scores in evaluating OYTs. A PA score is a highly subjective overall rating of a breeding line that reflects how the breeder perceives the line in relation to the program's priorities; thus, it indicates what the breeder intends to do with a line the following season.

Table 13.1. A typical scale for rating phenotypic acceptability (PA).

Score	Description[a]	Interpretation
1	Outstanding	Move to most advanced trial and include in hybridization block
3	Good	Move to more advanced trial or keep in same trial
5	Fair	Keep one more year or discard
7	Poor	Discard
9	Unacceptable	Discard

[a]Descriptors are from the *Standard evaluation system for rice (SES)* (IRRI 1988a).

Recording PA scores is particularly useful for large OYT nurseries where there is not enough time or resources to measure all traits directly. Although direct measurement of yield of OYT entries is desirable, yield measurements can be quite expensive, especially if multilocation OYTs are grown. Many breeding programs prefer to concentrate on measuring yields in replicated trials where statistical analysis can be performed. PA scores can thus be used to evaluate yields in the OYT so the most promising entries can be advanced to replicated trials. The scores are most reliable when the nurseries are grown under stress, as this makes it easier to differentiate the tolerant and susceptible entries.

While PA scores are commonly used by rice breeders, even for recording observations of RYTs, no standard scale is in use. However, the scale illustrated in Table 13.1 is typical. Some breeders assign different interpretations to the scores or use intermediate values (that is, even numbers).

Entries that perform especially poorly under stress in the trial can be maintained as susceptible checks. For example, an entry that receives a score of 9 at a location where drought has occurred may be highly susceptible to drought. If the entry performs well in other trials, the breeder may be able to assume that drought stress has not occurred at those sites.

PA scoring is merely a decision-making tool. The score given to an entry is relative to the conditions of the trial and, more importantly, to the response of the check cultivar. When growing conditions are unfavorable, all entries may look as if they deserve inferior scores, so comparison to the check entry becomes vital. For example, entries with only 50% survival due to a stress may ordinarily deserve scores of 7 or 9; however, if the check cultivars had less than 10% survival, entries with 50% survival merit a much better score than 7 or 9.

In using PA scoring,

- Try to score all lines so the mean is near 5 for all trials, making it easier to compare data between trials. This mean can be achieved by assigning the best performing lines a 1 or 3 and the worst performing lines a 7 or 9. Maintaining a mean score of 5 may be impossible, however, when the amount of stress differs greatly between sites.
- For trials in which mean PA scores are variable, compare the scores of the entries with mean score or with the scores of the check cultivars. For example, a score of 5 may indicate that an entry is mediocre if the

mean also is 5 and the check cultivars earned a score of 3. But if stress was particularly severe and the check cultivars scored only a 7 or 9, an entry's score of 5 is respectable.

The brief notes included in the field book about the characteristics of a line can give only limited guidance in composing the next season's nurseries. PA scores integrate all factors involved in the visual assessment of breeding lines; thus, they can help make these decisions easier and more apt.

Set up the field book with a column for the overall PA score as well as columns for noting a line's strengths and weaknesses (Fig. 13.2). When certain traits are especially important, assign columns to those traits and use the 1 to 9 scoring system to rank them. An entry that receives a 1 for lodging resistance and a 4 for plant height but has small panicles or other weakness may deserve an overall score of only 5 (see plot 4112 in Fig. 13.2). Thus, the PA score constitutes a final assessment of a genotype's worth in a single number that can be averaged over sites and used as the basis of decisions to advance or discard entries.

Evaluating data from several OYTs

Decisions about which entries to advance to replicated trials, which to keep in the nursery, and which to discard are more complicated for multilocation OYTs than for single-location OYTs. Each breeder must develop a strategy for making these decisions. Changes in objectives or the resources available influence the number of sites used and the number of entries that can be evaluated, which in turn dictate how many entries must be discarded each year to make room for new lines entering the OYT from the pedigree nursery.

	PA	Ldg	Ht	Comments	Yield
4101	4	1	5	SH, SPAN	3250
4102	3	1	2	ST	2500
4103	2	1	2	LPAN, T	3300
4104	7	2	6	SH	1450
4105	6	7	3	WK, T	2130
4106	2	1	2	ST	2970
4107	3	3	3		2845
4108	9	7	3	WK	1780
4109	1	1	2	VIG, LPAN, CLN	3230
4110	5	1	4	BB	2670
4111	4	3	3	BB	2840
4112	5	1	4	SPAN	2570

13.2. An example of a page from the OYT field book. Abbreviations are used to conserve space: PA = phenotypic acceptability, Ldg = lodging resistance, Ht = height, SH = short (height), SPAN = small panicles, ST = strong stems, LPAN = large panicles, T = tall, WK = weak stems, VIG = vigorous, CLN = clean, no foliar diseases, and BB = bacterial blight.

Table 13.2. Options for future use of breeding lines evaluated in multilocation OYTs.

Performance of breeding line	Action
Outstanding performance when averaged over all sites	Advance to higher level trial Include in hybridization block Consider nominating for international nurseries (INGER) If performance is maintained for 2 yr or more, consider for release
Good performance when averaged over all sites	Keep in nursery another year
Excellent performance at some sites but poor performance at others	Consider for on-farm trials in areas where performance is superior If it performs well in unfavorable sites, use in hybridization block as source of stress resistance
Average or poor performance at most or all sites	Discard

While neat theoretical classifications of material can be developed (Table 13.2), making real decisions about what to do with breeding lines is not a tidy process. In theory, when a large amount of data has been collected, it should be possible to apply an index from which an unambiguous score could be derived that would guide the breeder in accepting or rejecting lines. Most breeders would contend that a trained eye is more valuable than an index in rapidly evaluating the strengths and weaknesses of a breeding line and integrating all characters into an accurate score of a genotype's worth. They also would argue that the data collected from a series of trials are so numerous and complex that it would be impossible to develop a formula that would eliminate ambiguity.

Resolving this conflict is beyond the scope of this book. Nevertheless, programs should be careful not to use an evaluation process that prevents breeders from becoming intimately acquainted with their breeding material. In some extreme cases, breeders have had to devote so much time to administrative duties or paper work that they have made decisions based upon field data collected by their assistants. When the assistants are trained breeders who are allowed to provide subjective input into the selection process, this approach may be appropriate. When the assistants have limited experience or are not highly trained, it is not.

Breeders who choose to use mean PA over trials as a decision-making guide are supported by the rationale that the range of environments encountered at the OYT sites represent the range of environments in the target area. In rainfed lowlands, growing conditions vary widely between sites and between years. If a variety is to be adopted by rainfed lowland rice farmers, it must produce stable yields under these varying conditions. If several hundred entries are being evaluated in multiple OYTs, a mean PA score helps the breeder to focus on the lines that perform exceptionally in most or all of the trials. If the sites are diverse, however, different entries probably will be most promising at different sites, especially if that diversity involves conditions other than climate, such as adverse soils.

Using several well-chosen sites each year can help speed up the breeding process by compensating (at least partially) for the lack of several years of data. For example, if drought stress occurs on average once in 3 yr at any particular site and only one site is used, several years of OYT data may be needed to ensure that the entries are evaluated for drought under typical field conditions. If five sites are used, chances are much better that the entries will be exposed to drought in more than one trial. Breeding lines that consistently perform well at a single site should be maintained in the OYT and RYT at that site and considered for release in areas to which they are adapted (Table 13.2).

Finally, farmers' evaluation of breeding lines can alert breeders to problems often overlooked. Farmers often have different priorities in selecting lines, priorities that will ultimately play a role in their accepting or rejecting new cultivars. They are always eager to go through breeding nurseries and select their favorite lines, and their input should be highly valued.

Replicated yield trial

The entries that earn the highest scores in the OYTs are advanced to replicated yield trials (RYTs). The RYTs can be conducted at the same sites as were the OYTs and at additional sites, if desired.

An RYT typically has about 20-40% as many entries as the OYT; but plot size is larger—often 8 rows of 5-10 m. Most programs use four replications per site, but the number can be reduced to three if space or seed is limited. For example, an OYT might include 500 entries. The RYT that follows has only about 100 entries; but because the RYT involves four replications, the result is 400 plots.

The most common experimental design is the randomized complete block design. If the RYT is to test more than 20 entries, avoid the problems associated with large blocks by using an alternative design, such as incomplete blocks. If the RYT is to test entries in which growth duration differs greatly, separate entries into maturity groups that can be analyzed separately, or use the group balanced block design (Gomez and Gomez 1985).

Data collected from the RYT include those collected for the OYT plus evaluations of other traits such as milling quality, gel consistency, adaptation to problem soils, and grain dormancy. For more information about evaluating these traits, see Jennings et al (1979).

Monitoring hydrology in field tests

Previous sections have stressed the importance of evaluating rainfed lowland breeding material in observational and replicated yield trials across a range of sites. These sites will differ enormously in field hydrology, within and among years. Interpretation of performance will depend on knowing fairly precisely the pattern and depth of flooding during the growing season in all these trials.

Two simple types of gauges are needed to monitor field hydrology: a water depth gauge and groundwater observation wells.

To measure water depth in the flooded field, use a bamboo stake marked in centimeter gradations. Record water depth twice a week.

After the field has drained, the groundwater may remain near the soil surface or may drop below the rooting layer, inducing drought stress. To monitor the level of groundwater, install a set of three perforated plastic tubes to depths of 20, 40, and 80 cm. Directions for constructing, installing, and reading observation wells are found in Appendix 2. The data are plotted for the growing season, enabling the interpretation of the timing and severity of flooding or drought events. Cultivar performance is then assessed on the basis of quantitative knowledge of the nature of the hydrological stress observed.

CHAPTER 14

Releasing varieties

Breeders sometimes supervise national evaluation trials; more often, they only contribute breeding lines for evaluation. Thus, they usually do not decide directly what varieties are released to farmers, but they influence such decisions.

The system for varietal release varies in each country. In some cases, the testing and release of cultivars is completely separated from the breeding program, and breeders' input may be limited to nominating the most promising lines. The evaluation of the lines under farmers' conditions may be handled by a different group of workers, with the ultimate decisions about release being made by the national seed board or a similar agency. In other cases, data from breeders' screening and yield trials may be used in deciding which lines to release. In a few cases, the breeders themselves determine which lines are released.

Varieties intended for unfavorable areas, such as rainfed lowlands, require different testing and identification procedures than varieties intended for irrigated and otherwise favorable areas. Unfortunately, most breeding programs follow the same testing procedures for both types of areas. Scientists who are engaged in rainfed lowland rice improvement programs need to understand the appropriate criteria for selecting varieties for unfavorable areas, and must bring these factors vigorously to the attention of the decisionmakers.

This chapter discusses the special considerations that apply to a system for releasing rainfed lowland varieties.

Collecting data

Identifying and releasing varieties intended for rainfed lowlands proceeds logically from evaluating advanced lines according to their performance in field trials that simulate on-farm conditions (see Chapter 13). Thus, it is essential for the release process to consider all of the data collected by breeders. Observations of breeding lines in multilocation OYTs and RYTs should supplement data collected in trials performed by agencies responsible for varietal release (assuming these agencies are separate from the breeding program). To hasten the identification of new rainfed lowland varieties, as much information as possible must be obtained for advanced lines in each season.

Each program must develop an evaluation system that is appropriate for the level of resources available and target environments addressed. All programs, however, employ three basic types of trials for evaluating potential varieties. Preliminary observations are recorded for several hundred lines in small plots (OYTs). These trials are typically unreplicated or have two replications per site. Lines that perform well in this trial are advanced to RYTs. In these nurseries, larger plots and three or four replications per site are used to increase the accuracy of the yield evaluation. A few lines that show the most promise for release as varieties are then grown at a larger number of field sites to verify their superior performance. Farmer feedback at this stage is critical to avoid releasing varieties that will be unacceptable.

At least 5 yr are required for this series of trials, that is, 5 yr will elapse from the time a uniform bulk of a pedigree line is entered into OYTs until the line can be proposed for release. Due to year-to-year variability, it is essential to have at least 2 yr of data in RYTs and verification trials before making a decision about release.

During pedigree selection, each generation is screened for important traits (see Chapter 12). OYTs and RYTs involve fewer lines than pedigree selection, and the seed produced is more abundant than that produced in earlier generations. Once the number of lines being evaluated is reduced, the breeder can focus on characteristics that would be too costly to evaluate in a large number of lines, such as milling and cooking characteristics and tolerance for problem soils. The stage at which the lines art screened for each trait depends on the resources available and the relative importance of the traits to the program.

An analysis of the cumulative data from OYTs and RYTs, including data from multilocation trials, should form the basis of decisions about which varieties are selected for release. Thus, the breeding team should establish its own protocol for collecting data (see Table 14.1 for an example) and should decide how to vary the protocol for lines that are targeted for different environments.

The number of years needed for yield testing depends on the complexity of the target environment and the number of sites included each season. Irrigated environments are less complex than rainfed lowland environments and have much less site-to-site or year-to-year variability. Consequently, fewer years or seasons of data are required (usually at least four seasons). For rainfed lowlands, the amount and distribution of rainfall often varies greatly over years and sites; thus more trials are necessary to assess a line's performance accurately.

Breeding lines of rainfed lowland rices can be evaluated realistically only in the wet season. The dry season has a shorter photoperiod, which affects the growth duration of long-duration and photoperiod-sensitive lines (see Chapter 4). Rainfall is low and solar radiation is high. Dry-season trials therefore tend to favor the shorter, high-tillering types that are appropriate for irrigated conditions.

Table 14.1. Example of a protocol for collecting data that can be used to determine which lines to release as varieties.

Characteristic on which data are collected		Stage at which data are collected [a]			
Category	Trait	Pedigree nursery	OYT	RYT	Multilocation yield trials (verification and seed increase)
Agronomic	Height	o			
	Tillering	o			
	Panicle size	o			
	Yield		o	o	o
	Stability			o	o
	Shattering			o	
Pests	Bacterial blight	o			
	Blast	o			
	Tungro		o		
	Green leafhopper	o			
	Brown planthopper		o		
	Gall midge		o		
Grain quality	Size	o			
	Shape	o			
	Chalkiness	o			
	Amylose	o			
	Gel consistency		o		
	Milling			o	
	Dormancy				o
	Taste				o
Stress	Submergence	o	o	o	o
	Drought (during vegetative stage)		o	o	o
	Drought (during reproductive stage)		o	o	o
Soil	Phosphorus deficiency			o	
	Zinc deficiency			o	
	Iron toxicity			o	

[a] For each program, the stage at which a trait is measured depends on its ease of measurement, its importance, and the level of resources available.

It is unlikely that a variety could be recommended for release in rainfed lowlands with fewer than 3 yr of multilocation tests. On the other hand, 10 yr of multilocation trials—typical for some programs—are excessive. If an improved line is of potential benefit to farms, it should be moved through the system as quickly as possible.

Two options are available for reducing the number of years required to evaluate breeding lines:

- The number of locations and replications per year can be increased. Selecting a diverse set of sites increases the likelihood that lines can be evaluated for the diverse conditions encountered in the target environment. Thus, site-to-site variations in rainfall, soil nutrients, weed populations, and incidence of diseases and pests can substitute for year-to-year variations that are likely in the target area. At sites where growing conditions are poor, the stress resistance of the lines can be evaluated; at sites where conditions are favorable, yield potential can be assessed. The breeder can increase the validity of the results by choosing sites that are likely to experience the stresses of most interest; for example, if the lines being developed are intended for flood-prone areas, the sites chosen for trials should include typical flood-prone fields.

- Stress can be evaluated at special screening or off-season nurseries. For instance, dry-season nurseries can be used to screen varieties that are intended for drought-prone areas. Data resulting from these trials must be interpreted cautiously, however, since the screening conditions may not realistically represent farm conditions.

Interpreting the data from multilocation trials of irrigated varieties is straightforward; mean yield is the primary factor to consider. Interpreting data for rainfed lowland varieties is more complicated because rainfed lowland farmers tend to place higher priority on yield stability than on overall mean yield. Farmers often are most interested in how a variety performs during lower yielding years, when rice supplies are low and prices are high. Thus, varieties' responses to environmental stress must be emphasized in choosing lines to be released for use in rainfed lowlands.

No single variety can satisfy the needs of all rainfed lowland farmers. Ideally, farmers should be offered a choice of varieties from which they select according to their own priorities and field conditions; that is, some prefer a variety that has higher overall mean yield, and others prefer a variety with a lower mean yield that remains productive under greater stress. Farmers' preferences must figure prominently in decisions about varietal release; otherwise, farmers may not adopt the new varieties or, if they do, may find that the varieties do not fit their requirements.

One strategy for including farmers in the decision-making process is the practice of distributing seed samples (known as *minikits*) of promising lines to farmers for testing. Many farmers are eager to cooperate in such testing, and the feedback they provide is invaluable to breeders. Further, farmers tend to share seed from lines they accept; their voluntary distribution of seed to other farmers can be used as a measure of acceptability. In fact, sometimes a line ends up being grown on thousands of hectares as a result of the farmers' informal multiplication and distribution system. Some breeders are uncomfortable with the potential for widespread informal distribution of experimental lines; they fear that an unforeseen varietal weakness, such as susceptibility to an important pest, could severely damage the crops and destroy farmers' confidence in modern varieties. The advantages of voluntary on-farm testing probably outweigh the disadvantages; nevertheless, some kind of agreement should be established with farmers who receive minikits to minimize the potential dangers.

Location specificity and the number of released varieties

For irrigated rice improvement programs, determining the target area to which a variety should be released is seldom complicated. In many cases, an irrigated variety can be recommended for an entire country or even for several countries. In other cases, an irrigated variety is targeted to a niche; that is, it is released to meet a specific need or solve a specific problem in a certain area, such as

- a limited growing season—early varieties are more suitable for the dry season; varieties with some cold tolerance are suitable for the cooler months at higher latitude;
- a pest problem—varieties that are resistant to the pest but have other defects may be recommended for use in "hot spots," areas in which the pest severely limits production;
- a grain quality preference—a glutinous rice, for example, may be popular in some areas and unpopular in others; or
- a soil nutrient problem—a variety that tolerates iron toxicity, for example, may be needed in an area that has acid soils.

For rainfed lowland rice improvement programs, complex factors must be considered in determining the target area for varietal release. A breeding program may be called upon to develop varieties

- for several regions that have grossly different environments,
- for one region that has a range of growing conditions requiring lines of differing maturities—long-duration varieties for low-lying areas and short-duration varieties for drought-prone areas, or
- for a range of farmer preferences and priorities—for example, some farmers prefer short varieties that are responsive to fertilizer, while others prefer tall varieties that require few inputs.

Further, some recommended varieties eventually are rejected because they display defects under production conditions that were not apparent under test conditions. Thus, a rainfed lowland program usually must produce a larger number of new varieties than an irrigated program.

A potential problem in interpreting data from yield trials, with an eye to recommending varieties for release, is that a breeding line that does not produce an outstanding overall mean yield may perform remarkably well in a certain location. If the variety has been tested at an unsuitable site, its potential for production in certain niches probably will be overlooked. Therefore, trial sites should be chosen that accurately represent the environments for which the varieties are targeted (see Chapter 13).

An example of a program that characterizes its trial sites well is the rainfed lowland rice-improvement program of Thailand. This program releases varieties for four main regions of the country: north, northeast, central plains, and south. The regional divisions are based primarily on flowering dates of photoperiod-sensitive rices. Within each region, flowering ranges from early to late; but the dates that correspond to these periods differ between regions (Table 14.2). Endosperm type also distinguishes the regions;

that is, glutinous rices are prevalent in the north and northeast. As work on rainfed lowland rice improvement proceeds in Thailand, it is becoming clear that, even within a region, varieties must be targeted to different localities. Thus, in northeast Thailand, each of the six research stations is encouraged to develop its own breeding materials for the surrounding areas; their efforts are coordinated by the center at Ubon. When a variety is released, it bears the name of the station that was mainly responsible for its development.

In countries whose rice breeding programs focus on producing varieties for irrigated and favorable rainfed environments, policies for testing and releasing varieties often are inappropriate for rainfed lowland rice. These policies tend to

- limit the number of varieties that can be released, though a large number of varieties usually is needed for rainfed lowland areas;
- overemphasize high overall mean yields from experiment station trials, though varieties that are appropriate for rainfed lowland areas; may not produce such yields;
- rely little on farmers' input in selecting varieties, though farmers' feedback about performance and preference are critical to the success of rainfed lowland varieties; and
- avoid varieties that are adapted to specific areas, though niche varieties are important and valuable—sometimes critical—to rainfed lowland farms.

Changing such policies may not be easy. Extra money, staff, and other resources are required to develop, test, produce, and distribute a larger number of varieties; to conduct multilocation trials and collect and analyze the large amounts of data generated by these trials; and to provide experimenters with the necessary experience in appropriate research techniques; and to recruit experienced breeders. Still, the policies must be changed if varieties are to be developed that meet the needs of rainfed lowland areas. Researchers and administrators must identify and implement innovative solutions to these problems.

Table 14.2 Classification of rice varieties in Thailand, based on maturity and specific to region. Each maturity class can be subdivided into 5- to 7-d intervals, if necessary (Awakul 1980).

Maturity classification	Flowering date		
	North/northeast	Central plains	South
Very early	Before 1 Oct	Before 15 Oct	Before 1 Dec
Early	1-15 Oct	15-31 Oct	1-15 Dec
Medium	16-31 Oct	1-15 Nov	16-31 Dec
Late	1-15 Nov	16-20 Nov	1-20 Han
Very late	After 15 Nov	After 30 Nov	After 20 Jan

Producing seed

Many rice improvement programs place the plant breeders in charge of producing seed for varieties to be released. Many experiment stations devote much of their area to producing quality seed for distribution through an extension system or directly to farmers. While breeders usually are capable of managing these production tasks, the administrators or sponsors of a breeding program must consider whether managing seed production is the best use of a breeder's time and expertise. When feasible, seed production specialists should be hired to manage seed multiplication for approved varieties, freeing breeders to concentrate on developing new varieties and maintaining breeders' seed—seed of released varieties to be used to produce foundation seed in future years.

By the time breeding lines are beginning the final stages of multilocation testing, the breeder should begin to multiply seed of those lines that are candidates for release. Jennings et al (1979) have outlined a procedure for purification and multiplication of potential cultivars.

Inspect the most outstanding breeding lines for uniformity of grain types, and thresh individual plants (or panicles) separately. Plant seed from these plants in *head rows.* Transplant the material into single-plant hills to facilitate roguing; be sure each row contains progeny from only one plant (or one panicle). Inspect each row frequently as the crop develops, and remove any off-type plants from otherwise normal rows. Eliminate deviant rows.

Bulk harvest, dry, clean, and bag the seed from each row. Be extremely careful to avoid mixing seed from different rows. About 1,000 kg of seed can be harvested from 600 panicle rows.

Store about 300 kg of the seed of each line in an air-conditioned room to be used as breeders' seed. Under these conditions—moderately low temperature and relative humidity—the seed should retain its viability for at least 5 yr. If questions arise about varietal characters in future plots, some of the breeders' seed can be planted, grown out, and compared with the questionable plots to be sure they are the correct variety.

Break the dormancy of the remaining 700 kg of seed and replant it in regional trials and at the experiment station to produce foundation seed, from which seed is multiplied for distribution. Depending on the planting method used, the 700 kg of seed should produce 10-20 ha of foundation seed. When a variety has been formally released, turn its foundation seed over to be produced and distributed through normal channels. See Douglas (1980) for a complete description of seed production practices. See Jennings et al (1979) for a complete exposition of procedures for preparing varietal descriptions.

References cited

Acharya S, Sharma K D (1983) Genetics of cold tolerance at rice reproductive stage. Int. Rice Res. Newsl. 8(2):10-11.

Adkins S W, Shiraishi T, McComb J A (1988) Callus physiology of rice varieties with differing sensitivity to submergence. Pages 343-350 *in* Proceedings of the 1987 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Ahmad M S (1979) Photoperiod sensitivity in rainfed lowland rice. Pages 135-147 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Ahn S N, Bollich C N, Tanksley S D (1992) RFLP tagging of the gene for aroma in rice. Theor. Appl. Genet. 84:825-828.

Ahn S W, dela Peña R C, Candole B L, Mew T W (1986) A new scale for rice sheath blight (ShB) disease assessment. Int. Rice Res. Newsl. 11(6):17.

Akbar M, Senadhira D (1985) Emerging scenario in rice research: rice breeding for adverse soils. Paper presented at the International Rice Research Conference, 1-5 Jun 1985, International Rice Research Institute, Los Baños, Philippines.

Akbar M, Gunawardena I E, Ponnamperuma F N (1986a) Breeding for soil stresses. Pages 263-272 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Akbar M, Khush G S, HilleRisLambers D (1986b) Genetics of salt tolerance in rice. Pages 399-409 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Akita S (1989) Physiological aspects for improving yield potential in tropical rice cultivation. Pages 41-76 *in* Progress in irrigated rice research. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Akita S, Cabuslay G S (1990) Physiological basis of differential response to salinity in rice cultivars. Plant Soil 123:277-294.

Amante M M, Mackill D J (1988) Performance of rice breeding lines under medium deepwater conditions. Int. Rice Res. Newsl. 13(5):17-18.

Amante-Bordeos A, Sitch L A, Nelson R, Dalmacio R D, Oliva N P, Aswidinnoor H, Leung H (1992) Transfer of bacterial blight and blast resistance from the tetraploid wild rice *Oryza minuta* to cultivated rice, *Oryza sativa.* Theor. Appl. Genet. 84:345-354.

Armenta-Soto J, Chang T T, Loresto G C, O'Toole J C (1983) Genetic analysis of root characters in rice. SABRAO J. 15:103-115.

Aslam M, Qureshi R H (1989) A rapid screening technique for salt tolerance in rice. Int. Rice Res. Newsl. 14(3):24-25.

Awakul S (1980) Photoperiod-sensitive transplant rice in Thailand. Pages 269-275 *in* Proceedings of the International Seminar on Photoperiod-sensitive Transplant Rice, 24-28 Oct 1977, Bangladesh Rice Research Institute, Dhaka.

Balakrishna Rao M J (1973) Problems of rice varietal improvement in India. Int. Rice Comm. Newsl. 22(2):21-33.

Balakrishna Rao M J, Biswas S (1979) Rainfed lowland rice in India. Pages 87-94 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Balakrishna Rao M J, Murty K S, Sreedharan V K, Muralidharan V K, Srinivasalu K, Gangadharan C, Choudhury D (1971) Breeding varieties for water-logged areas. Oryza 8(2, suppl.):33-43.
Baloch K K, Bonman J M (1985) Rice seedling resistance to brown spot (BS). Int. Rice Res. Newsl. 10(5):8-9.
BRRI—Bangladesh Rice Research Institute (1980) Proceedings of the International Seminar on Photoperiod-sensitive Transplant Rice, 24-28 Oct 1977. Dhaka, Bangladesh.
Bardhan Roy S K, Mondal J, Chatterjee B N, Bhattacharya S, Debnath P, Mondal B (1988) Potential for rice ratooning in eastern India, with special reference to photoperiod-sensitive rices for deepwater areas. Pages 135-142 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Barker R, Herdt R W (1979) Rainfed lowland rice as a research priority—an economist's view. Pages 3-50 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Barker R, Herdt R W, Rose B (1985) The rice economy of Asia. Resources for the Future, Washington, D.C., USA.
Bent A F, Kunkel B N, Dahlbeck D, Brown K L, Schmidt R, Giraudat J, Leung J, Staskawicz B J (1994) RPS2 of *Arabidopsis thaliana:* a leucine-rich repeat class of plant disease resistance genes. Science 265:1856-1860.
Bhattacharya S N, Vergara B S (1979) Importance of seedling age in transplanted rice. Pages 173-183 *in* Proceedings of the 1978 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Bidinger F R, Mahalakshmi V, Talukdar B S, Alagarswamy G (1982) Improvement of drought resistance in pearl millet. Pages 357-376 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Binh L T, Oono K (1992) Molecular cloning and characterization of genes related to chilling tolerance in rice. Plant Physiol. 99:1146-1150.
Biswas S, Mallick S, Mitra N K (1986) Integrated breeding program for medium-deep, stagnant-water, rainfed rice in India. Pages 207-216 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Bloom, A L (1969) The surface of the earth. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
Blum A (1982) Evidence for genetic variability in drought resistance and its implications for plant breeding. Pages 53-68 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Boje-Klein, G (1986) Problem soils as potential areas for adverse soils-tolerant rice varieties in south and southeast Asia. IRRI Res. Pap. Ser. 119,
Bollich C N, Webb B D, Scott J E (1988) Breeding and testing for superior ratooning ability of rice in Texas. Pages 47-53 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Bonman J M, Estrada B A, Bandong J M (1989) Leaf and neck blast resistance in tropical lowland rice cultivars. Plant Dis. 73:388-390.
Bonman J M, Khush G S, Nelson R J (1992) Breeding rice for resistance to pests. Annu. Rev. Phythopathol. 30:507-528.
Bonman J M, Mackill D J (1988) Durable resistance to rice blast disease. Oryza 25:103-110.

Borrough, P A (1986) Principles of geographic information systems for land resources assessment. Clarendon Press, Oxford.
Brim C A (1966) A modified pedigree method of selection in soybeans. Crop Sci. 6:220.
Bruce R C, Morris R A (1981) Landforms in the rice-growing areas of the Cagayan River Basin. IRRI Res. Pap. Ser. 65.
Buddenhagen I W (1978) Rice ecosystems in Africa. Pages 11-27 *in* Rice in Africa. I. W. Buddenhagen and G. Pursley, eds. Academic Press, London.
Buddenhagen I W (1983) Breeding strategies for stress and disease resistance in developing countries. Annu. Rev. Phytopathol. 21:385-409.
Cabunagan R C, Tiongco E R, Flores Z M, Hibino H (1989) Resistance of TKM6 and IR20 to rice tungro spherical virus (RTSV). Int. Rice Res. Newsl. 14(3):19-20.
Carruthers I, Chambers R (1981) Rapid appraisal for rural development. Agric. Adm. 8:407-422.
Catling D (1992) Rice in deep water. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Champoux M, Wang G, Sarkarung S, Huang N, Mackill D J, O'Toole J C, McCouch S R (1995) Locating genes associated with root morphology on the molecular linkage map of rice. Theor. Appl. Genet. 90:969-981.
Chang T T (1976) The origin, evolution, cultivation, dissemination, and diversification of Asian and African rices. Euphytica 25:425-441.
Chang T T, Bardenas E A (1965) The morphology and varietal characteristics of the rice plant. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Chang T T, Tagumpay O (1973) Inheritance of grain dormancy in relation to growth duration in 10 rice crosses. SABRAO Newsl. 5(2):87-94.
Chang T T, Li C C, Vergara B S (1969) Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. Euphytica 18:79-91.
Chang T T, Loresto G C, Tagumpay O (1974) Screening rice germplasm for drought resistance. SABRAO J. 6:9-16.
Chang T T, Loresto G C, OToole J C, Armenta-Soto J L (1982) Strategy and methodology of breeding rice for drought-prone areas. Pages 217-244 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Chaturvedi G S, Ingram K T (1989) Accumulation and remobilization of assimilates for drought tolerance of rice. Agronomy abstracts. pp. 109-110.
Chaubey C N, Senadhira D S, Gregorio G B (1994) Genetic analysis of tolerance for phosphorous deficiency in rice (*Oryza sativa* L.) Theor. Appl. Genet. 89:313-317.
Chaudhary B P, Srivastava P S, Srivastava M N, Khush G S (1986) Inheritance of resistance to gall midge in some cultivars of rice. Pages 523-527 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Chaudhary R C, Khush G S, Heinrichs E A (1984) Varietal resistance to rice stem-borers. Insect. Sci. Appl. 5:447-463.
Chauhan J S, Lopez F S S, Vergara B S (1989) Genetic analysis of ratooning ability of rice *(Oryza sativa* L.). Euphytica 40:97-102.
Cheng K S (1985) A statistical evaluation of the classification of rice cultivars into hsien and keng subspecies. Rice Genet. Newsl. 246-48.
Coffman W R, Herrera R M (1980) Rice. Pages 511-522 *in* Hybridization of crop plants. W. R. Fehr and H. H. Hadley, eds. American Society of Agronomy, Madison, Wisconsin, USA.
Coffman W R, Juliano B O (1976) Current status of breeding high protein rice. Pages 150-153 *in* Improving the nutrient quality of cereals 11. H.L. Wilcke, ed. U.S. Agency for International Development, Washington, D.C., USA.

Coffman W R, Juliano B O (1979) Seed protein improvement in rice. Pages 261-277 *in* Proceedings of the international symposium on seed protein improvement in cereal and grain legumes, Vol. 2, September 1978, Neuherburg, Germany. IAEA, Vienna.

Conway G (1986) Agroecosystems analysis for research and development. Winrock International Institute for Agricultural Development, Bangkok.

Cruz R T, O'Toole J C, Dingkuhn M, Yambao E B, Thangaraj M, De Datta S K (1986) Shoot and root responses to water deficits in rainfed lowland rice. Aust. J. Plant Physiol. 13:567-575.

Cruz R T, OToole J C, Moody K (1983) Leaf water potential of weeds and rice. Weed Sci. 31:410-414.

Cuevas-Pérez F E (1980) Inheritance and associations of six agronomic traits and stem-based carbohydrate concentrations on ratooning ability in rice *Oryza sativa* L. Ph D dissertation, Oregon State University, Corvallis, Oregon, USA.

Dahal G, Aguiero V M, Cabunagan R C, Hibino H (1988) Varietal reaction to tungro (RTV) with change in leafhopper "virulence." Int. Rice Res. Newsl. 13(5):12-13.

Dao T T, Nguyen H N (1982) Varietal tolerance for acid sulfate soils in north Vietnam. Int. Rice Res. Newsl. 7(4):12-13.

De Datta S K (1981) Principles and practices of rice production. John Wiley & Sons, New York.

De Datta S K, Malabuyoc J A, Aragon E L (1988) A field screening technique for evaluating rice germplasm for drought tolerance during the vegetative stage. Field Crops Res. 19:123-134.

Denning G L (1985) Adaptation and adoption of dry-seeded rice in the rainfed lowlands of Iloilo and South Cotabato, Philippines. Ph D dissertation, University of Reading, United Kingdom.

Dingkuhn M, Cruz R T, O'Toole J C, Doerffling K (1989) Net photosynthesis, water use efficiency, leaf water potential and leaf rolling as affected by water deficit in tropical upland rice. Aust. J. Agric. Res. 40(6):1171-1191.

Dingkuhn M, Schnier H F, De Datta S K, Doerffling K, Javellana C, Pamplona R (1990) Nitrogen fertilization of direct-seeded flooded vs. transplanted rice: II. Interactions among canopy properties. Crop Sci. 30:1284-1292.

Douglas J E (1980) Successful seed programs: a planning and management guide. Westview Press, Boulder, Colorado, USA.

Eberthart S A, Russell W A (1967) Stability parameters for comparing varieties. Crop Sci6:36-40.

Eiguchi M, Sano R, Hirano H Y, Sano Y (1993) Genetic and developmental bases for phenotypic plasticity in deepwater rice. J. Hered. 84:201-205.

Ekanayake I J, De Datta S K, Steponkus P L (1989) Spikelet sterility and flowering response of rice to water stress at anthesis. Ann. of Bot. 63:257-264.

Ekanayake I J, Garrity D P, Masajo T M, O'Toole J C (1985a) Root pulling resistance in rice: inheritance and association with drought resistance. Euphytica 34:905-913.

Ekanayake I J, Garrity D P, OToole J C (1986) Influence of deep root density on root pulling force resistance in rice. Crop Sci. 26:1181-1186.

Ekanayake I J, O'Toole J C, Garrity D P, Masajo T M (1985b) Inheritance of root characters and their relations to drought resistance in rice. Crop sci. 25:927-933.

Emes M J, Wilkins C P, Smith P A, Kupkanchanakul K, Hawker K, Charlton W A, Cutter E G (1988) Starch utilization by deepwater rices during submergence. Pages 319-326 *in* Proceedings of the 1987 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Philippines.

Evans L T, Visperas R M, Vergara B S (1984) Morphological and physiological changes among rice varieties used in the Philippines over the last seventy years. Field Crops Res. 8:105-124.

Federer W T (1956) Augmented (or Hoonuiaku) designs. Hawaiian Planter's Rec. 55:191-208.

Flowers T J, Yeo A R (1990) Salinity and rice: a physiological approach to breeding for resistance. Pages 953-959 *in* Proceedings of the International Conference on Plant Physiology, Vol. 2,15-20 Feb 1988, New Delhi. Society for Plant Physiology and Biochemistry, New Delhi.

Fry W E (1982) Principles of plant disease management. Academic Press, New York.

Fujimaki H (1979) Recurrent selection by using genetic male sterility for rice improvement. JARQ 13:153-156.

Fujimoto H, Itoh K, Yamamoto M, Kyozuka J, Shimamoto K (1993) Insect resistant rice generated by introduction of a modified delta-endotoxin gene of *Bacillus thuringiensis*. Bio/Technology 11:1151-1155.

Fujisaka S (1988) Rice agroecosystems, fanner management, and social organization in Kampuchea: a preliminary assessment and research recommendations. IRRI Res. Pap. Ser. 136.

Fujisaka S (1990a) Agroecosystem and farmer practices and knowledge in Madagascar's central highland: toward improved rice-based systems research. IRRI Res. Pap. Ser. 143.

Fujisaka S (1990b) Rainfed lowland rice: building research on farmer practice and technical knowledge. Agric. Ecosyst. Environ. 33:57-74.

Fujisaka S (1991) Crop establishment (beusani) in Cuttack District, India. IRRI Res. Pap. Ser. 148.

Futsuhara Y, Kitano H (1985) Inheritance of a root growth-inhibiting mutant in rice. Rice Genet. Newsl. 2:70-71.

Futsuhara Y, Toriyama K (1969) Genetic studies on tolerance in rice. IV. Direct and indirect effects of selection for cold tolerance. Jpn. J. Breed. 19:286-292.

Futsuhara Y, Toriyama K (1971) Genetic studies on cool tolerance in rice. V. Effectiveness of individual and line selections for cool tolerance. Jpn. J. Breed. 21:181-188.

Garrity D P (1984) Rice environmental classifications: a comparative review. Pages 11-35 *in* Terminology for rice-growing environments. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Garrity D P, O'Toole J C (1995) Selection for reproductive stage drought avoidance in rice by infrared thermometry. Agron. J. 87:773-779.

Garrity D P, O'Toole J C (1994) Screening rices for drought resistance at the reproductive stage. Field. Crops Res. 39:99-110.

Garrity D P, Novero R P, Cruz R T, O'Toole J C (1982) Improving the reproductive stage drought resistance in rice. Paper presented at IRRI Saturday Seminar, June 19, International Rice Research Institute, Los Baños, Philippines.

Garrity D P, Oldeman L R, Morris R A, Lenka D (1986b) Rainfed lowland rice ecosystems: characterization and distribution. Pages 3-24 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Garrity D P, Vidal E T, O'Toole J C (1986a) Manipulating panicle transpiration resistance to increase rice spikelet fertility during flowering stage water stress. Crop Sci. 26:789-795.

Ghani M U, Khush G S (1988) A new gene for resistance to green leafhopper *Nephotettix virescens* (Distant) in rice. J. Genet. 67:151-159.

Ghildyal B P, Tomar V S (1982) Soil physical properties that affect rice root systems under drought. Pages 83-96 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Gines H C, Pernito R G, Morris R A (1985) The rationale of photoperiod-sensitive rice cultivars in rainfed rice-based cropping systems. Philipp. J. Crop Sci. 10:77-80.

Glaszmann J C (1987) Isozymes and classification of Asian rice varieties. Theor. Appl. Genet. 74:21-30.

Glaszmann J C, Arraudeau M (1986) Rice plant type variation: "Japonica"-"Javanica" relationships. Rice Genet. Newsl. 3:41-43.

Glaszmann J C, Kaw R N, Khush G S (1990) Genetic divergence among cold tolerant rices (*Oryza sativa* L.). Euphytica 45:95-104.
Glaszmann J C, de los Reyes B G, Khush G S (1988) Electrophoretic variation of isozymes in plumules of rice (*Oryza sativa* L.)—a key to the identification of 76 alleles at 24 loci. IRRI Res. Pap. Ser. 134.
Gomez K A, Gomez A A (1984) Statistical procedures for agricultural research. 2d ed. John Wiley & Sons, Inc., New York.
Grant J W (1957) The rice crop in Burma: its history, cultivation, marketing and improvement. Agricultural Department Burma, Rangoon.
Gregorio G B, Senadhira D (1993) Genetic analysis of salinity tolerance in rice (*Oryza sativa* L.). Theor. Appl. Genet. 86:333-338.
Guiderdoni E, Galinato E, Luistro J, Vergara G (1992) Anther culture of tropical japonica x indica hybrids of rice *(Oryza sativa* L.). Euphytica 62:219-224.
Guo W M, Chen R Y (1988) Modified screening method for salt tolerance. Int. Rice Res. Newsl. 13(5):19.
Haque E M, Loresto G C, Chang T T, Tepora N (1992) A comparative study of rice root chracters related to the mechanisms of drought resistance under aeroponic and hydroponic cultures. SABRAO J. 21:111-122.
Haque M M, Mackill D J, Ingram K T (1992) Inheritance of epicuticular wax content in rice. Crop Sci. 32: 865-868.
Haque Q A, HilleRisLambers D, Tepora N M, dela Cruz Q D (1989c) Inheritance of submergence tolerance in rice. Euphytica 41:247-251.
Hasanuddin A, Cabauatan P Q, Hibino H (1987) Tolerance of rice varieties to tungro disease and its possible use for disease management. Pages 98-106 *in* Proceedings of Workshop on Rice Tungro Virus, 24-27 Sep 1986, Maros, Indonesia. Min. Agric. AARD—Maros Res. Inst. Food Crops, Indonesia.
Heinrichs E A, Katanyukuk W, Karim A N M, Misra B C (1986) Management of insect pests in rainfed lowland rice. Pages 349-358 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Heinrichs E A, Medrano F G, Rapusas H R (1985) Genetic evaluation for insect resistance in rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Heinrichs E A, Pathak P K (1981) Resistance to the rice gall midge, *Orseolia oryzae* in rice. Insect Sci. Appl. 1:123-132.
Herdt, R W (1982) Focusing field research on future constraints to rice production. IRRI Res. Paper Ser. 76.
Herdt R W, Barker R (1977) Multi-site tests, environments, and breeding strategies for new rice technology. IRRI Res. Pap. Ser. 7.
Herdt R W, Palacpac A C (1983) World rice facts and trends. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Herrera R M, Coffman W R (1974) Emasculation of rice by vacuum extraction. Proc. Crop Sci. Soc. Philippines 5:12-14.
Herrera R, HilleRisLambers D (1984) Off-season growing of photoperiod-sensitive rices in Los Baños at 13°40'N. Int. Rice Res. Newsl. 9(1):6.
Hibino H (1987) Rice tungro virus disease: current research and prospects. Pages 2-6 *in* Proceedings of Workshop on Rice Tungro Virus, 24-27 Sep 1986, Maros, Indonesia. Min. Agric. AARD—Maros Res. Inst. Food Crops, Indonesia.
Hibino H, Roechan M, Sudarisman S (1978) Association of two types of virus particles with penyakit habang (tungro disease) of rice in Indonesia. Phytopathology 68:1412-1416.
HilleRisLambers D, Seshu D V (1982) Some ideas on breeding procedures and requirements for deepwater rice improvement, Pages 29-44 *in* Proceedings of the 1981 International Deepwater Rice Workshop. International Rice Research Institute. Los Baños, Philippines.

HilleRisLambers D, Vergara B S (1982) Summary results of an international collaboration on screening methods for flood tolerance. Pages 347-353 *in* Proceedings of the 1981 International Deepwater Rice Workshop. International Rice Research Institute, Los Baños, Philippines.
HilleRisLambers D, Gomosta A R, Kupkanchanakul T (1986) Screening for submergence tolerance. Pages 177-190 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Hsiao T C (1982) The soil-plant-atmosphere continuum in relation to drought and crop production. Pages 39-52 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Hsiao T C, O'Toole J C, Yambao E B, Turner N C (1984) Influence of osmotic adjustment on leaf rolling and tissue death in rice. Plant Physiol. 75:338-341.
Huke R E (1982a) Agroclimatic and dry-season maps of south, southeast and east Asia. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Huke, R E (1982b) Rice area by type of culture: South and southeast Asia. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Ichii M (1988) Some factors influencing the growth of rice ratoon. Pages 41-46 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Ikehashi H, Araki H (1986) Genetics of F1 sterility in remote crosses of rice. Pages 119-130 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Ikehashi H, HilleRisLambers D (1979) Integrated international collaborative program in the use of rapid generation advance in rice. Pages 261-276 *in* Proceedings of the 1978 International Deepwater Rice Workshop. International Rice Research Institute, Los Baños, Philippines.
Ikehashi H, Khush G S (1979) Methodology of assessing appearance of the rice grain, including chalkiness and whiteness. Pages 224-229 *in* Chemical aspects of rice grain quality. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Ikehashi H, Nieto E (1980) Rapid generation advance as a breeding method for photoperiod-sensitive rice. Pages 45-52 *in* Proceedings of the International Seminar on Photoperiod-sensitive Transplant Rice, 24-28 Oct 1977. Bangladesh Rice Research Institute, Dhaka.
Ingram K T, Real J G, Maguling M A, Obien M A, Loresto G C (1990) Comparison of selection indices to screen lowland rice for drought resistance. Euphytica 48: 253-260.
IRRI—International Rice Research Institute (1964) Annual report for 1964. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1976) Research highlights for 1975. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1978) Annual report for 1977. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1979) Future research for rainfed lowland rice. Pages 329-331 *in* Rainfed lowland rice: selected papers from the 1978 international rice research conference. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1980) Annual report for 1979. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1981) Reactions of differential varieties to the rice gall midge, *Orseolia oryzae,* in Asia: report of an international collaborative research project. IRRI Res. Pap. Ser. 61.
IRRI—International Rice Research Institute (1983a) Annual report for 1982. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1983b) Field problems of tropical rice. Rev. ed. P.O. Box 933, Manila, Philippines.

IRRI—International Rice Research Institute (1984a) Annual report for 1983. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1984b) Rice improvement for adverse soils, with emphasis on acid sulfate and coastal salinity. Proceedings of an IRTP/ INSFFER monitoring program. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1984c) Terminology for rice growing environments. Los Baños, Philippines.
IRRI—International Rice Research Institute (1985) Annual report for 1984. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1987) Annual report for 1986. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1988a) Annual report for 1987. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1988b) Late-flowering rainfed lowland rice in Cambodia, Vietnam and Thailand, 8-18 Dec 1989. A report of an IRTP monitoring tour. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1988c) Rice ratooning. Los Baños, Philippines.
IRRI—International Rice Research Institute (1988d) Standard evaluation system for rice, 3d ed. Los Baños, Philippines.
IRRI—International Rice Research Institute (1989a) Annual report for 1988. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1989b) Final report of the fifteenth international rice observational nursery (15th IRON) 1988. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1989c) IRRI toward 2000 and beyond. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1990) Program report for 1989. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1991) Direct seeded flooded rice in the tropics. Selected papers from the IRRC, 27-31 Aug 1990. Los Baños, Philippines.
IRRI—International Rice Research Institute (1992) Program report for 1991. P.O. Box 933, Manila, Philippines.
IRRI—International Rice Research Institute (1993) Program report for 1992. P.O. Box 933, Manila, Philippines.
Ito N, Hayase T, Satake T, Nishiyama I (1970) Male sterility caused by cooling temperature at the meiotic stage in rice plants. III. Male abnormalities at anthesis. Proc. Crop Sci. Soc. Japan 39:60-64.
Jayawardena G (1979) Adaptability of deepwater rice varieties to flash floods and partial submergence in Sri Lanka. Pages 103-106 *in* Proceedings of the 1978 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Jennings P R (1964) Plant type as a rice breeding objective. Crop Sci. 4:13-15.
Jennings P R, Herrera R M (1968) Studies on competition in rice. II. Competition in segregating populations. Evolution 22:332-336.
Jennings P R, Coffman W R, Kauffman H E (1979) Rice improvement. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Johnson R (1981) Durable resistance: definition of, genetic control, and attainment in plant breeding. Phytopathol. 71:567-568.
Jones D A, Thomas C M, Hammondkosack K E, Balintkurti P J, Jones J D G (1994) Isolation of the tomato *cf-9* gene for resistance to *Cladosporium fulvum* by transposon tagging. Science 266:789-793.
Jones M P (1986) Genetic analysis of salt tolerance in mangrove swamp rice. Pages 411—422 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Jones M P (1989) Rapid generation and improvement of salt tolerance in photoperiod sensitive mangrove swamp rice varieties and breeding lines. Env. Exp. Botany 29:417-422.
Juliano B O (1979) Chemical basis of rice grain quality. Pages 69-90 *in* Chemical aspects of rice grain quality. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Juliano B O (1985) Criteria and tests for rice grain qualities. Pages 443-524 *in* Rice: Chemistry and technology. B. O. Juliano, ed. American Association of Cereal Chemists, Inc., St. Paul, Minnesota, USA.
Juliano B O, Perez C M, Cuevas-Pérez F (1993) Screening for stable high head rice yields in rough rice. Cereal Chem. 70:650-655.
Kalode M B, Bentur J S (1988) Donors for resistance to Andhra Pradesh biotype 4 gall midge (GM). Int. Rice Res. Newsl. 13(6):16-17.
Kalode M B, Bentur J S (1989) Characterization of Indian biotypes of the rice gall midge, *Orseolia oryzae* (Wood-Mason) (Diptera:Cecidomyiidae). Insect Sci. Applic. 10:219-224.
Kalode M B, Rezaul Karim A N M, Pongprasert S, Heinrichs EA (1986) Varietal improvement and resistance to insect pests. Pages 240-252 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Kandasmy S (1981) Response of rice roots to simulated soil compaction with emphasis on water uptake. Master's thesis, University of the Philippines at Los Baños, Laguna, Philippines.
Kaneda C, Beachell H M (1974) Response of indica-japonica rice hybrids to low temperatures. SABRAO J. 6:17-32.
Karin S, Vergara B S, Mazaredo A M (1982) Anatomical and morphological studies of rice varieties tolerant of and susceptible to complete submergence at seedling stage. Pages 287-291 *in* Proceedings of the 1981 international Deepwater Rice Workshop. International Rice Research Institute, Los Baiios, Philippines.
Katayama T (1963) Photoperiod responses of *Oryza* species. V. Annu. Rep. Nat. Inst. Genet. (Jpn) 13:51-52.
Kauffman H E, Reddy A P K, Hsieh S P Y, Merca S D (1973) An improved technique for evaluating resistance of rice varieties to *Xanthomonas oryzae.* Plant Dis. Rep. 57:537-541.
Kaw R N, Moon H P, Yae J D, Visperas R M (1989) Estimates of combining ability for cold tolerance at reproductive stage in rice. Korean J. Breed. 21:188-195.
Khan D R, Mackill D J, Vergara B S (1986) Selection for tolerance to low temperature-induced spikelet sterility at anthesis in rice. Crop Sci. 26:694-698.
Khush G S (1984a) Breeding rice for resistance to insects. Prot. Ecol. 7:147-165.
Khush G S (1984b) Terminology for rice-growing environments. Pages 5-10 *in* Terminology for rice-growing environments. International Rice Research institute, P.O. Box 933, Manila, Philippines.
Khush G S, Virmani S S (1985) Breeding rice for disease resistance. Pages 239-279 *in* Progress in plant breeding. G.E. Russell, ed. Butterworth, London.
Khush G S, Mackill D J, Sidhu G S (1989) Breeding rice for resistance to bacterial blight. Pages 207-217 *in* Bacterial blight of rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Kilian J, Teissier J (1973) Methodes d'investigation pour l'analyse et la classement des bas-fonds dans quelques regions de 1'Afrique de l'oest: Proposition de classification d'aptitudes des terres a la riziculture. Agronomie tropical 28:156-171.
Kobayashi N, Ikeda R, Domingo I T, Vaughan D A (1993) Resistance to infection of rice tungro viruses and vector resistance in wild species of rice (*Oryza* spp.) Jpn. J. Breed. 43:377-387.
Koch M (1989) Methods for assessing resistance to bacterial blight. Pages 111-123 *in* Bacterial blight of rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Koch M, Parlevliet J E (1991a) Genetic analysis of, and selection for, factors affecting quantitative resistance to *Xanthomonas campestris* pv. *oryzae* in rice. Euphytica 53:235.245.

Koch M, Parlevliet J E (1991b) Residual effects of the *Xa-4* resistance gene in three rice cultivars when exposed to a virulent isolate of *Xanthomonas campestris* pv. *Oryzae.* Euphytica 55:187-193.

Koike S (1990) Rice low temperature tolerance research in Japan. Paper presented at the International Rice Research Conference: Focus on Irrigated Rice, 27-31 Aug 1990, Seoul, Korea.

Kramer P J (1983) Water relations of plants. Academic Press, New York.

Krishnamurthy K (1988) Rice ratooning as an alternative to double cropping in tropical Asia. Pages 3-15 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Krishnasamy V, Seshu D V (1989) Seed germination rate and associated characters in rice. Crop Sci. 29:904-908.

Krishnayya G R, De R N, Lodh S B (1990) Physiological basis for submergence tolerance in rice. Oryza 27:286-290.

Kumar I, Khush G S, Juliano B O (1987) Genetic analysis of waxy locus in rice (*Oryza sativa* L.). Theor. Appl. Genet. 73:481-488.

Kyaw O, Escuro P B (1979) Rainfed lowland rice in Burma. Pages 81-86 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, Los Baños, Philippines.

Lamb C J (1994) Plant disease resistance genes in signal perception and transduction. Cell 76:419-22.

Lamb C J, Ryals J A, Ward E R, Dixon R A (1992) Emerging strategies for enhancing crop resistance to microbial pathogens. Biotechnology 10:1436-1445.

Levitt J (1980) Responses of plants to environmental stresses, Vol. 2. Academic Press, New York.

Levy M, Romao J, Marchetti M A, Hamer J E (1991) DNA fingerprinting with a dispersed repeated sequence resolves pathotype diversity in the rice blast fungus. Plant Cell 3:95-102.

Li S, Chen T (1988) Inheritance of ratooning ability in Chinese rice varieties (*O. sativa* subsp. xian (or indica)). Pages 239-245 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Li T G, Vergara B S (1981) Use of small pots for testing cold tolerance of crosses at seedling and flowering stages under rapid generation advance. Int. Rice Res. Newsl. 6(3):13.

Lim K T, Yamamoto R (1978) Studies on the lodging resistance of rice plant growing under submerged condition and its preventive measure. I. Regarding to morphological changes of rice plant under submersion [in Japanese, English summary]. Jpn. J. Crop Sci. 47:674-680.

Mackel R (1974) Dambos: a study in morphodynamic activity on the plateau regions of Zambia, Catena 1:327-365.

Mackill D J (1986) Varietal improvement for rainfed lowland rice in south and southeast Asia: results of a survey. Pages 115-144 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Mackill D J, Coffman W R (1983) Inheritance of high temperature tolerance and pollen shedding in a rice cross. Z. Planzenzuchtg. 91:61-69.

Mackill D J, Ekanayake I J (1986) Rice backcross progeny differing in heat and drought tolerance at anthesis. Agronomy Abstracts. p. 71.

Mackill D J, Amante M M, Vergara B S, Sarkarung S (1993) Improved semidwarf rice lines with tolerance to submergence of seedlings. Crop Sci. 33:749-753.

Mackill D J, Bonman J M, Suh H S, Srilingam R (1985) Genes for resistance to Philippine isolates of the rice blast pathogen. Rice Genet, Newsl. 2:80-81.

Mackill D J, Garrity D P, Seshu D V, Zan K (1986) The breeding experience from Asia. Pages 115-132 *in* The wetlands and rice in subSaharan Africa. A.R. Juo and J.A. Lowe, eds. International Institute of Tropical Agriculture, Ibadan, Nigeria.
Mackill D J, Salam M A, Wang Z Y, Tankslev S D (1993) A major photoperiod-sensitivity gene tagged with RFLP and isozyme markers in rice. Theor. Appl. Genet. 85:536-540.
Maegawa H, Usui E, Uchida N, Yasuda T, Yamaguchi T (1987) Studies on the mechanism of salt tolerance in rice (*Oryza sativa* L.): relation between salt content and photosynthesis. Japan. J. Trop. Agr. 31:92-98.
Magor N P (1984) Potential in rainfed transplanted rice production in north-east Bangladesh. Bangladesh Rice Research Institute, Joydebpur, Bangladesh.
Mahadevappa M, Ikehashi H, Noorsyamsi H, Coffman W R (1981) Improvement of native rices through induced mutation. IRRI Res. Pap. Ser. 57.
Mahapatra P C, Reddy B B (1982) Varietal management in flood-prone and waterlogged rice fields—A case study. Oryza 19:148-150.
Majumder M K, Seshu D V, Shenoy V V (1989) Implication of fatty acids and seed dormancy in a new screening procedure for cold tolerance in rice. Crop Sci. 29:1298-1304.
Mak C, Harvey B L, Berdahl J D (1978) An evaluation of control plots and moving means for error control in barley nurseries. Crop Sci. 18:870-873.
Malabuyoc J A, Aragon E L, De Datta S K (1985) Recovery from drought-induced desiccation at the vegetative growth stage in direct-seeded rainfed rice. Field Crops Res. 10:105-112.
Martin G B, Brommonschenkel S H, Chunwongse J, Frary A, Ganal M W, Spivey R, Wu T Y, Earle E D, Tanksley S D (1993) Map-based cloning of a protein kinase gene conferring disease resistance in tomato. Science 262:1432-1436.
Martinez, C P (1990) Uses of anther culture in rice breeding at CIAT. Page 35 *in* Proceedings of 23rd Rice Technical Working Group, 26-28 Feb 1990, Biloxi, MS, USA.
Matsushima S (1966) Some experiments and investigations on rice plants in relation to water in Malaysia. Pages 115-123 *in* Water resource utilization in Southeast Asia. Y. Fujioka, ed. Center for Southeast Asian Studies, Kyoto University, Japan.
Maurya D M, Mall C N (1986) Breeding rice varieties for rainfed lowland areas. Pages 159-166 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Mazaredo A M, Vergara B S (1982) Physiological differences in rice varieties tolerant of and susceptible to complete submergence. Pages 327:341 *in* Proceedings of the 1981 international deepwater rice workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
McCouch S R, Kochert G, Yu Z Y, Wang Z Y, Khush G S, Coffman W R, Tanksley S D (1988) Molecular mapping of rice chromosomes. Theor. Appl. Genet. 76:815-829.
McKenzie K S, Bollich C N, Rutger J N, Moldenhauer K A K (1987) Rice. Pages 497-532 *in* Principles of cultivar development. Vol. 2, Crop species. W.R. Fehr, ed. Macmillan, New York.
Medrano F G, Heinrichs E A, Alam S, Alam M S, Jackson Y Y, Senadhira D, Wickramasinghe N (1987) Modified seedbox screening test to identify field resistance to brown planthopper (BPH). Int. Rice Res. Newsl. 12(3):17-18.
Mew T W, Shahjahan A K M, Mariappan V (1986) Diseases and disease management of rainfed lowland rice. Pages 339-348 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Miah N M, Miah M A A, Dewan S B A (1986) Integrated breeding program for medium-deep, stagnant-water, rainfed rice in Bangladesh. Pages 217-222 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Millington A C, Helmich F, Rhebergen G J (1985) Inland valley swamps and bolis in Seirra Leone: hydrological and pedological considerations for agricultural development. Zeitschrift fuer Geomorph Bd. 52:l-8.

Misra A K, Mathur S C (1983) Sheath rot incidence in cultivars grown at different nitrogen levels. Int. Rice Res. Newsl. 8(2):5-6.

Mohan M, Nair S, Bentur J S, Prasada Rao U, Bennett J (1994) RFLP and RAPD mapping of the rice *Gm2* gene that confers resistance to biotype 1 of gall midge (*Orseolia oryzae*). Theor. Appl. Genet. 87:782-788.

Mohanty H K, Chaudhary R C (1986) Breeding for submergence tolerance in rice in India. Pages 191-200 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Mohanty H K, Roy A, Das S R (1984) Varietal improvement in lowland rice. Oryza 21:72-87.

Mohanty H K, Suprihatno B, Khush G S, Coffman W R, Vergara B S (1982) Inheritance of submergence tolerance in deepwater rice. Pages 121-134 *in* Proceedings of the 1981 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Moormann F R, van Breeman N (1978) Rice: soil, land, water. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Morgan J M (1971) The death of spikelets in wheat due to water deficit. Aust. J. Agric. Anim. Husb. 11:349-351.

Mori K, Kinoshita T (1987) Salt tolerance of rice callus clones. Rice Genet. Newsl. 4:112-113.

Morris R A, Kim J H, Valera J B (1986) Landforms and modern rice varieties. IRRI Res. Pap. Ser. 121.

Murayama K (1989) Using rapid generation advance with single seed descent in rice breeding. Pages 253-259 *in* Progress in irrigated rice research. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Namuco O S, Hsiao T C, O'Toole J C (1980) Water stress sensitivity of rice at flowering. Paper presented at the 11th Annual Meeting, Crop Science Society of the Philippines, 27-29 Apr, Visayas State College of Agriculture, Baybay, Leyte, Philippines.

Nanda J S, Coffman W R (1979a) Alternative plant types and other agronomic characteristics for rainfed lowland rice. Pages 123-133 *in* Rainfed lowland rice: selected papers from the 1978 international rice research conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Nanda J S, Coffman W R (1979b) IRRI's efforts to improve the protein content of rice. Pages 33-47 *in* Chemical aspects of rice grain quality. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Narasimman R, Rangasamy S R S (1993) Comparison of fertility between the F_1, F_2 and anther derived lines in crosses of indica/japonica and japonica/indica in rice (*Oryza sativa* L). Euphytica 66:19-25.

Nelson R R (1973) The meaning of disease resistance in plants. Pages 13-25 *in* Breeding plants for disease resistance: concepts and applications. R.R. Nelson, ed. Pennsylvania State University Press, University Park, Pennsylvania, USA.

Neue H U, Lantin R S, Cayton M T C, Autor N U (1990) Screening of rices for adverse soil tolerance. Pages 523-531 *in* Genetic aspects of plant mineral nutrition. M. El Bassam, M. Dambroth, and B.C. Lougham, eds. Kluwer, Netherlands.

Novero R P, Garrity D P, O'Toole J C, Cruz R T (1983) Mass screening of rices for drought resistance at the reproductive stage. IRRI Saturday Seminar, 9 Jul. International Rice Research Institute, Los Baños, Philippines.

Nwe K T, Mackill D J (1986) Photoperiod sensitivity in three rice crosses. Euphytica 35:751-760.

Ogawa T, Khush G S (1989) Major genes for resistance to bacterial blight in rice. Pages 177-192 *in* Bacterial blight of rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Oka H I (1958) Intervarietal variation and classification of cultivated rice. Indian J. Genet. Plant Breed. 18:79-89.
Oka H I (1988) Origin of cultivated rice. Elsevier, Amsterdam.
Oldeman L R (1980) The agroclimatic classification of rice-growing environments in Indonesia. Pages 47-55 *in* Proceedings of a symposium on the agrometeorology of the rice crop. R.L. Cowell, ed. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Ookawa T, Ishihara K (1993) Varietal difference of the cell wall components affecting the bending stress of the culm in relation to the lodging resistance in paddy rice. Jpn. J. Crop Sci. 62:378-384.
Oshima I, Kikuchi F, Watanabe Y, Asahi C (1993) Genetic analysis of heading time in a cross between two indica varieties with inhibitor genes for photoperiod sensitivity. Jpn. J. Breed. 43:101-106.
O'Toole J C (1982) Adaptation of rice to drought-prone environments. Pages 195-213 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
O'Toole J C (1984) Lodging resistance in cereals—a review. (Mimeo available from International Rice Research Institute, P.O. Box 933, Manila, Philippines.)
OToole J C, Baldia E P (1982) Water deficits and mineral uptake in rice. Crop Sci. 22:1144-1150.
O'Toole J C, Chang T T (1979) Drought resistance in cereals—rice: a case study. Pages 373-405 *in* Stress physiology in crop plants. H. Mussell and R.C. Staples, eds. John Wiley and Sons, New York.
OToole J C, Cruz R T (1980) Response of leaf water potential, stomatal resistance, and leaf rolling to water stress. Plant Physiol. 65:428-432.
OToole J C, De Datta S K (1986) Drought resistance in rainfed lowland rice. Pages 145-158 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
OToole J C, Maguling M A (1981) Greenhouse selection for drought resistance in rice. Crop Sci 21:325-327.
OToole J C, Namuco O S (1983) Role of panicle exsertion in water stress induced sterility. Crop Sci 23:1093-1097.
OToole J C, Soemartono (1981) Evaluation of a simple technique for characterizing rice root systems in relation to drought resistance. Euphytica 30:283-290.
OToole J C, Wolfe J E (1990) Aeroponic culture system for root studies. Texas Agric. Exp. Stn. MP01704, February 1990.
OToole J C, Cruz R T, Seiber J N (1979) Epicuticular wax and cuticular resistance in rice. Physiol. Plant. 47:237-244.
OToole J C, Hsiao T C, Namuco O S (1984) Panicle water relations during water stress. Plant Sci. Lett. 33:137-143.
Ou S H (1985) Rice diseases. 2d ed. Commonwealth Mycological Institute, Kew, United Kingdom.
Painter R H (1951) Insect resistance in crop plants. The MacMillan Co., New York.
Palada M C, Vergara B S (1972) Environmental effects on the resistance of rice seedlings to complete submergence. Crop Sci. 12:209-212.
Pande H K, Mittra B N, Ghosh B C (1979) Flood susceptibility of semidwarf rices and their suitability for low-lying areas. Pages 185-195 *in* Proceedings of the 1978 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Pandey D K, Gupta H S (1993) Genetics of panicle exsertion in cold-tolerant rice (*Oryza sativa*). Plant Breed. 111:82-85.
Paterson A H, Lander E S, Hewitt J D, Peterson S, Lincoln S E, Tanksley S D (1988) Resolution of quantitative traits into Mendelian factors by using a complete RFLP linkage map. Nature 335:721-726.
Pathak M D (1972) Resistance to insect pests in rice varieties. Pages 325-341 *in* Rice breeding. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Pathak M D, Saxena R C (1980) Breeding approaches in rice. Pages 421-455 *in* Breeding plants resistant to insects. F.G. Maxwell and P.R. Jennings, eds. John Wiley and Sons, New York.
Perdon A A, Juliano B O (1975) Amylose content of rice and quality of fermented cake. Starke 27:196-198.
Ponnamperuma F N (1981) Role of varietal tolerance in rice production on acid sulfate soils. Paper presented at the International Rice Research Conference, 27 Apr-1 May 1981, International Rice Research Institute, Los Baños, Philippines.
Ponnamperuma F N, Ikehashi H (1979) Varietal tolerance for mineral stresses in rainfed wetland rice fields. Pages 175-185 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Poonyarit M, Mackill D J, Vergara B S (1989) Genetics of photoperiod sensitivity and critical daylength in rice. Crop Sci. 29:647-652.
Prakasa Rao P S (1989) Yield losses due to gall midge *Orseolia oryzae* Wood-Mason in some rice varieties and characterisation of tolerance. Trop. Pest. Manage. 35:205-213.
Premalatha Dath A (1985) A better criterion in rating the reaction of rice cultivars against sheath blight. Indian Phytopath. 38:678-682.
Purkayastha R P, Ghosal A (1982) Sheath rot of rice. Oryza 19:78-83.
Pushpavesa S, Jackson B R (1979) Photoperiod sensitivity in rainfed rice. Pages 139-147 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Rao M J B, Biswas S (1979) Rainfed lowland rice in India. Pages 87-94 *in* Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. International Rice Research Institute, Los Baños, Philippines.
Rao M S, Murthy P S S (1986) Effect of shallow submergence on agronomic characters. International Rice Research Newsletter 11(6):4.
Reddy A P K, Miah S A, Mew T W (1986) Disease resistance in rainfed lowland rice. Pages 253-262 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Resurreccion A P, Hara T, Juliano B O, Yoshida S (1977) Effect of temperature during ripening on grain quality of rice. Soil Sci. Plant Nutr. 23:109-112.
Reyniers F N, Truong-Binh, Jacquinot L, Nicou R (1982) Breeding for drought resistance in dryland rice. Pages 273-292 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute. P.O. Box 933, Manila, Philippines.
Rezaul Karim A N M, Pathak M D (1982) New genes for resistance to green leafhopper, *Nephotettix virescens* (Distant) in rice, *Oryza sativa* L. Crop Prot. 1:483-490.
Richharia R H (1966) Rices of India. Scientific Book Co., Patna, India.
Ro P V, Hoang V T (1986) Progress in breeding rice for medium deep water rainfed lowland areas in Vietnam. Pages 233-240 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Rosielle A A, Hamblin J (1981) Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21:943-945.
Saha A, Roy B, Adak M K, Gupta D (1993) Effect of waterlogging on yield parameters in rice (Oryza *sativa).* Indian J. Agric. Sci. 63:367-368.
Salam M A, Mackill D J (1993) Effects of a photoperiod sensitivity gene on morphological characters in rice. Field Crop Res. 33:267-268.
Samoto S (1965) Rice breeding. Pages 24-35 *in* Rice culture in Malaya. Center for Southeast Asian Studies, Kyoto University, Kyoto, Japan.
Sano Y (1992) Genetic comparisons of chromosome 6 between wild and cultivated rice. Jpn. J. Breed. 42:561-572.
Sano Y (1993) Is an egg-killer present in rice? Theor. Appl. Genet. 86:1038-1042.

Sano Y, Sano R (1990) Variation of the intergenic spacer region of ribosomal DNA in cultivated and wild rice species. Genome 33:209-218.

Sarkarung, S (1991) A simplified crossing method for rice breeding: a manual. Centro Internacional de Agricultura Tropical, Cali, Columbia.

SAS—SAS Institute, Inc. (1990) SAS/STAT=AE User's Guide, vol. 2. Cary, NC, USA.

Satake T (1976) Sterile-type cool injury in paddy rice plants. Pages 281-300 *in* Climate and rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Satake T (1986) Anther length as indicator to estimate chilling tolerance at booting stage in rice plants. Pages 221-228 *in* Napomapeth B, Subhandrabandhu S (eds). Proceedings of the 5th international Congress of SABRAO, "New frontiers in breeding researches." Kasetsart University, Bangkok, Thailand.

Satake T, Hayase H (1970) Male sterility caused by cooling treatment at the young microspore stage in rice plants. V. Estimation of pollen developmental stage and the most sensitive stage to coolness. Proc. Crop Sci. Soc. Jpn. 39:468-473.

Satake T, Koike S (1983) Sterility caused by cooling treatment at flowering stage in rice plants. I. The stage and organ susceptible to cool temperature. Jpn. J. Crop Sci. 52:207-214.

Sato Y I (1987) Character association patterns among Japonica rice varieties of Asian origin. *In* Crop exploration and utilization of genetic resources. S.C. Hsieh, ed. Taichung District Agricultural Improvement Station, Changhua, Taiwan.

Saviddes L (1981) Guidelines to improving valley swamps (fadamas): a procedure and approach followed in the Bida Agricultural Development Project. Bida, Nigeria.

Saxena R C (1986) Biochemical bases of insect resistance in rice varieties. Pages 142-159 *in* Natural resistance of plants to pests: roles of allelochemicals. M.B. Green and P.A. Hedin, eds. American Chemical Society, Washington, D.C., USA.

Scott R A, Miliken G A (1993) A SAS program for analyzing augmented randomized complete block designs. Crop Sci. 33:865-867.

Second G (1982) Origin of the genic diversity of cultivated rice (*Oryza* spp.): study of the polymorphism scored at 40 isozyme loci. Jpn. J. Genet. 57:25-57.

Seshu D V (1986) Rice varietal testing in the rainfed lowlands of south and southeast Asia. Pages 77-101 *in* Progress in rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Seshu D V (1989) Salient findings from the multilocation evaluation of the International Rice Bacterial Blight Nursery. Pages 167-176 *in* Bacterial blight of rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Seshu D V, Akbar M (1990) Salient findings from multilocation evaluation of rice for cold stress tolerance. Paper presented at the International Rice Research Conference: Focus on Irrigated Rice, 27-31 Aug 1990, Seoul, Korea.

Seshu D V, Cady F B (1984) Response of rice to solar radiation and temperature estimated from international yield trials. Crop Sci. 24:649-654.

Seshu D V, Sorrells M E (1986) Genetic studies on seed dormancy in rice. Pages 369-382 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Setter T L, Jackson M B, Waters I, Wallace I, Greenway H (1988) Floodwater carbon dioxide and ethylene concentrations as factors in chlorosis development and reduced growth of completely submerged rice. Pages 301 -310 *in* Proceedings of the 1987 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Sha X Y, Zhu L H (1989) Resistance to sheath blight (ShB) in China. Int. Rice Res. Newsl. 14(2):14-15.

Shahi B B, Khush G S (1986) Genetic analysis of cold tolerance in rice. Pages 429-435 *in* Rice genetics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Shahjahan M, Jalani B S, Zakri A H, Imbe T, Othman O (1990) Inheritance of tolerance to rice tungro bacilliform virus (RTBV) in rice (*Oryza sativa* L.). Theor. Appl. Genet. 80:513-517.

Shen G, Fan K, Chu Q (1987) Genetic analysis of gelatinization temperature in 35 rice cross combinations. Acta Agric. Shanghai 3(3):14.

Silué D, Tharreau D, Notteghem J L (1992) Evidence of a gene-for-gene relationship in the *Oryza sativa-Magnaporthe grisea* pathosystem. Phytopathology 82:577-580.

Singh B N, Mackill D J (1991) Genetics of leaf rolling under drought stress. Pages 159-166 *in* Rice genetics II. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Singh P P, Mazaredo A M, Vergara B S, Singh B N, Mackill D J (1989) Tolerance of rainfed lowland rice cultivars and breeding lines for submergence at seedling stage. Int. Rice Res. Newsl. 14(5):16-17.

Singh R N (1988a) Evaluation of indigenous rice varieties for resistance to brown spot. Indian Phytopath. 41:635-637.

Singh R N (1988b) Status of sheath rot (ShR) in eastern Uttar Pradesh (UP), India. Int. Rice Res. Newsl. 13(6):33.

Singh S, Bhattacharjee D P (1988) Effect of waterlogging on yield and yield attributes in late high yielding rice varieties. Oryza 25:315-318.

Sinha M M, Saran S (1988) Inheritance of submergence tolerance in lowland rice. Oryza 25:351-354.

Sinha S K, Mackill D J, Singh B N, Amante M M (1989) Promising breeding lines for submergence-prone and medium-deep rainfed lowland conditions. Int. Rice Res. Newsl. 14(4):20-21.

Smith P A, Kupkanchanakul K, Emes M J, Cutter E G (1988) Changes in fluorescence and photosynthesis during submergence of deepwater rice. Pages 327-335 *in* 1987 International Deepwater Rice Workshop. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Srivastava D P (1984) Importance of panicle weight types in breeding rice varieties for intermediate water depth. Rice Res. Newsl. 5(1/2):1.

Srivastava D P, De R N (1982) Changes in internode pattern in rice under intermediate water depth. Oryza 19:151-154.

Steponkus P L, Shahan K W, Cutler J M (1982) Osmotic adjustment in rice. Pages 181-194 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Supapoj N, Boonwite C, O'Toole J C, De Datta S K, Jackson B R (1982) Using check varieties to adjust visual scores for nonuniform soil drying in drought resistance field screening. Int. Rice Res. Newsl. 7(4):12.

Tanaka M (1980) Role of the circulation at the 150 mb level in the winter and summer monsoon in the Asian and Australasian regions. Climatological Notes 26, pp. 1-134. Institute of Geoscience, University of Tsukuba, Japan.

Tang S X, Khush G S, Juliano B S (1991) Genetics of gel consistency in rice (*Oryza sativa* L.). J. Genet. 70:69-78.

Taniyama T, Ikeda K, Subbaiah S V, Rao M L N, Sharma S K (1988) Cultivation and ecophysiology of rice plants in the tropics V. Yield and yield components of several rice cultivars of India grown under usual cultural methods. Japan. J. Crop Sci.57:728-732.

Teng P S (1994) Integrated pest management in rice. Exp. Agr. 30:115-137.

Thakur R, HilleRisLambers D (1987) Inheritance of plant elongation ability at seedling stage in rice. Euphytica 41:227-233.

Tiongco E R, Flores Z M, Hibino H (1987) Reaction of selected varieties to tungro (RTV) and green leafhopper (GLH). Int. Rice Res. Newsl. 12(4):15-16.

Tomar J B, Prasad S C (1992) Genetic analysis of resistance to gall midge (*Oryseolia oryzae* Wood Mason) in rice. Plant Breed. 109:159-167.

Toriyama K, Futsuhara Y (1960) Genetic studies on cool tolerance in rice. I. Inheritance of cool tolerance (In Japanese, English summary). Jpn. J. Breed. 10:143-152.

Tsuzuki E, Shimokawa E (1990) Inheritance of aroma in rice. Euphytica 46:157-159.

Turner N C (1982) The role of shoot characteristics in drought resistance of crop plants. Pages 115-134 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Turner N C (1986). Adaptation to water deficits: a changing perspective. Aust. J. Plant Physiol. 13:175-90.

Turner N C, O'Toole J C, Cruz R T, Namuco O S, Ahmad S (1986) Responses of seven diverse rice cultivars to water deficits. I. Stress development, canopy temperature, leaf rolling and growth. Field Crops Res. 13:257-271.

Valusamy R, Saxena R C (1989) Genes conditioning resistance to brown planthopper (BPH). Int. Rice Res. Newsl. 14(1):12-13.

Valusamy R, Heinrichs E A, Khush G S (1987) Genetics of field resistance of rice to brown planthopper. Crop Sci. 27:199-200.

Van der Plank J E (1968) Disease resistance in plants. Academic Press, New York.

Vaughan D A (1989) The genus *Oryza* L: current status of taxonomy. IRRI Res. Paper Ser. 138.

Vergara B S, Chang T T (1985) The flowering response of the rice plant to photoperiod: a review of the literature, 4th ed. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Vergara B S, Lilis R (1966) Studies on the responses of the rice plant to photoperiod. II. Effect of the number of photoinductive cycles on a seasonal rice variety—BPI-76. Philipp. Agric. 50:9-14.

Vergara B S, Mazaredo A (1975) Screening for resistance to submergence under greenhouse conditions. Pages 67-70 *in* Proceedings of the International Seminar on Deep-water rice, 21-26 Aug 1974. Bangladesh Rice Research Institute, Joydepbur, Dhaka.

Vergara B S, Sehadhira D (1990) Future direction of research on rice cold tolerance. Paper presented at the International Rice Research Conference: Focus on Irrigated Rice, 27-31 Aug 1990, Seoul, Korea.

Vergara B S, Lopez F S S, Chauhan J S (1988) Morphology and physiology of ratoon rice. Pages 31-40 *in* Rice ratooning. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Vergara B S, Pateña G, Lopez F S S (1982) Rapid generation advance of rice at the International Rice Research Institute. IRRI Res. Pap. Ser. 84.

Villareal C P, dela Cruz N M, Juliano B O (1994) Rice amylose analysis by near-infrared transmittance spectroscopy. Cereal Chem. 71:292-296.

Wang G L, Mackill D J, Bonman J M, McCouch S R, Nelson R J (1994) RFLP mapping of major and minor genes for blast resistance in a durably resistant rice cultivar. Genetics 136:1421-1434.

Wang S B, Hoshikawa K (1991) Studies on lodging in rice plants: 2. Morphological characteristics of the stem at the breaking position. Jpn. J. Crop Sci. 60:566-573.

Wang Z, Mackill D J, Bonman J M (1989) Inheritance of partial resistance to blast in indica rice cultivars. Crop Sci. 29:848-853.

Wang Z Y, Tanksley S D (1990) Restriction fragment length polymorphism in *Oryza sativa* L. Genome 32:1113-1118.

Wasano K, Hirota Y, Kido Y (1985) Varietal differences in the resistance to sheath blight of rice, *Rhizoctonia solani* Kuhn, and the effectiveness of selection for the resistance from the cross, Tetep X CN4-4-2 [in Japanese, English summary]. Crop Sci. Soc. Japan Kyushu Br. 52:16-22.

Widawsky D A, O'Toole J C (1990) Prioritizing the rice technology research agenda for eastern India. Rockefeller Foundation, New York.

Xu K, Mackill D J (1995) RAPD and RFLP mapping of a submergence tolerance locus in rice. Rice Genet. Newsl. 12. (in press)
Xu Y, Shen Z (1988) Inheritance of seedling stage cold tolerance in six indica and japonica crosses. Int. Rice Res. Newsl. 13(4):15-16.
Yambao E B, Ingram K T, Real J G (1992) Root xylem influence on the water relations and drought resistance of rice. J. Exp. Bot. 43:925-932.
Yan X L, Zheng S L, He Y K, Huang N R (1992) Rice genotypes differing in salt tolerance. 1. Growth response and NaCl accumulation of whole plants and their corresponding callus cultures. J. Plant Nutr. 15:2653-2666.
Yeh W H, Bonman J M (1986) Assessment of partial resistance to blast in six rice cultivars. Plant Pathol. 35:319-323.
Yeo A R, Flowers T J (1986) Salinity resistance in rice *(Oryza sativa* L.) and a pyramiding approach to breeding varieties for saline soils. Aust. J. Plant Physiol. 13:161-173.
Yokoo M, Fujimaki H (1971) Tight linkage of blast resistance with late maturity observed in different Indica varieties of rice. Jpn. J. Breed. 21:35-39.
Yokoo M, Kikuchi F (1977) Multiple allelism of the locus controlling heading time in rice by the aid of the linkage with blast resistance [in Japanese, English summary]. Jpn. J. Breed. 27:123-130.
Yokoo M, Kikuchi F (1992) The *Lm* locus controlling photoperiod sensitivity in rice differs from *E1* -loci, *E2* -loci and *E3* -loci. Jpn. J. Breed. 42:375-381.
Yokoo M, Okuno K (1993) Genetic analysis of earliness mutations induced in the rice cultivar Norin-8. Jpn. J. Breed. 43:l-11.
Yokoo M, Kikuchi F, Nakane A, Fujimaki H (1980) Genetic analysis of heading date by aid of close linkage with blast resistance in rice. Bull. Nat. Inst. Agric. Sci. Ser D:31:95-126.
Yoshida S (1977) Physiological consequences of altering plant type and maturity. Int. Rice Comm. Newsl. 26(1):5-16.
Yoshida S (1981) Fundamentals of rice crop science. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Yoshida S, Hasegawa S (1982) The rice root system: its development and function. Pages 97-114 *in* Drought resistance in crops, with emphasis on rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Yoshimura A (1989) Genetic behavior of quantitative resistance to bacterial blight in rice. Pages 193-197 *in* Bacterial blight of rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
Yoshino M M, ed. (1984) Climate and agricultural land use in monsoon Asia. University of Tokyo Press, Japan.
Yu C J, Yao T T (1968) Genetische studien beim Reis. II. Die Koppelung des Langhüllspelzengens mit dem Photoperiodizitätsgen. Bot. Bull. Acad. Sin. 9:34-35.
Yu Z H, Mackill D J, Bonman J M, Tanksley S D (1991) Tagging genes for blast resistance in rice via linkage to RFLP markers. Theor. Appl. Genet. 81:471-476.
Zapata F J, Akbar M, Senadhira D, Seshu D V (1989) Salt tolerance of anther culture-derived rice lines. Int. Rice. Res. Newsl. 14(1):6-7.

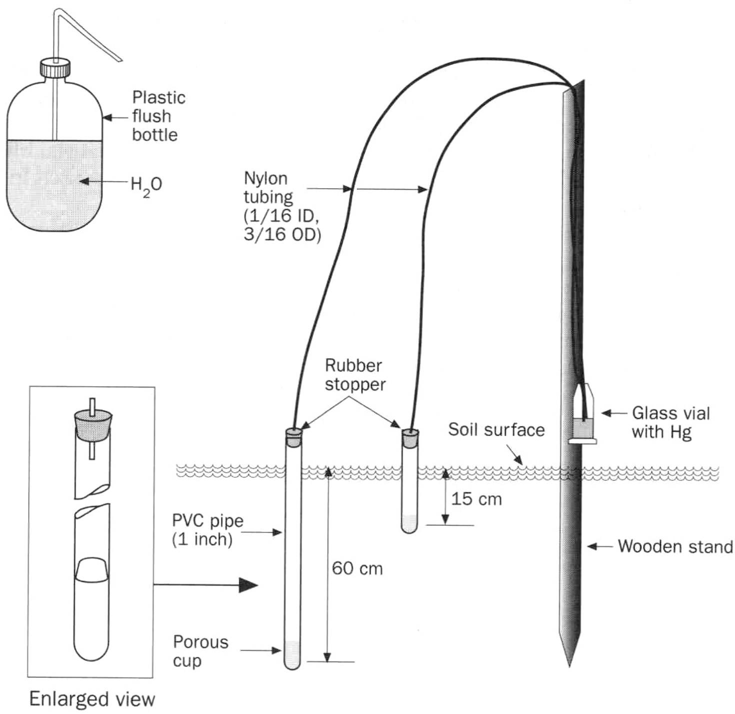
How to fabricate a simple tensiometer for monitoring soil water potential

A tensiometer is an instrument that is used to determine soil water potential. It consists of one or more water-filled tubes embedded in the soil and connected to a mercury well that is suspended on a wooden stand (Fig. 1). Each water-filled tube is attached at the lower end to a small porous cup. The tensiometer measures the pressure at which the soil draws water from the cup. This pressure equals the soil water potential.

Materials

To build a simple tensiometer, you need the following materials:

- PVC pipe, 2.5 cm in diameter
- fine sandpaper
- glue
- porous cup, 1.5 cm in diameter



1. Conventional mercury tensiometer setup in the field (o'Toole and maguling [nd]).

- nylon tubing with an internal diameter of 1.6 mm or less
- drill bits no larger than the diameter of the tubing
- two rubber stoppers large enough to fit snugly into the PVC pipe
- grease
- glass vial, 1.5 cm in diameter
- distilled water
- enough mercury to fill the vial to about 1 cm depth
- wooden slat, 5 cm × 2.5 cm × 150 cm
- graph paper with 1-mm gradations

If nylon tubing is not available, you can substitute plastic or tygon tubing. Keep in mind, however, that plastic tubing is more brittle than nylon and may not be available with an internal diameter of 1.6 mm or less. Tygon tubing is durable and comes in all sizes but is more expensive than either nylon or plastic; and, because it is soft, it may be difficult to pass through a rubber stopper.

Fabrication

Follow these steps to assemble the tensiometer:

1. Decide the location and depth at which you will place the water-filled tube and the location of the stand to hold the mercury-filled vial.
2. Cut a section of PVC pipe 15 cm longer than the depth at which it will be placed. For example, if a tube is to be embedded 30 cm deep, cut a section of PVC pipe that is 45 cm long. The extra length lets the tube project above the soil's surface.
3. Sand the end of the pipe to help the glue adhere and, thus, assure an airtight fit. Glue the cup to the sanded end of the pipe.
4. Drill a hole through each rubber stopper. The holes must be slightly smaller than the diameter of the nylon tubing to assure a snug, airtight fit.
5. Cut a length of nylon tubing long enough to reach from the tube to the wooden stand plus 1 m. For example, if the tube is to be located 2 m from the stand, cut a piece of nylon tubing 3 m long.
6. Grease one end of the tubing and pass it through the hole drilled in one rubber stopper. Use a sharp blade to cut off the end of the tubing, which may have become clogged when you greased it and passed it through the stopper. Insert the rubber stopper into the end of the tube opposite the porous cup. Follow the same procedure to insert the tubing through the other rubber stopper, which will be inserted into the mercury well. Be sure the tubing extends far enough through the stopper to reach the bottom of the glass vial.
7. Place the mercury in the glass vial and insert the stopper.
8. Sharpen one end of the wooden slat and glue graph paper to one face of the slat.

Installation

Follow these steps to install the tensiometer:

1. Push the PVC tube, with the porous cup attached, into the soil to the desired depth. If the soil is dry or compacted, use an auger to drill a pilot

hole in the soil that is smaller in diameter than the porous cup; then push the PVC tube into the pilot hole. Be sure the fit is snug.

2. Remove the stopper, fill the tube with distilled water, and reinsert the stopper.

3. At the location you have chosen for the wooden stand, push the sharp end of the wooden slat into the soil until the slat stands firmly.

4. Suspend the mercury well from the wooden stand by the nylon tubing. Be sure the distance from the well to the top of the stand is at least 1 m. Also be sure that the well is next to the face of the stand to which you have glued the graph paper. Tape the tubing in place at the top of the stand.

5. Flush the air from the nylon tubing by removing the stopper from the well and inserting it into a plastic bottle filled with distilled water. Remove the stopper from the PVC tube, too. Squeeze the plastic bottle until water flows out the end of the tubing. Place your finger over the end of the tubing while water is still flowing to prevent air from reentering. Reinsert the stopper into the PVC tube. Carefully withdraw the stopper from the plastic bottle, placing your finger over the end of the tubing to prevent air from reentering it. Reinsert that stopper into the mercury well.

Tips

- The tensiometer can accurately measure tensions between 0 and 0.80 bar. When the tension in the porous cup exceeds this limit, air enters the tensiometer through its walls, the mercury column is released, and further measurement is inaccurate or impossible.
- A number of water-filled tubes can be attached to the same mercury well, and these tubes may measure soil moisture potential over a range of depths (Fig. 1).
- Check the tensiometer regularly for air leaks.
- In expanding types of clay, tensiometers tend to break down because the soil cracks extensively. To ensure that you get an accurate reading in these types of soil, install as many tensiometers as possible.

Performing the calculations

Water moves in and out of the tensiometer's porous cup in response to capillary potential—the force that causes a fluid to rise or remain at a given level in a narrow-diameter tube against the force of gravity. At any given time, the opposing forces within the system are as shown in Figure 2. These forces may be expressed in terms of *head of water* by the following equation:

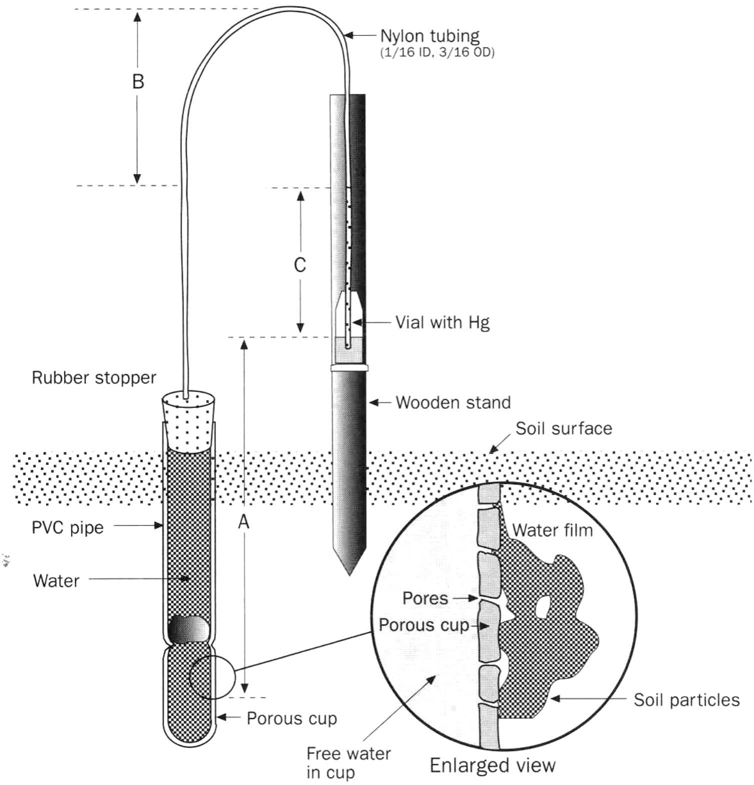
$$\mathrm{SMT} = \frac{(13.6\text{-}1)C - A}{(13.60)(0.7534)} = \frac{(12.6)C - A}{10.246}$$

where

SMT	=	soil moisture tension (cb)
C	=	mercury height in the tubing (cm)
A	=	distance from the upper surface of the mercury in the well to the center of the porous cup (cm)

13.6	=	density of mercury (g/cm^3)
1.0	=	density of water (g/cm^3)
0.7534	=	factor for converting mercury rise from centimeters to centibars

When the water table is higher than the midpoint of the porous cup, water may pass from the soil into the tensiometer, and SMT may have a negative value. Change all negative values to zero.



2. Various dimensions used in calculating soil moisture tension with a mercury tensiometer (O'Toole and Maguling [nd]).

Reference

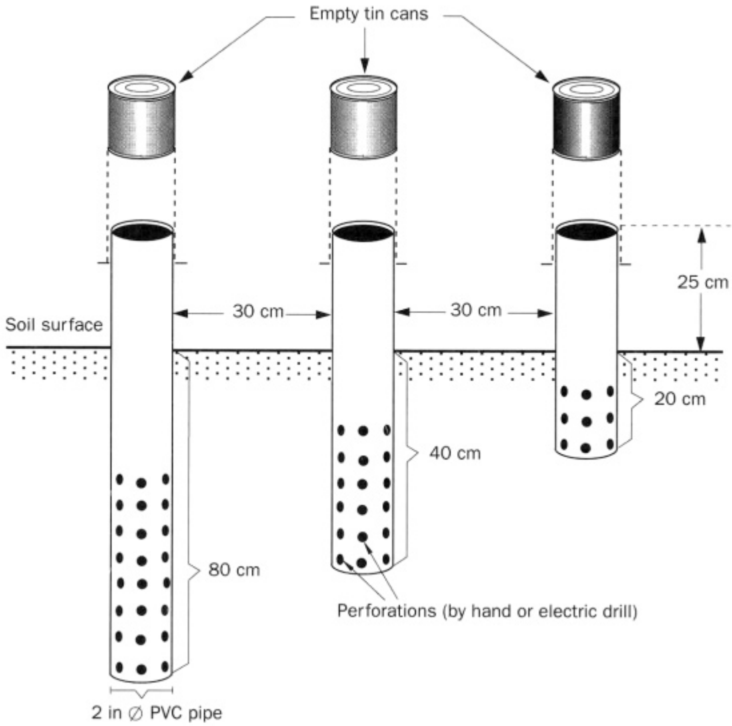
O'Toole J C, Maguling M A (no date). Drought screening greenhouse operations manual. Agronomy Department. International Rice Research institute, P.O. Box 933, Manila, Philippines. 39 p.

Fabrication and installation of groundwater observation wells

Groundwater observation wells are invaluable for determining the nature of water fluctuation in rainfed lowland test fields and interpreting the duration and intensity of drought stress. Their use in nurseries of advanced breeding lines is discussed in Chapter 13.

Groundwater observation wells are fabricated from 5 cm inside diameter polyvinylchloride (PVC) pipe as shown (Fig. 3). Perforations are drilled in the lower half of each tube. The top and bottom of each tube are open. The tube is wrapped with a layer of porous cotton cloth before installation to prevent the entry of mud in the bottom of the tube. A soil auger of similar diameter to the tube is used to bore the holes to the desired depth.

This type of groundwater well measures the free water level in the soil. Tubes with unperforated sidewalls are called piezometers. They measure the artesian water pressure in the soil. Data from piezometers are more difficult to interpret.



3. Construction and installation features of 80-, 40-, and 20-cm PVC tubes for groundwater monitoring in rainfed lowland ricefields.

Keyword index

Note: page numbers in italics refer to tables and figures.

Variety index

Note: page numbers in italics refer to tables and figures.

9 789712 200717
ISBN 971-22-0071-X