Breeding Strategies for Rainfed Lowland Rice in Drought-prone Environments

Proceedings of an International Workshop held at Ubon Ratchathani, Thailand, 5–8 November 1996

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Foreword

The ACIAR Crops Program develops projects that have as their objective the enhancement of the profitability and sustainability of field and horticultural crops. Plant breeding is a major activity area targeted by the program. As the major part of Australian agriculture takes place under marginal rainfed conditions, much agricultural research in recent years, including plant breeding and crop physiology, has focused on methods for improving the performance of rainfed cropping.These proceedings represent the result of five years collaboration between scientists in Australia, Thailand and the Lao People's Democratic Republic on the ACIAR-funded project 'Plant Breeding Strategies for Rainfed Lowland Rice in Northeast Thailand and Laos' (CS1/95/100).

This project has built upon knowledge gained in an earlier ACIAR project (PN/9045), which explored more broadly the potential for rainfed lowland rice improvement in the region. The current project aims to improve the efficiency of breeding programs under the rainfed lowland conditions in Thailand and Lao PDR. To achieve this aim, breeding strategies are being developed that take account of the water stresses imposed by prevailing soil and climate conditions in the area. Modifications of this difficult environment have been attempted through agronomic management, such as direct seeding and fertiliser application. Strategies are being developed that also take account of longer-term breeding objectives, such as grain quality, disease resistance and sustainability. The project complements existing Thai and Lao national breeding programs and other collaborative projects with the International Rice Research Institute (IRRI) and the Rainfed Lowland Rice Research Consortium (RLRRC).

The International Workshop on Breeding Strategies for Rainfed Lowland Rice in Drought-Prone Environments was sponsored by ACIAR, RLRRC and the Department of Agriculture, Thailand. It provided an opportunity for scientists involved in the rainfed rice research to share relevant knowledge, assess future research needs and plan further research to improve yields. These proceedings are one indication of how well this was achieved. They comprise most papers presented at the workshop, as well as a record of the discussions amongst the more than 100 participants from nine rice-growing countries. I trust that you find it valuable.

Thanks are due to the organising committee, principally Associate Professor Shu Fukai and Dr Mark Cooper from The University of Queensland, Dr Boriboon Somrith from the Thai Department of Agriculture, Mr Phoumey Inthapanya from the Lao Department of Agriculture and Extension, and Dr Len Wade and Dr Surapong Sarkarung from IRRI. Thanks are also due to the local organising committee in Ubon Ratchathani, chaired by Mr Nopporn Supapoj, Director of the Ubon Rice Research Centre.

Tony Fischer
Research Program Coordinator Crops 1
ACIAR

Introduction

Shu Fukai*, C. Piggin† and M. Cooper*

Rice Production Systems

RICE is grown over an area totalling 140 million ha worldwide. Of this area, 53, 26, 13 and 8% is estimated to be under irrigated, rainfed lowland, upland and flood-prone systems, with 73, 17, 4 and 6% of total rice production, respectively (Crosson 1995). It has been projected that total production of rice must be increased by 70% by the year 2025 to meet the increasing food demands generated by the increasing human population (Fischer 1996). While it is anticipated that the majority (70%) of this increase will come from irrigated systems, Scobie et al. (1993) estimated that 21% needs to come from the rainfed lowlands, 6% from the uplands and the remaining 3% from the flood-prone system. Critical questions are whether such improvements can be achieved and whether production can be sustained at these levels if they can be achieved. Given these expectations, it is timely that we evaluate the resource base for each rice ecosystem and assess the potential avenues for improving production above the current levels. Where opportunities for improvement are identified, clear research plans need to be formulated, implemented and supported if an impact is to be achieved in the farmer's field.

In the 1970s and 1980s the green revolution contributed to large increases in total rice production in the Asian region. However, these increases occurred mainly where there were reliable irrigation facilities and associated adoption of improved modern cultivars that were responsive to inputs. In the more unfavourable production systems, which are prone to a heterogeneous mixture of biotic and abiotic stress conditions, there has been a reluctance to adopt modern cultivars and traditional cultivars are still grown (Hossain 1995). As a consequence, there has been limited genetic improvement of the yield of rice in the unfavourable rice production environments (rainfed lowland, upland and flood-prone).

The rainfed lowland rice ecosystem covers vast areas (about 35 million ha) in South and Southeast Asia (Fig. 1). A feature common across rainfed production environments, and one that clearly distinguishes these from the irrigated system, is uncertain water supply. This provides a highly heterogeneous target population of environments for any plant breeding program. The combinations of environmental conditions that can be encountered in any one region are diverse and range from extremes of severe drought to damaging floods, with both events possible in a single cropping season. The soils of rainfed lowland areas are often infertile and may be acidic or saline. The soil problem, combined with the problem of uncertain water supply, is a major limitation for yield improvement in the rainfed lowland ecosystem. Genetic improvement of rice under these complex and adverse conditions is perhaps the major challenge facing rice breeders today. Apart from the direct effects of low and unstable production levels, a consequence of failure to achieve improvements in the rainfed systems is an increase in pressure on the irrigated systems to deliver improvements in production. Even if the irrigated systems could achieve the required gains to compensate for a lack of yield improvement in rainfed systems, problems of sustainability, and the distribution of excess rice from the improved irrigated production systems to the resource-poor farmers of the rainfed systems, would remain. Therefore, achieving higher levels of rice production from the rainfed lowland ecosystem is pivotal for improving food security at international, national and regional levels.

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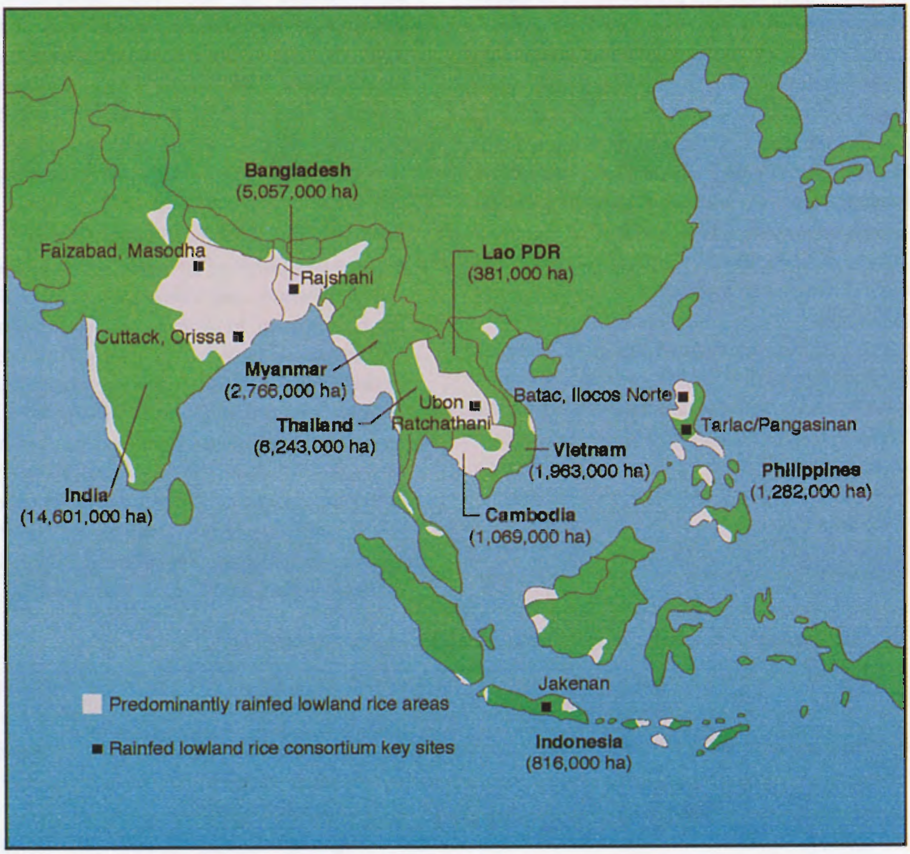

Figure 1. Rainfed lowland rice areas in South and Southeast Asia.

Given the complexity of the challenge faced, the lack of genetic progress to date, and the expectation of higher yields from the rainfed lowland ecosystem, international research organisations have developed team work approaches, involving National Agricultural Research Systems (NARS), in an attempt to improve the efficiency of plant breeding programs for the rainfed lowland ecosystem. This process has been assisted in recent years by two major research initiatives:

1. the Rainfed Lowland Rice Research Consortium (RLRRC), which is supported by the Asian Development Bank/Netherlands and coordinated by the International Rice Research Institute (IRRI); and

2. the project *Plant Improvement/Breeding Strategies for Rainfed Lowland Rice in Drought-Prone Areas of Thailand and Laos*, which is supported by the Australian Centre for International Agricultural Research (ACIAR) and coordinated by The University of Queensland.

These projects collaborate formally with NARS from six countries (Bangladesh, India, Indonesia, the Lao People's Democratic Republic [Lao PDR], Philippines, and Thailand), and informally with others from the Asian region.

RLRRC (Rainfed Lowland Rice Research Consortium)

The existence of several strong national systems in the rainfed lowlands, with research already under way, led to the formation of the RLRRC in 1991. This consortium of national research centres develops and runs a common research agenda aimed at resolving the principal strategic challenges of the less favourable ecosystems that are predominant in South and Southeast Asia.

The RLRRC operates at seven sites in five Asian countries (Bangladesh, India, Indonesia, Philippines, and Thailand). Member institutes are Bangladesh Rice Research Institute, Central Rice Research Institute (India), Narendra Deva University of Agriculture and Technology (India), Central Research Institute for Food Crops (Indonesia), Philippine Rice Research Institute, Ubon Rice Research Centre (Thailand) and IRRI (Table 1). Each site represents a subecosystem and research focus.

The overall goal of the consortium is to improve sustainable rice production in the lowland rice ecosystem of Asia, while maintaining and enhancing the resource base. This will be achieved through a regionally-based research effort with knowledge sharing among member institutions. More specific objectives are described below.

- *Development of improved germplasm.* Current germplasm for rainfed lowlands is low-yielding and of long growth duration. Populations are needed that are adapted to the environment (through sensitivity to photoperiod) and tolerant to the principal stresses yet still responsive to inputs in favourable years. Population development for the major subecosystems will continue to be an important thrust throughout the project.
- *Characterisation of agroecology and understanding of diversity and variability of the rainfed lowland ecosystem.* In order to predict the potential and limitations of new technologies, it is necessary to understand the physical and socioeconomic characteristics of rainfed lowland environments, including the processes leading to environmental degradation. This characterisation will continue using the database, geographic information system (GIS) and simulation models, to understand the extent, distribution, and variability of the abiotic and biotic stresses in major rainfed areas.

Table 1. Sites and research focus of the Rainfed Lowland Rice Research Consortium.

Country	Site	Institution	Umbrella agency	Research focus	Subecosystem
Bangladesh	Rajabari, Rajshahi	BRRI	BRRI	Root system development under moderate drought Photoperiod sensitivity	Drought-prone
India	Cuttack, Orissa	Central Rice Research Institute (CRRI)	ICAR	Regional breeding, stagnant flooding, and socioeconomics	Drought- and submergence-prone
	Faizabad/Masodha, Uttar Pradesh	Experiment Station, Narendra Deva University of Agriculture and Technology (NDUAT)	NDUAT	Salinity/shallow flash flooding, agroecological characterisation	Drought- and submergence-prone
Indonesia	Jakenan, Central Java	Jakenan Experiment Station	CRIFC	Sustainability of system intensification, dry direct seeding (*gogorancah*), potassium deficiency, efficient water capture and utilisation	Drought- and submergence-prone
Philippines	Batac, Ilocos Norte	Philippine Rice Research Institute (PhilRice)/MMSU	DOA	Long-term sustainability of production system	Favourable
	Tarlac	IRRI	IRRI	Nutrient and water interactions, dry direct seeding	Drought-prone
Thailand	Ubon Ratchathani	Ubon Rice Research Centre (URRC)	DOA	Severe drought/poor soil fertility, blast and other diseases, regional breeding	Drought-prone

BRRI = Bangladesh Rice Research Institute; ICAR = Indian Council of Agricultural Research; CRIFC = Central Research Institute for Food Crops; DOA = Department of Agriculture; MMSU = Mariano Marcos State University

Other activities include the development of input-efficient technologies for sustainable production, strengthening of scientific capacity and transfer of technology for impact. The expected outputs of the collaboration are:

- rice cultivars with increased stress (submergence and drought) tolerance and disease resistance;
- high-yielding cultivars with enhanced input efficiency;
- more productive and sustainable cultural practices for rainfed conditions;
- enhanced understanding of the extent, distribution and variability of the abiotic and biotic stresses in major rainfed areas;
- enhanced training of participating scientists in rainfed lowland technology; and
- transfer of appropriate technology to NARS and farmers in cooperation with involved international agencies.

ACIAR (Australian Centre for International Agricultural Research)

An ACIAR project on genetic improvement of drought resistance in rice was started in 1992 and will continue until 1999. The major goal is to evaluate drought problems and to identify appropriate strategies for genetic improvements of yield in rainfed lowland rice in drought-prone areas of Thailand and Lao PDR. The University of Queensland has collaborated with the Thai Rice Research Institute and the Lao Department of Agriculture and Extension. The rainfed lowland rice ecosystem is very important in these countries; in Thailand, 75% of the total rice area is in rainfed lowlands, and much of this occurs in the country's northeast. Poor soils—sandy, infertile and often highly acidic—add to the impact of inadequate rainfall in constraining production. Average yield in Northeastern Thailand is about 1.7 t/ha. Conditions are similar across the border in Lao PDR where the rainfed lowland system accounts for 64% of the rice area.

The major goal of the first phase of the ACIAR project (1992–96) was to provide the key information required to enable definition of strategies for the development of cultivars that produce higher yields than existing cultivars in dry environments. Specific objectives were:

- characterisation of drought development in rainfed lowland rice and identification of genotypic variation in drought resistance in the Northeastern and Northern Regions of Thailand and rainfed lowland areas of Lao PDR;
- evaluation and improvement of current drought resistance screening methods used in the Rice Research Institute of the Thai Department of Agriculture; and
- evaluation of rice cultivars suitable for minimising water stress problems in a new rice-growing system in Australia, based on reduced irrigation inputs.

Plant breeders, agronomists, plant physiologists and soil scientists from 15 research stations in Thailand and Lao PDR conducted the extensive experimental work for the project (Fig. 2). Australian scientists visited frequently for discussions on planning and progress. A total of 128 experiments were conducted in Thailand, Lao PDR and Australia. In addition a rice simulation model was used to estimate the impact of drought problems in Thailand. A summary of these activities is shown in Table 2.

The major goal of the second phase of the ACIAR project (1996–99) is to assess existing and alternative breeding strategies for their potential to increase yield and yield stability of rainfed lowland rice in drought-prone areas of Northeastern Thailand and Lao PDR and to identify appropriate strategies for genetic and agronomic improvements of rice yield in these areas. Specific objectives are:

- to evaluate existing and alternative selection strategies for rainfed lowland rice in Northeastern Thailand;
- to develop a screening method for resistance to late-season droughts and to identify physiological and morphological traits that confer drought resistance;
- to examine whether screening under high fertiliser input is appropriate for selection of genotypes and to identify reasons for superiority of some genotypes under different soil fertility conditions;
- to evaluate the genotypic requirement for direct seeding to minimise the adverse effects of drought; and
- to quantify the effect of various environmental factors on phenological development of different rice cultivars.

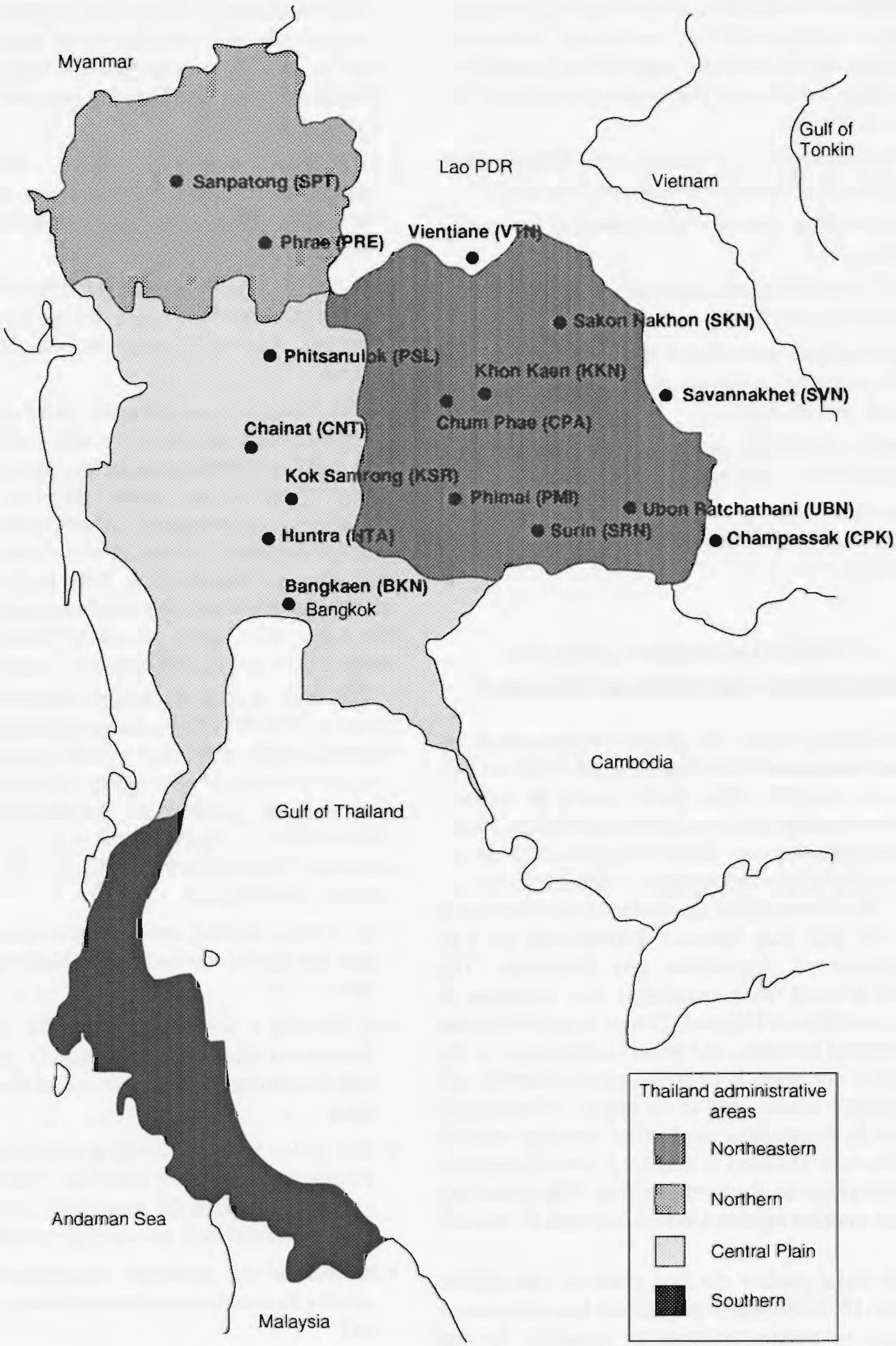

Figure 2. Rice research stations in Thailand and Lao PDR used in the ACIAR project.

Table 2. Experiments and simulation modelling exercises conducted in the first phase of the ACIAR project.

Project type	Number of locations			Number of experiments	Number of scientists involved
	Thailand	Lao PDR	Australia		
1. Multilocation trials	10	2	0	41	17
2. Seedling screening					
–glasshouse	5	0	1	12	9
–field	5	0	1	14	12
3. Response to drought and crop management					
–growth studies	4	0	0	13	7
–fertiliser	6	0	0	10	8
–lime	2	0	0	2	2
–direct seeding	3	0	0	14	5
4. Physiology of drought resistance	1	0	1	8	5
5. Development of RILs	7	0	0	11	8
6. Rice growth model	1	0	1	0	4
7. Saturated soil culture	0	0	3	3	3
Total	10	2	3	128	c.60

RIL = recombinant inbred line

Workshop Objectives and Structure

The International Workshop on Breeding Strategies for Rainfed Lowland Rice in Drought-Prone Environments was held at Ubon Ratchathani, Northeastern Thailand, on 5–8 November 1996. The workshop had several objectives:

- to analyse current breeding strategies in relation to environmental constraints;
- to evaluate impacts of environmental constraints, particularly drought and adverse soil conditions, on rice production in the rainfed lowland ecosystem;
- to examine agronomic methods and genotypic adaptation to minimise these impacts;
- to provide future research direction for breeding programs for the drought-prone rainfed lowland ecosystem.

The workshop was sponsored by ACIAR, RLRRC and the Thai Department of Agriculture and attracted 117 participants from nine countries and two international rice research organisations. Twenty-nine papers were presented and discussed. These papers, which are presented in these proceedings, addressed the characteristics of the rainfed production systems targeted in breeding programs, current breeding practices, constraints to increasing production above present levels, and the genetic progress that has been made to date.

In addition, one afternoon was spent in general discussion to prioritise future research directions. An overview of this session is presented in the last paper of these proceedings and also provides recommendations for future research and development addressing breeding strategies for rainfed lowland rice in drought-prone environments.

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Rainfed Lowland Rice Research: Challenges and Priorities for the 21st Century

Sushil Pandey*

Abstract

A rapid increase in production of rice is required to meet the future increases in demand arising from population growth and increasing incomes. Although over two-thirds of the current rice supply comes from irrigated areas, which have been the traditional rice bowls following the success of the green revolution, an increase in the productivity of rainfed lowlands is essential to ensure food security, especially for the poorer segments of the population. There are over 40 million ha of rainfed lowlands worldwide and these areas have the potential for further improvements in productivity. However, rice production in rainfed ecosystems is constrained by a range of biotic and abiotic stresses, which limit yield, as well as by a range of socio-economic factors that determine the type of technology demanded by farmers. Given that the socio-economic conditions vary across countries and regions, a targeted approach to technology research in rainfed lowlands is advocated. Trends such as increasing urbanisation, commercialisation and diversification of agricultural production systems will increasingly shape the nature of rice production systems in the rainfed lowlands. A challenge for agricultural researchers is to develop technologies that not only increase and stabilise yield, but also help farmers maintain higher levels of income through input saving, product diversification and farm consolidation.

THE challenge facing rice researchers in the coming decades is to increase the supply of rice to feed a growing world population. The success of green revolution technology based on high-yielding varieties, irrigation, fertilisers and other complementary inputs, led to a rapid increase in the supply of food grains and helped to prevent hunger and mass starvation. The relative homogeneity of irrigated ecosystems made widespread adoption of modern technologies possible.

As we move into the next century, additional supplies of rice must come from rainfed as well as irrigated environments. There are early signs that productivity growth in irrigated areas alone may not be enough to produce the additional supplies required to meet increased demand in an environmentally sustainable manner. Increased productivity in rainfed lowland ecosystems will be increasingly important in ensuring food security, especially in areas with poor economic performance and widespread poverty. It is therefore timely to reassess the potential role of rainfed lowland rice ecosystems in ensuring food security in the light of the emerging trends and to develop a research agenda.

Rainfed Lowland Ecosystems

In the context of rice production, rainfed lowland ecosystems are defined as areas where rice is grown in unirrigated, levelled and bunded fields that have shallow flooding with rain water (Mackill et al. 1996). Worldwide, about 40 million ha of land is planted with rainfed lowland rice. This is approximately 28% of the total rice-growing area, and rainfed lowland rice forms about 18% of the global rice supply. More than 90% of the area planted to rainfed lowland rice is in Asia. India and Bangladesh in South Asia and Thailand, Myanmar and Indonesia in Southeast Asia together account for more than 80% of the total area and production in Asia (Table 1).

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Table 1. Rainfed lowland rice area of selected Asian countries.

Country	Area (million ha)	Area as % of total rice area	Yield (t/ha)
Bangladesh	5.17	47	2.5
India	13.93	35	2.4
Nepal	0.94	66	2.2
Sri Lanka	0.45	53	2.5
Cambodia	0.86	48	1.5
Indonesia	0.71	7	3.0
Lao PDR	0.32	56	2.1
Malaysia	0.13	21	1.5
Myanmar	2.51	52	3.0
Philippines	1.20	35	2.0
Thailand	8.57	85	1.8
Vietnam	1.76	28	2.0

Source: IRRI (1993)

The yield of rainfed lowland rice is low and varies from 1.5 t/ha in Cambodia and Malaysia to 3 t/ha in Indonesia and Myanmar. The overall average yield for Asia is 2.3 t/ha. It is not possible to examine the pattern of yield growth by ecosystem for most countries as time-series data by ecosystems are generally not available. Limited data for India and the Philippines indicate that, as compared to irrigated ecosystems, yield growth in rainfed lowland rice is not only low but also variable, as measured by the coefficient of variation (Table 2). The existing level of yield in the different states of India correlates well with the proportion of the rice-growing area that is irrigated (Fig. 1). Rainfed lowlands not only have low and variable yields but also have a higher incidence of poverty. For example, the proportion of poor people is greater in Bihar, Orissa and Madhya Pradesh, where rice is produced mostly under rainfed conditions (Fig. 2), than in other states, where rice is predominantly irrigated. The green revolution, which led to a rapid growth in productivity of irrigated rice, has had a relatively modest impact on the yield of rainfed rice.

Depending on the environmental conditions, rainfed lowlands may be classified into favourable and unfavourable ecosystems. In favourable rainfed areas, which are intermediate between rainfed and irrigated ecosystems, field water cannot be completely controlled but rainfall is usually adequate and well distributed. Favourable rainfed areas account for about 20% of the total rainfed lowlands (Mackill et al. 1996). Farmers mostly grow modern varieties and yields are on the higher side of the range for rainfed ecosystems. More than 50% of the favourable rainfed lowlands are in Southeast Asia. The remaining 80% of the rainfed lowland area is less favourable and rice in these areas suffers from varying degrees of

Table 2. Growth rate and coefficient of variation (CV) of rice yields by ecosystem.

	Irrigated	Rainfed lowland	Upland
India (1956–87)			
Growth rate in yield (%)	2.5	1.0	0.3
CV of yield (%)	10.0	12.0	16.0
Philippines (1961–87)			
Growth rate in yield (%)	3.2	2.4	1.4
CV of yield (%)	6.0	8.0	8.0

Source: IRRI Rice Data Base

drought, submergence and both drought and submergence. As a result, yields are low and highly variable. More than 60% of the unfavourable rainfed lowlands are in southern Asia.

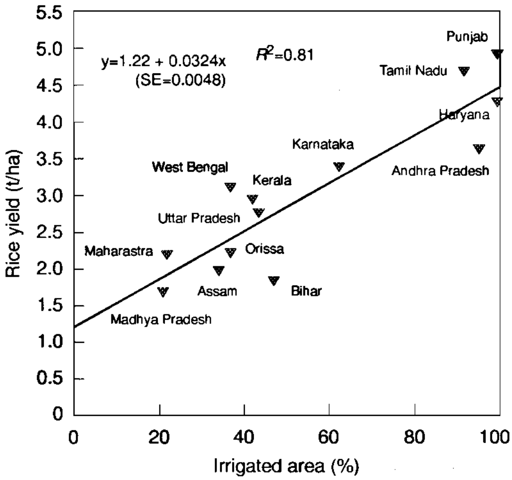

Figure 1. Association between the percentage of the rice-growing area that is irrigated and rice yield, in selected Indian states, 1991–92 (Hossain 1995).

Although the classification of rice-growing areas by ecosystem helps focus on major constraints relevant to each of the ecosystems, the boundaries are not static. Changes may occur for several reasons. Previously rainfed areas may become irrigated areas with expansion of irrigation systems. Similarly, areas classified as irrigated may actually resemble rainfed conditions due to lack of irrigation. Although the physical area under a particular ecosystem may remain the same, the area of rice planted changes with changes in the cropping intensity of rice. Although the *total* rice area in Asia remained more or less the same from the late 1970s to early 1990s, the distribution between the different ecosystems has changed considerably. Upland, deepwater and rainfed areas have shown a decline but the irrigated area, especially during the dry season, has increased. The total rainfed lowland area has decreased by about 10% compared to the late 1970s but the distribution across the Asian countries is not uniform. There has been a substantial increase in Cambodia, Lao People's Democratic Republic (Lao PDR), Vietnam, Myanmar and Thailand and a reduction in the Philippines, Nepal, Bangladesh, Malaysia, China and India (Huke and Huke 1996).

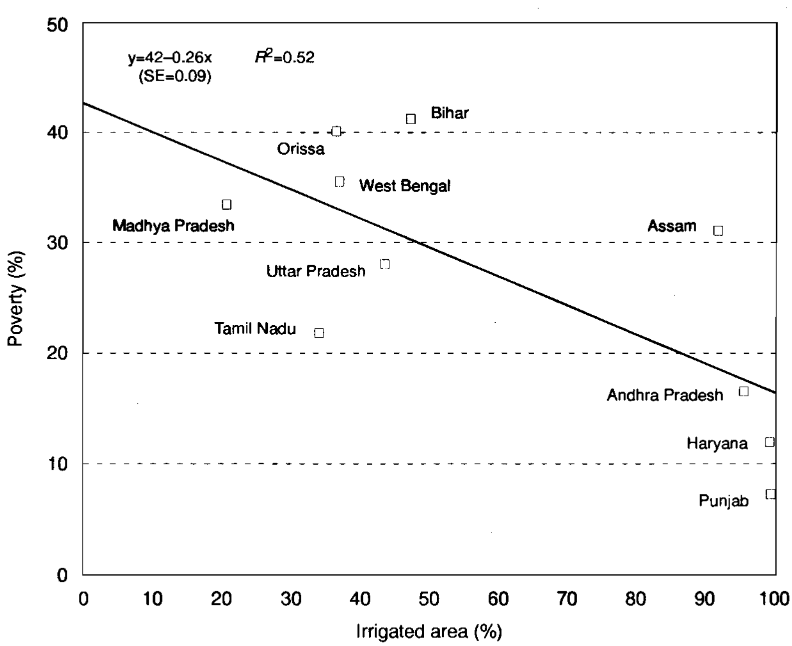

Figure 2. Association between the percentage of the rice-growing area that is irrigated and poverty level in Indian rice-growing states (Hossain 1995).

Emerging Trends

Population growth and increasing demand for food

Population growth will continue to be a major factor determining the rate of growth of demand for food grains in the coming decades. According to recent projections, by the year 2010 global food demand will increase by about 40% from the 1989–91 level (Rosegrant et al. 1995). If the current growth rate of 1.7% per year continues, the Asian population of about 3 billion will increase by another 2 billion in the next 30 years. In addition to this population-induced increase in demand for rice, income increases in countries such as India, Bangladesh, Indonesia and China in the coming decades will lead to further increases in demand for rice. These countries account for more than 70% of the total rice consumption and have a positive income elasticity of demand. Although higher income countries, such as Japan, Korea and Taiwan, have a negative income elasticity of demand and hence will reduce their consumption of rice with further increases in income, the net effect of income growth on rice demand will be positive due to the greater importance of low income countries in determining the total demand. Recent projections show that at the prevailing price level, the demand for rice is likely to increase from the current level of 500 million tonnes by as much as 69% by 2025 (Hossain 1995).

Urbanisation

The percentage of the total population living in urban areas has increased in almost every country in Asia (Table 3). During 1990–95, the average annual growth rate of the urban population in various rice-producing Asian countries was at least 3%. In 1994, about a quarter of the Asian population was living in urban areas. It has been estimated that by 2015, there will be at least 16 cities with populations exceeding 10 million (Table 4).

This trend towards increased urbanisation has several implications for the organisation of rice production systems in the coming decades. First, an increasing number of rice consumers will be dependent on the marketed surplus of rice, and rice production systems need to be geared towards producing a marketed surplus. Second, demand for water for urban use will increase, creating pressure to divert water from agricultural use. Rice production systems of the future will therefore need to be water efficient. Third, urbanisation competes with agricultural use of land, creating pressure for increased rice production with less land.

Table 3. Urban population as a percentage of total population.

Country	Urban population (%)		
	1975	1985	1994
Bangladesh	9.3	13.7	17.0
India	21.3	24.3	26.0
Nepal	5.0	8.5	12.0
Sri Lanka	22.0	21.1	22.0
Cambodia	10.3	10.8	12.0
Indonesia	19.4	25.3	32.0
Lao PDR	11.4	15.9	20.0
Malaysia	30.7	38.8	44.0
Myanmar	23.9	24.0	25.0
Philippines	35.6	40.0	44.0
Thailand	15.1	19.5	35.0
Vietnam	18.8	19.6	20.0

Source: ADB (1995)

Table 4. Asian cities with populations above 10 million.

1994	2015
Tokyo	Tokyo
Shanghai	Shanghai
Bombay	Bombay
Jakarta	Jakarta
Calcutta	Calcutta
Seoul	Seoul
Beijing	Beijing
Osaka	Osaka
Tianjin	Tianjin
	Delhi
	Manila
	Dhaka
	Lahore
	Hyderabad
	Bangkok
	Karachi

Source: World Bank

Increase in wage rate

The Asian economies are currently growing at an unprecedented rate. The annual GNP growth rate for many Asian countries in 1994 was more than 5% (Table 5). Economic growth leads to structural changes, reducing the share of agriculture in GNP and in employment. As a result of an increase in labour productivity and income in the non-farm sector, there is movement of labour from the agricultural to non-agricultural sector. This is accompanied by a rapid increase in agricultural wages, not only due to the demand pull from the non-farm sector, but also due to increased peak labour demand in agriculture, which results from increased intensity of land use. The extent of wage increases depends on the rate of growth of the economy, the capital intensity in the non-farm sector, the rate of population growth and the nature of agricultural production technology. Variations in these factors create differences in the growth rate of agricultural wages and the subsequent degree of labour scarcity across countries. However, it is inevitable that agricultural production systems ultimately have to face the problem of labour scarcity.

Commercialisation of agriculture

Commercialisation refers to the process by which non-traded inputs are substituted for traded inputs, and outputs are primarily sold rather than consumed by the farm households. Examples of non-traded inputs are family labour and farmyard manure and those of traded inputs are hired labour, machinery and chemical fertilisers. Compared to subsistence farming, where the farm household is both a producing and a consuming unit, commercialisation leads to the separation of these two units. The consumers and the producers may be spatially separated, as in the case of urban consumers obtaining their food supplies from the rural areas. The separation occurs even in the case of rural producers who, instead of consuming their own produce, purchase from the market. Commercialisation thus leads to an increased reliance in the market for both inputs and outputs.

Commercialisation of agricultural production is another facet of structural change whereby traded inputs become relatively cheaper than non-traded inputs, leading to a substitution of the latter by the former. An increase in the opportunity costs of land and labour makes labour-intensive inputs, such as farmyard manure, more expensive compared to chemical fertilisers. The price ratio swings further in favour of manufactured fertilisers as technological changes in these industries reduce the unit cost of production. The price of chemical fertilisers has been declining for some time, encouraging their increased application for rice production. Similarly, other manufactured inputs, such as machinery and herbicides, are being increasingly used as a result of rises in wage rates.

Commercialisation has major implications for the organisation of agricultural production. Technologies that are based on the use of non-traded inputs are not appropriate for commercialised agriculture. When inputs and outputs are valued at the market price, the main factor that governs decisions on what and how to produce becomes the economic profit. Integration with the non-farm sector also means that the performance of agriculture becomes much more sensitive to the performance of the non-farm economy.

Table 5. GNP per capita (US$, 1993) and percentage growth rate (1985–94).

	1993 GNP per capita (US$)	1985–94 Growth rate of GNP per capita (%)
Nepal	160	2.3
Bangladesh	220	2.0
India	290	2.9
Sri Lanka	600	2.9
Indonesia	730	6.0
Philippines	830	1.7
Thailand	2040	8.6
Malaysia	3160	5.6
China	530	7.8

Source: ADB (1995)

Diversification of agriculture

Commercialisation of agriculture leads to the development of a diversified market-oriented production system. Diversification can be considered at the farm, regional, sectoral and intersectoral levels. Farm-level diversification implies an increase in the number of agricultural enterprises that a farm household undertakes. Farm-level diversification performs at least three functions. It enables agricultural resources to be spread more evenly across activities and over the agricultural season; provides protection against yield and price risks; and provides flexibility to take advantage of improved market opportunities by shifting resources across activities. Although traditional farming systems are highly diversified, the more recent trend towards diversification away from rice in the humid and subhumid tropics, especially in the rapidly growing economies of Southeast Asia, has been in response to slower growth of farm income due to increased rice productivity and the subsequent decline in the long-term price of rice (Timmer 1992). This trend towards diversification has been encouraged by the availability of irrigation and the income-induced growth in demand for high value products such as fruits, vegetables and meat.

The potential for diversification out of rice depends both on both the biophysical and economic environments (Pingali 1992). In the lowland, the trend towards diversification is most evident in irrigated ecosystems. The potential for diversification is low in the wet season due to drainage constraints but in the dry season, irrigation facilitates the successful cultivation of a range of upland crops such as vegetables, wheat, oilseeds and other seasonal crops. In addition to this seasonal diversification, year-round diversification into activities such as fruit trees, aquaculture and poultry have occurred in response to the declining profitability of rice. As the farmers' incentive for diversification is to supplement their income by engaging in enterprises whose outputs have increasing market demand, diversification has only been successful in areas with good marketing infrastructure.

In rainfed lowland areas, the possibilities for seasonal diversification are limited due to the lack of irrigation. Non-rice crops are unsuitable during the rainy season, except in well-drained fields. In poorly drained fields, it is more advantageous to grow rice. During the dry season, possibilities exist for diversification if supplementary irrigation is available. Seasonal diversification in Batac, northern Luzon, is based on the availability of groundwater. Farmers grow a range of vegetable crops during the dry season using groundwater (Lucas et al. 1996). Similarly, the expansion of the rice–wheat system in eastern India is supported by the availability of groundwater to provide supplementary irrigation to wheat. Depending on the length of the rainy season, some opportunities also exist for growing short-duration non-rice crops before or after rice.

Overall, drainage constraints during the rainy season and the lack of supplementary water during the dry season limit the extent of diversification of rainfed lowland areas. Rapid expansion of groundwater irrigation, as in the case of eastern India, may relax the water supply constraint and encourage farmers to grow a range of post-rice crops with high market demand. Without the expansion of irrigation, the majority of rainfed lowlands will continue to be used for rice monocropping. However, year-round diversification is possible, if strong market demand for non-rice crops makes investment in drainage and irrigation profitable. These pressures are likely to exist in peri-urban areas and farmers may switch out of rice completely to engage in year-round production of fruit trees, vegetables, sugarcane, cattle, poultry, etc. Since the demand for these products increases only when incomes are rising rapidly, countries with faster rates of economic growth are first to experience such diversification.

Reduced profitability of irrigated rice production

The success of the green revolution in irrigated rice ecosystems during the past three decades has made these ecosystems the main rice bowl of the world. Currently, irrigated ecosystems generate over 75% of the total rice supply although they account for only 55% of the total rice area. Rice yield in irrigated areas ranges from 3–9 t/ha with an average yield level of 4.9 t/ha. Despite the overwhelming importance of irrigated ecosystems in generating the bulk of the rice supply, there are indications that this ecosystem alone will not be able to provide all the additional supplies required to meet the increasing demands in the coming decades. Relatively higher costs associated with providing new irrigation facilities, the maintenance of existing irrigation infrastructure, trends towards diversification out of rice in order to maintain farm incomes, environmental concerns associated with further intensification of irrigated rice production and the lack of an economically exploitable 'yield-gap'are some of the major factors limiting the possibility of further increases in rice production from irrigated ecosystems (Rosegrant and Svendsen 1993; Pingali 1994).

Reduced profitability of intensified irrigated rice production in rapidly growing economies such as Malaysia, China and Indonesia — countries relying mainly on irrigated rice production — could lead to serious rice deficits. According to estimates made by Hossain (1995), the average yield in irrigated ecosystems would have to increase from the existing level of 4.9 t/ha to 9.5 t/ha by 2025 to satisfy the total demand, if yields under rainfed conditions remained at the existing level of 1.9 t/ha. Even if cultivars can be developed with the potential to produce such high yields, the levels of input usage required for such yields will generate substantial negative externalities.

Trade Liberalisation

Trade liberalisation under the World Trade Organisation will put pressures on the rice production systems of the future to be more cost-efficient. This will require an increase in yield and/or a reduction in the cost of production. High-cost producers will find it difficult to compete with low-cost producers. To the extent that environmental constraints limit productivity gains, production will shift from the more difficult environments towards more favourable ones because the per unit cost of production in these environments will be relatively high compared to more favourable areas. This tendency will be reinforced if the production of other commodities suitable to such areas becomes more profitable with trade liberalisation. For example, it may be possible to switch from rice to agroforestry in the uplands and marginal rainfed environments.

The effect of trade liberalisation on rice production systems may therefore be to reinforce the trends towards increasing wage rates, increasing commercialisation and diversification of agriculture.

A Conceptual Framework

Overall, the nature of rice production systems may be determined by population density, the stage of economic development and the agroclimatic conditions. These factors determine the nature of production systems through their effects on rice demand and supply. The first two variables work by influencing both the supply and demand factors. The agroclimatic conditions influence the supply by determining the production potential.

Population density

Population density affects food demand in relation to the available land area for production. When the population density increases there is greater pressure to intensify production to meet the demand. The labour supply needed to intensify production also increases with an increase in population density. Population pressure is one of the major factors determining land-use intensity (Boserup 1965, 1981). When the population density is low, any increase in population pressure initially results in expansion of agricultural areas because the returns to labour, which is a relatively scarce factor, are maximised by such a land-extensive strategy.

As the land frontier approaches its limit due to continuous expansion of population, however, and the labour productivity declines as a consequence, methods are sought to increase production from the limited land area by intensification. The production system will be predominantly subsistence-oriented unless possibilities exist for trading with other societies. If technologies are not available to increase the yield rapidly enough, labour productivity will continue to decline. Low and falling labour productivity encourages exploitation of marginal land, thus leading to a cycle of low productivity, poverty and resource degradation. Thus, low productivity, high levels of poverty, small farm size and subsistence-oriented production systems are typical of densely populated agricultural societies, which are not able to intensify production rapidly enough to meet the demand or to trade with other societies due to limited market access.

Economic growth

Economic growth affects the agricultural sector in two ways. Firstly, it alters the income-induced demand for staples, and, secondly, it draws resources away from agriculture. The effect of economic growth on food demand depends on the current levels of income. When incomes are low, demand for staples tends to increase with an increase in income due to positive income elasticity of demand. Consumption levels increase as people are able to afford more staples. Many low-income countries in Asia have a positive income elasticity of demand for rice and will increase their rice demand in the future. However, at high levels of income, income elasticity for rice becomes negative, leading to a decline in its consumption, as vegetables, fruits and meat are substituted for rice. East Asian economies, such as Japan and Korea, and rapidly growing Southeast Asian countries are now in this stage. Rice production systems change as farmers attempt to respond to such income-induced changes in consumption patterns. As mentioned earlier, a more diversified production system is likely to evolve with economic growth.

The second effect of economic growth results from the structural transformation that results in withdrawal of resources from agriculture. A shrinking agricultural sector has to increasingly compete with an expanding non-farm sector for land, labour and capital. In response, technologies and production methods are adopted that help maintain profits in the face of rising input costs. The increasing cost of land encourages the adoption of yield-increasing technologies while the growing scarcity of labour forces the adoption of mechanical technologies. Because of the economy of scale associated with mechanised farming there is a trend towards increased farm size.

The effects of population density and income levels on the nature of production systems

The combined effect of population density and the level of economic growth (as indicated by income levels) on the nature of the agricultural production systems is depicted in Figure 3. When both income levels and population density are low, agricultural production systems tend to be land-extensive and subsistence-oriented because of the lack of demand from a relatively smaller non-farm sector (e.g. Cambodia, Myanmar and Lao PDR). Population density in these countries ranges from 18 persons/km^2 in Lao PDR to 63 persons/km^2 in Myanmar with per capita annual incomes of around US$300. On the other hand, subsistence-oriented, labour-intensive and small farm-based production systems dominate when the population density is high but the income level is low (e.g. India, Bangladesh and Nepal). The population density in these countries ranges from 134 persons/km^2 in Nepal to 768 persons/km^2 in Bangladesh, with per capita income of less than US$300. In these densely populated areas, the non-farm sector has a limited capacity to absorb the rapidly increasing population, resulting in high levels of poverty in the farm

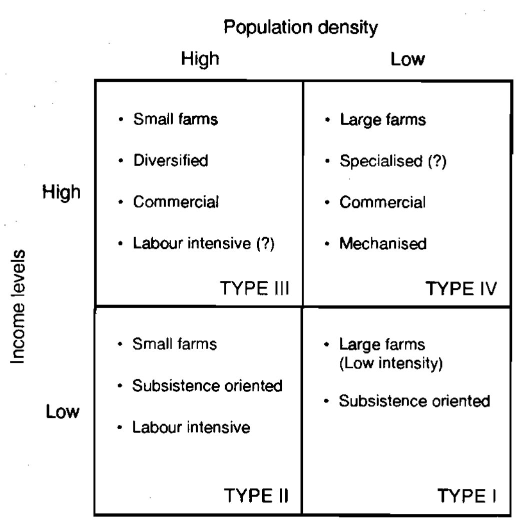

Figure 3. The effects of population density and income levels on the nature of production systems.

sector. As the level of poverty is inversely related to the productivity of the agricultural sector, at low levels of income, poverty reduction requires rapid technological innovation in the agricultural sector.

When countries with high population pressure and low levels of income are finally able to increase their incomes, diversified and commercialised production systems are likely to evolve. Initially, the farms will be small due to the high population pressure but increased demand for a range of agricultural products at higher levels of income encourages diversification. Similarly, increased linkages between the farm and non-farm sectors through both the input and output markets provide incentives for commercialisation. Thailand, Sri Lanka, the Philippines and Indonesia all fall into this category. The per capita income in these countries is more than US$600 and the population density is greater than 90 persons/km^2.

Specialised, commercialised and mechanised production systems tend to evolve when income levels increase further but the population density is low. Under these conditions, labour scarcity in the farm sector will force the adoption of labour-saving innovations. Whether or not specialisation at the farm level occurs depends not only on the agroclimatic factors but also on the nature of the evolving marketing systems. Malaysia, with a per capita income of US$3160 and a population density of 56 persons/km^2, provides an example of a highly commercialised and mechanised production system that is becoming increasingly specialised. Agroclimatic conditions permitting, farm-level specialisation occurs as management-intensive methods of production, which become desirable at high levels of income, limit farmers' abilities to efficiently manage multiproduct farms.

Figure 3 is a representation of the major long-term determinants of the characteristics of agricultural production systems. At any point in time, a country can display all four characteristics, especially if market imperfections and/or agroclimatic characteristics make a different pattern of growth possible in each region. For example, income levels are high and the agricultural production systems are increasingly commercialised in the Indian Punjab, where agricultural productivity increased rapidly due to the green revolution. In contrast, eastern India has subsistence-oriented production systems with low income and high population pressure. Although the policy environments are similar in both these regions, a less favourable agroclimatic environment combined with a slower growth of the non-farm sector in eastern India has resulted in a different type of production system.

The somewhat static pattern depicted in Figure 3 could also be used to trace out an evolutionary path as agricultural production systems undergo change. For example, agricultural production systems of Type I could change directly to Type IV if societies with low population are able to grow rapidly and achieve structural transformation before a major increase in population density occurs. This was mainly the pattern of growth of the contemporary developed countries. Rapid economic growth generated by the industrial revolution in the 19th century led to the transformation of subsistence-oriented production systems to commercialised and specialised farms (Type IV).

The production system could change from Type I to Type II if the economic growth is slow but the population is expanding rapidly. The production system will then change from Type II to Type III if rapid economic growth is achieved. The Type III production system may ultimately change to Type IV as increased labour absorption by the non-farm sector results in labour scarcity in agriculture.

The relevance of the scheme shown in Figure 3 for designing agricultural development strategies in developing countries is that reduction in poverty cannot be achieved without rapid growth in agricultural productivity, at least in the initial stages of economic growth. The increase in agricultural productivity since the green revolution has been a major factor in reducing poverty in many developing countries. However, a sustainable reduction in poverty cannot be achieved without a rapidly expanding non-farm sector so that population pressure on the agricultural sector is reduced as the country undergoes structural transformation. Unless interventions are in place that make the process of structural transformation relatively easy, some areas within a region move ahead while others lag behind and suffer from poverty. Therefore, agricultural research targeted to these lagging areas alone may not be an efficient way of addressing poverty resulting from the problems of structural transformation. For example, if an economy has a Type II agricultural sector only, economic growth and poverty alleviation cannot be achieved without a rapid growth in agricultural productivity. However, if the overall growth in income is rapid enough for a major section of the agricultural sector to acquire the characteristics of Type III and Type IV, poverty problems in areas that still have Type II characteristics will most likely require interventions designed to exploit the opportunities of income enhancement offered by the rapidly growing non-farm sector.

This implies that policies designed to increase the incomes of rural producers in these areas by developing better linkages with the non-farm sector are likely to be more effective in poverty alleviation than attempts to increase the productivity of food crops under subsistence production systems. A switch in agricultural research policies from improving the productivity of subsistence food production to developing a more flexible and responsive agricultural sector, which can adapt to and benefit from new opportunities arising from economic growth, is needed for addressing the poverty problem in the long run.

A Research Agenda for the Rainfed Lowland Rice System

What are the high priority research areas in the rainfed lowland rice ecosystems of Asia, given the emerging trends and the likely evolution of the nature of the agricultural production systems? As compared to irrigated rice environments, which have benefited from yield-increasing green revolution technologies, most rainfed lowland rice ecosystems currently have low and unstable yields due to a host of abiotic and biotic stresses. Land-use intensity is low, production systems are predominantly subsistence-oriented and farmers mostly practice rice monocropping in the wet season. As a result of these characteristics, the level of poverty among rural households is high. Most of the countries where rainfed lowland rice ecosystems predominate also have a low per capita national income that is growing slowly, although some countries in Southeast Asia have now achieved a higher rate of economic growth. Thus rainfed lowland rice production systems mainly fall into the Type I and II systems shown in Figure 3, with some fast-growing countries having Type III characteristics (Table 6). Given the underlying trend towards increased commercialisation of agriculture, the long-term goal of rice research for rainfed lowlands should be to develop technologies that facilitate the transition from subsistence oriented to commercially oriented production systems. In the medium term, differences in the economic structure of countries in the above categories indicate that a somewhat targeted approach is needed for rice research.

Broadly speaking, low productivity in Type I regions is not due to the lack of production potential per se but is the result of lack of demand due to low population density or limited access to export markets. Farmers lack incentives to adopt yield-increasing input-intensive technologies as land is not a restricting factor.

Table 6. Major characteristics of selected Asian countries with rainfed lowland rice.

Country	Population density (per km^2)	Income per capita US$ (1993)	Major types of rainfed[1] rice system	Rainfed lowland rice area (million ha)
Cambodia	47	na	I	0.86
Myanmar	63	519	I	2.51
Lao PDR	18	290	I	0.32
India	264	290	II	13.93
Nepal	134	160	II	0.94
Bangladesh	768	220	II	5.17
Vietnam	209	170	II	1.76
Thailand	113	2040	III	8.57
Philippines	218	830	II,III	1.20
Indonesia	97	730	II,III	0.71
Sri Lanka	265	600	II,III	0.45

na = not available
[1] See Figure 3
Source: IRRI (1993)

Rice research technologies that enhance labour productivity are more suitable for these areas. Labour-saving technologies for land preparation, crop establishment and weeding can help improve labour productivity. The adoption of these technologies will be constrained, however, unless the non-farm sector or export market grows rapidly enough to increase the demand for rice and marketing infrastructures are sufficiently developed to make additional supplies available to consumers cost-effectively.

For areas that have the dominant rainfed lowland system with Type II characteristics, improvements in rice productivity could be the key to income enhancement and poverty reduction. Multiplier effects associated with income growth from improvement in rice productivity could encourage other non-farm rural activities and provide additional sources of income. As abiotic constraints such as submergence and drought are the major factors limiting rice yields in rainfed environments (Widawsky and O'Toole 1990), technologies to stabilise and enhance rice yields can play a major role in improving food security. Breeding for rice cultivars which can escape or withstand the effects of these abiotic stresses is hence likely to have high payoff. Similarly, improved crop management technologies, which lead to better crop establishment and more effective utilisation of moisture and nutrients, are needed to stabilise and improve rice yields. In addition, technologies such as shorter-duration rice cultivars and improved crop management practices can help intensification of agriculture based on a rice–upland cropping pattern. Even in countries with Type II characteristics, the long-term reduction in poverty cannot, however, be achieved without the demand pull exerted by a rapidly growing non-farm sector.

Regions belonging to category III have mostly achieved a high rate of economic growth and are undergoing rapid structural transformation. Producers of food grains suffer not so much from low yields as from low incomes. Research for rainfed rice systems in these countries should be targeted towards increasing the income of rice farmers rather than just the yield of rice. Even if rice yields are low, income could be increased by designing input-efficient methods of production (such as mechanisation), by growing premium quality rice, by creating opportunities for diversification of farm enterprises and by developing technologies which help generate income from processing and marketing of agricultural products. The vertical integration of both input and output markets will also pave the way for an efficient and specialised rice production system. In the drive for improving the cost-efficiency of rice production, marginal rainfed rice-growing areas in these economies will switch out of rice to other crops and production will be concentrated in the more favourable rainfed and irrigated areas. In addition, relatively higher costs of production of rice in these countries may encourage them to import rice from other low-cost countries withType I and Type II characteristics.

Conclusions

Increased rice production from rainfed lowlands is critical for ensuring global food security in the coming decades. Although the green revolution led to a rapid increase in rice production in irrigated areas during the past two decades, future demand for rice is unlikely to be met without an increase in the productivity of rainfed lowland ecosystems. Also, as rainfed rice producers are often poor and unable to purchase rice from the marketplace, the importance of investing in improved productivity for rainfed rice ecosystems is evident.

Rice productivity in rainfed lowland rice ecosystems is constrained mainly by abiotic stresses such as drought and submergence. Improvement in rice productivity therefore requires research on breeding cultivars that can either escape or withstand the effects of such stresses as well as on crop management to develop techniques that help the crop to perform better in adverse conditions.

Although abiotic stresses are the main limiting factors for increasing yields in rainfed lowland ecosystems, socioeconomic factors determine the type of technologies demanded by farmers. Population density and the level of economic growth are major factors determining the nature of farming systems and the type of technology that will be employed. Based on different levels of these two socioeconomic variables, a somewhat targeted approach to rice research in rainfed areas is suggested. In areas where low effective demand (due to low population density and/or poorly developed export markets) constrains rice productivity, labour-saving methods of rice production are likely to be more important than yield-increasing technologies. In addition, investment in infrastructure and policy reforms are often preconditions for substantial output expansion in such areas. In areas with rapidly growing non-farm economies and increasing demand for non-rice food products, rice farmers are likely to be more concerned about maintaining their income than increasing yields per se. Rice research that helps farmers maintain their incomes at parity with those of the non-farm sector would hence be demanded. Research to improve the quality of rice and for developing opportunities for diversification out of rice would therefore be desirable. Yield-enhancing technologies are most appropriate when the rainfed rice production system is predominantly subsistence-oriented, poverty is widespread and the non-rice economy is poorly developed.

It is essential to envisage how rainfed rice ecosystems are likely to be affected by emerging trends when viewed in the broader context of economic development and structural change. Urbanisation, increasing wage rates, commercialisation and diversification of agriculture and trade liberalisation are the major factors that will force farmers to be more competitive and cost-efficient. These trends will hence make subsistence-oriented modes of rice production — so common in many rainfed rice areas — increasingly obsolete. Farmers will increasingly demand technologies that will help them maintain a higher level of income through input saving, product diversification and expansion of farm sizes. The challenge to rainfed rice researchers is not only to develop and supply such technologies but also to make them affordable to rice farmers.

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Rice-Based Cropping Systems in Northeastern Thailand

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Abstract

Examination of existing rice-based cropping systems in Northeastern Thailand has shown an important role for upland crops planted before and after rice in increasing the intensity of land use and productivity. Examples of upland crops in the rainfed wetland rice system are sesame and kenaf before and after rice, peanut after rice and watermelon before rice. During the dry season, soil moisture around the root zone is important for the success of the existing cropping patterns. In Northeastern Thailand there are large paddy areas where the water table during the dry season is low. In these areas, research aiming to improve rice-based systems by growing upland crops before or after rice has shown that the yield of upland crops is highly variable from field to field and from year to year, depending on rainfall distribution. The upland crop species that have been grown most reliably before or after rice are mungbean, grain and green pod cowpea, and baby corn. However, successful rice-based cropping systems require rice cultivars that are suitable for double cropping, with early-maturing rice cultivars to accommodate upland crops after the rice harvest. Alternatively, if cultivars could be transplanted late in the season but still produce a high yield, an upland crop could be included before rice.

The characteristics of the farming systems in Northeastern Thailand, including decision-making processes and objectives within farm households, also need to be considered when developing rice-based cropping systems to suit the socioeconomic and human setting of farmers in Northeastern Thailand.

THE Northeastern Region is the largest region of Thailand, with total land area of approximately 64.9 million ha. The region has a population of about 20 million, which is over one-third of the population of the country. Most of the people in this region are engaged in agriculture and it is the largest rice and field crop production region in the country. However, per capita income is the lowest in the country, due to low and unstable agricultural productivity. The critical constraints are lack of sufficient irrigation (less than 30%), erratic rainfall, and poor soil.

The rainfall patterns observed in most of the meteorological stations in Northeastern Thailand are best fitted to a bimodal distribution, according to gamma distribution analysis (Vorasoot et al. 1985). The first peak occurs during May–June and the second in July–October. A dry period of 3–4 weeks usually occurs between the two rainfall peaks.

There are 35 different soil types in Northeastern Thailand, but, with the exception of some limestone areas in the hills, they are all derived from sandstone, shale or silt-stone and are therefore inherently low in potassium, calcium, magnesium and phosphorus and have extremely low organic matter and cation exchange capacity (Craig and Pisone 1988).

Northeastern Thailand can be classified into four landform types: hilly, undulating (mini-watershed), non-floodplain and floodplain (KKU-Ford Cropping Systems Project 1982).

Rice-based cropping systems are practiced widely in the traditional agriculture of Northeastern Thailand (Polthanee 1988). This paper describes the existing rice-based cropping systems and the results of field trials designed to develop improved systems in the region. However, growing rice is only one of many activities within a farm household. Therefore, exist-

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ing farming systems, decision-making processes and the overall objectives of farm households also need to be reviewed. This review is designed to help researchers develop rice-based cropping systems that suit the local physical, biological, socioeconomic and human setting of farmers in Northeastern Thailand, and also rice breeders who wish to develop plant-breeding strategies in the region.

Agroecological Systems in Northeastern Thailand

Farming in Northeastern Thailand is traditionally crop-based. Four distinctive agroecological systems can be identified in the region: mini-watershed, non-floodplain, floodplain and hilly land (Fig. 1).

Of the total agricultural land area of about 8.9 million ha in Northeastern Thailand, mini-watershed covers about 4.9 million ha, non-floodplain 2.9 million ha and floodplain 1.1 million ha. The mini-watershed areas comprise 2.2 million ha of upland fields (field crops 1.8 million ha and fruit tree and grazing land 0.43 million ha) and about 2.7 million ha of paddy fields (upper paddies 0.91 million ha and lower paddies 1.8 million ha).

In economic terms, the mini-watershed areas are the most important for field crop production, while non-floodplains play an important role for rice production in the region. However, within the mini-watershed landscape, the lower paddies are most important for home consumption of rice.

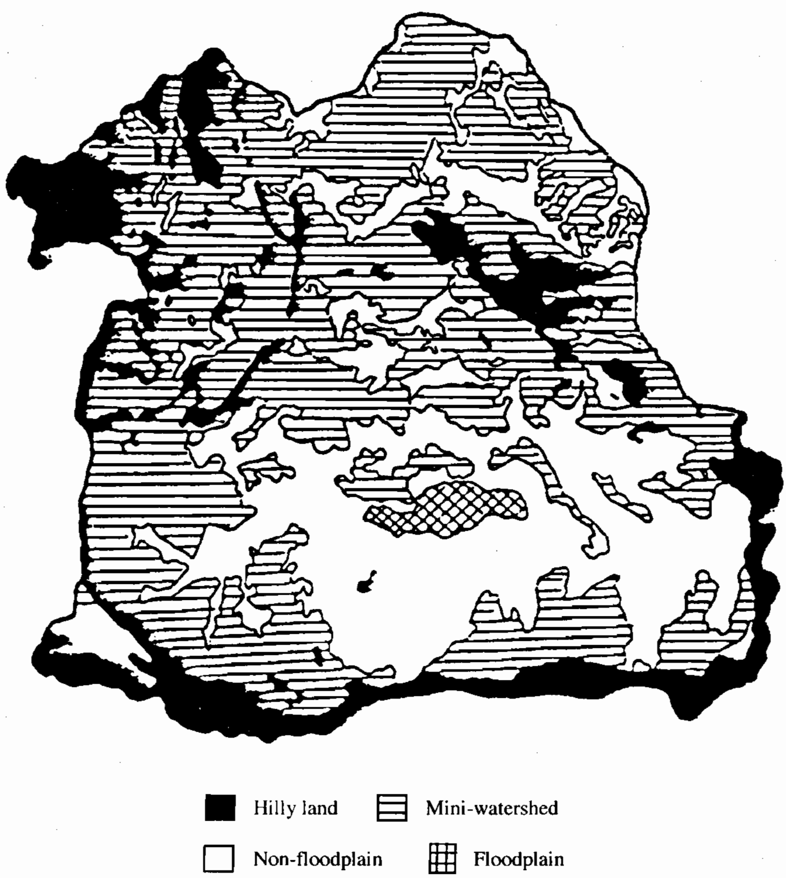

Figure 1. Landform map of Northeastern Thailand (adapted from Department of Agricultural Extension 1995); see map on page x (Introduction).

Mini-watershed

The watershed occurs throughout the northeast. It includes three types of land: upland, upper paddy and lowland paddy. Paddy fields occupy a slightly greater area than upland fields. The upland areas are planted each year to sugarcane, cassava, kenaf, peanut, watermelon, cucumber, green corn, and other field crops. Monocropping of rice is commonly practiced in upper paddies. However, upper paddies are usually left fallow in drier years when there is insufficient water available for transplanting rice. To avoid the problem some farmers grow direct-seeded rice in upper paddies, and transplant rice only in lower paddies. In addition, some farmers have converted the upper paddies to upland fields for growing sugarcane or cassava. Lowland paddies are planted with rice, followed by vegetables in some areas, with hand-irrigation using water from a small pond.

In general, crop yield is low due to the low water-holding capacity and low fertility of the soil in the watershed. Rice production from each farm may only be sufficient (or be insufficient) for home consumption. Generally, the major cash income is from upland crops. Farm labour in traditional systems is evenly distributed throughout the year (Fig. 2).

Non-floodplain

Non-floodplains are at a slightly higher elevation than the floodplains. There are two types of field: upland and paddies. Upland areas within the non-floodplain are usually small, and are used to grow field crops such as sugarcane, cassava, kenaf and peanut. Monocropping of rice is a common cropping pattern in paddy fields. However, in some limited areas, for example in Bureram, sesame or watermelon is grown before the rice crop. Farmers often construct small ponds or dig shallow wells in areas where the water table is shallow and hand-irrigate vegetables and tobacco after the rice crop, for example in Roi-Et and Yasothon Provinces. Many farmers have changed from transplanting to direct-sown (wet-seeded or dry-seeded) rice in order to adjust to the current labour shortage.

The soils are usually good paddy soils, and there is always sufficient water accumulated from rainfall to allow planting of rice in July–August. Rice production is usually sufficient for home consumption and excess is sold.

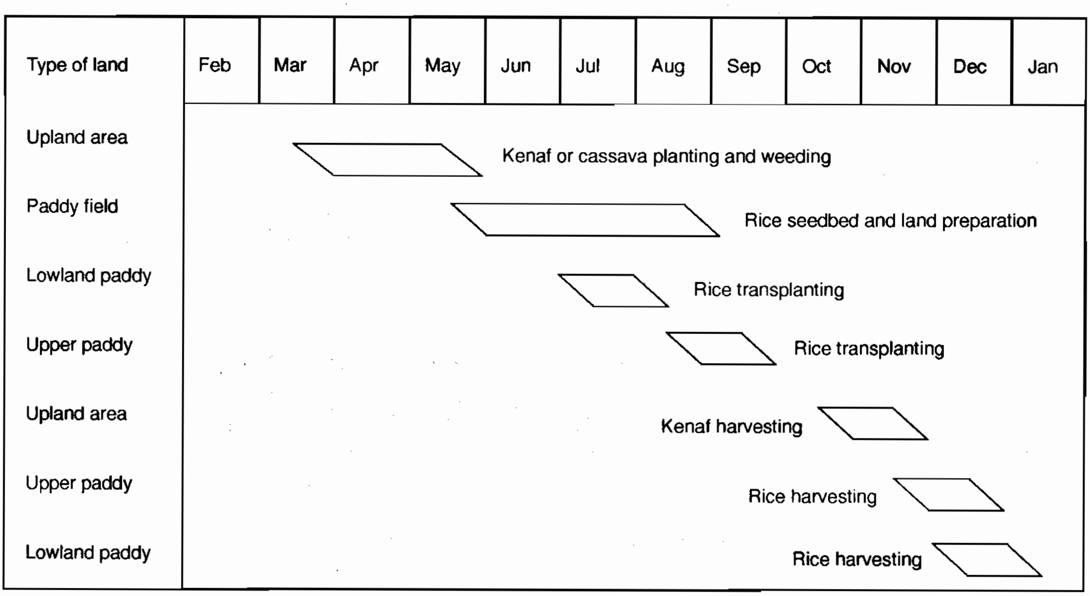

Figure 2. Seasonal distribution of labour for a farmer cultivating small plots on lowland paddy, upper paddy and upland (Polthanee 1988).

Floodplain

The floodplains occur along the Chi and Mun rivers in the northeast. The pattern of cultivation is very similar to that of the non-floodplains. Rice is the main crop. Commonly, vegetables are grown after the rice crop along the lower reaches of the Chi and Mun. Because of the current family labour shortage, direct-sown rice is preferred.

The soils are usually good paddy soils. Flooding can become a problem for rice production in some years. Both fishing and rice are sources of household income.

Hilly land

The hilly lands occur along the Petchabun and Dong Prayayen mountains in the west, Sankampaeng and Pranomdongrak mountains in the south, and Pupan mountains across the northeast and southeast of the region.

In some limited areas, field corn, mungbean, cowpea, cassava and upland rice are planted. However, rice production is usually insufficient for home consumption. Cattle are an additional source of household income, and non-timber products such as bamboo and mushrooms are collected from forest lands.

Decision Making in Farm Households

Farmers in Northeastern Thailand often experience drought problems. Their decision to grow crops such as cassava, kenaf and sugarcane is associated with minimising risks from drought, because the productivity of these three crops seems to be more stable than that of grain crops in this highly variable rainfall environment. Also, these three crops are harvested for vegetative materials rather than grain, and this reduces drought risk. Generally, farmers prefer to grow at least two crops. For example, farmers may decide to grow cassava and kenaf to minimise the risk associated with falling prices, or receive cash income from kenaf in November for payment in the new year. Cassava is harvested early in the rainy season, providing cash to buy inputs such as chemical fertiliser for rice production. In addition, the farmers who grow cassava prefer to plant twice (early and late rainy season), for a more even family labour and income distribution.

Objectives of farm households

The primary objective of farming in Northeastern Thailand is household food security. Rice is the most important crop for most farms. For home consumption, both quantity and quality of the products (e.g. taste) is very important. Rice yield usually depends on rainfall and this leads to the organisation of village ceremonies. For example, the purpose of the Bun Bang Fai ceremony is to request the best rainfall distribution for crop growth. Rice therefore serves as a social link. Three of the 11 main ceremonies during the year (Bun Punkaochi, Bun Kaotoktak and Bun Kaosart) use rice to request happiness for family members who have died (see Fig. 3). Because rice is such an important factor in their lives, farmers often grow rice even if the land is not suitable for rice production; when there is a labour shortage, time spent planting or weeding for rice production receives priority over that for other crops.

Rice-Based Cropping Systems

In rice-based cropping systems sequential cropping is common. Two important patterns occur in the rice paddies of Asia: first, the all-rice sequential cropping patterns (rice–rice, rice–rice–rice); and secondly, the mixed rice and upland crops sequential cropping patterns (rice–upland crop, upland crop–rice, rice–rice–upland crop, upland crop–rice–upland crop (Gomez and Gomez 1983). In Northeastern Thailand, growing upland crops before or after rice has been practiced for many years (Polthanee 1988). Several factors have influenced the existing double-cropping patterns. However, the primary factor that determines cropping patterns in the northeast is water availability. Generally, crop land can be distinguished according to the source of water (rainfed or irrigated).

Double Cropping Under the Rainfed System

In some places residual soil moisture at the end of the rainy season is sufficient for germination and initial growth of a crop that follows rice. Water obtained through the roots from a lower-lying water table allows the completion of crop growth. Therefore, crop yield is stabilised by using soil moisture provided from groundwater during the dry period (Fig. 4). The level of rainfall before the wet season determines the annual variation in yield.

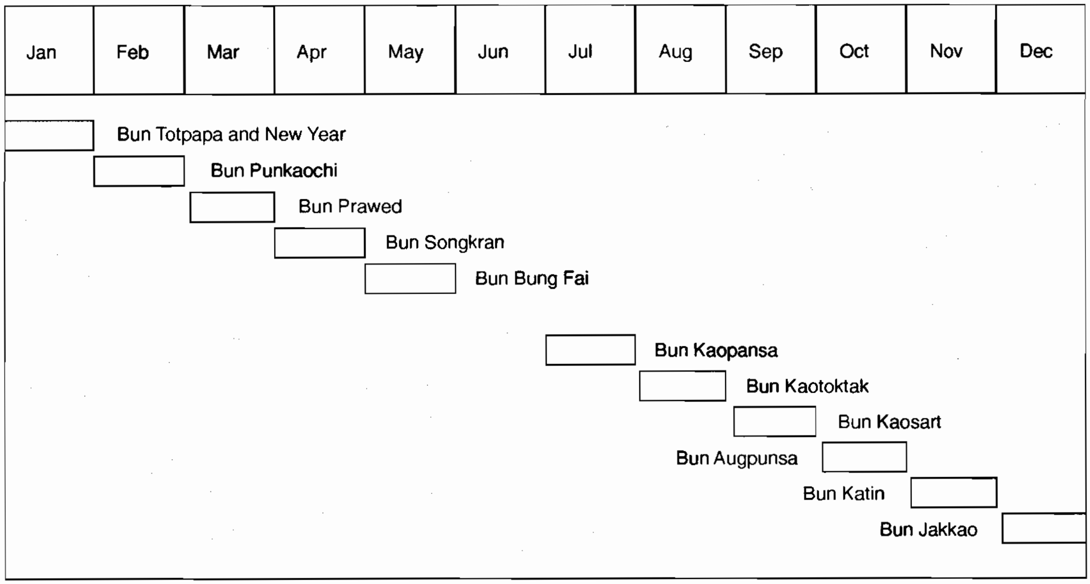

Figure 3. Annual calendar of family and village festivals (Polthanee 1988).

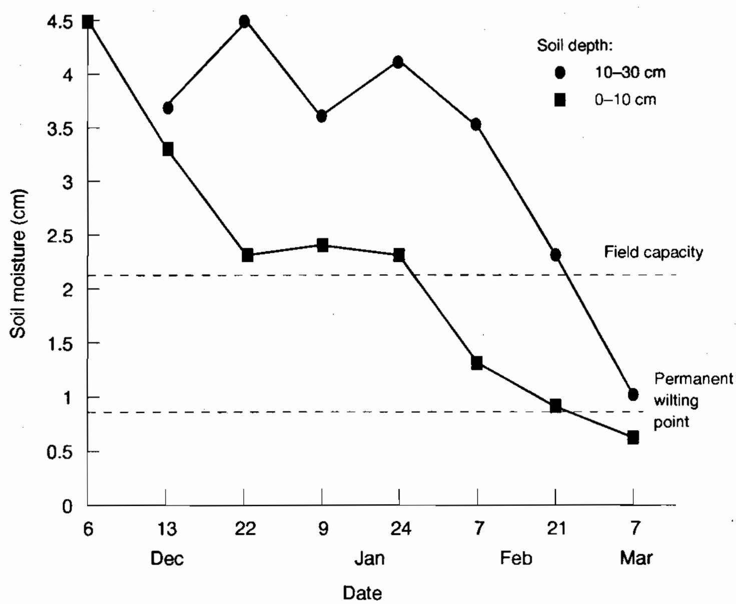

Figure 4. Soil moisture (cm) during the growing season after rice (farmer's field, Surin Province) (Jintrawet et al. 1983).

In some areas the groundwater level after rice harvesting is usually 1.5–2 m below the top soil layer around planting (Polthanee 1990), and additional rainfall before the wet season (February–March) is required for germination and early growth. In general, before deciding to plant, the farmers estimate the minimum amount of rainfall that would moisten soil to at least 30 cm soil depth. This ensures that soil moisture is sufficient for plant growth up to a certain stage, even though the amount and distribution of rainfall in the period before the wet season is quite poor. Roots must elongate to take up soil moisture from depths where sufficient water is provided from a low-lying water table. In this cropping pattern, the yield of the field crop before rice is stabilised due to a low-lying water table during the drought period in June–July.

Rice/peanut cropping systems

Peanut after rice

In certain areas of Surin Province peanut is planted after harvesting rice, from the last week of November to the second week of December (Fig. 5). Land is prepared by ploughing followed by harrowing (three to four times) followed by a last ploughing that makes a slightly deeper furrow between rows. Seed is dropped in the furrow and covered by soil when the next row is ploughed. Farmers in some villages pregerminate seeds before planting by submerging them in water for a day, draining the water, and covering the seed with a soaked cloth for a day. There is no need for weeding, and no insecticides are used during the growing season. Generally, peanuts give best yields when the rains come early in February, indicating that soil moisture is commonly inadequate for maximum pod development. Peanut is a fairly drought-resistant crop because the plants have deep roots that can extract water from deep in the soil (Allen et al. 1976).

Rice/sesame cropping systems

Sesame before rice

In certain areas of Bureram Province, sesame is planted when the rain comes during February–April (Fig. 6). There is a single ploughing, followed by broadcasting of seed and harrowing. Some farmers plough twice — at the end of the rainy season (after harvesting the rice) and immediately before planting the sesame, when the rain comes. Generally, sesame is harvested during a dry period in June–July.

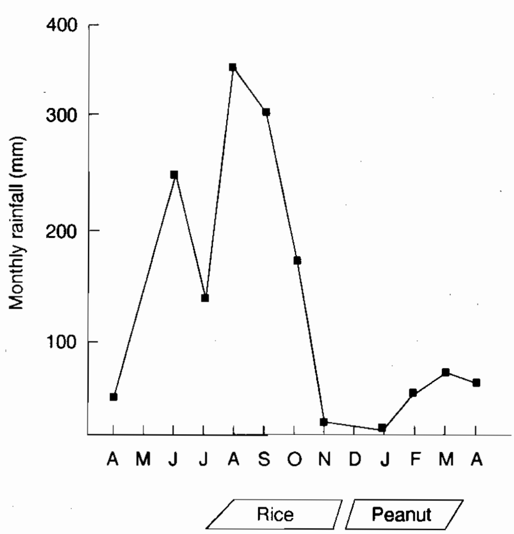

Figure 5. Cropping system for peanut after rice in Surin Province; monthly rainfall.

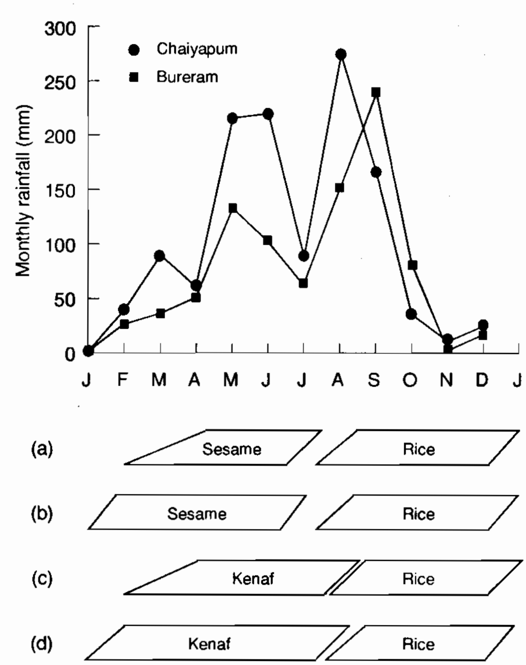

Figure 6. Cropping systems for sesame before (a) and after (b) rice in Bureram Province; kenaf before (c) and after (d) rice in Chaiyaphum Province; monthly rainfall.

Sesame after rice

In other areas of Bureram Province, sesame is usually planted in January, after harvesting rice (Fig. 6). In general, the crop will be harvested during a dry period in June–July. Land is prepared by ploughing once and the soil is allowed to dry for two weeks. Seeds are then broadcast into the soil and the land is ploughed again.

Rice/kenaf cropping systems

Kenaf before rice

In certain areas of Chaiyaphum Province, kenaf (*Hibiscus cannabinus*) is planted in February–March, after harvesting rice in December (Fig. 6). Land is prepared by one or two ploughings after burning the rice straw. At the last ploughing, seeds are dropped on the soil surface and covered by soil when the next row is ploughed, with a plant spacing of 50 × 40 cm. Weeds are removed one or two times during the growing season. Chemical fertiliser 15-15-15 (N, P_2O_5, K_2O) at the rate of 100–200 kg/ha is applied at planting. A similar cropping pattern is found in certain areas of Roi-Et Province. However, kenaf grown in this area is *H. sabdariffa* instead of *H. cannabinus*, because this area is drier than the area in Chaiyaphum Province where *H. cannabinus* is grown. *H. sabdariffa* is better adapted to drought, while *H. cannabinus* is better adapted to waterlogging. Some farmers prepare land after harvesting rice in December and plant kenaf at the onset of rainfall. This ensures a longer growth period before rice is transplanted, and also fewer weed problems, stabilising the kenaf yield.

Kenaf after rice

In other areas of Chaiyaphum Province, kenaf (*H. cannabinus*) is planted in January, after harvesting rice in December (Fig. 6). Land is prepared by one or two ploughings after burning the rice straw, and is harrowed several times immediately after ploughing. Seeds are dropped in furrows made by a hoe at a plant spacing of 40 × 40 cm, and covered with soil. In some years, the crop may suffer from waterlogging at later stages of crop growth. However, kenaf is considered to be a waterlogging-tolerant crop (Pruchareonvanich 1996). Plants develop adventitious roots, which are an adaptation to waterlogging, allowing absorption of oxygen (Jackson 1955).

Rice/watermelon cropping systems

Watermelon before rice

In Bureram Province, planting of sesame before rice is gradually being replaced by a cropping pattern of watermelon before rice. Farmers think that during the last five years sesame has produced poor yields due to the lack of additional rainfall after planting, before the wet season. In addition, watermelon gives a higher net income than does sesame.

Double Cropping Under Irrigation

Only a limited area is covered by the state irrigation scheme where irrigation water is taken from dams and main rivers using electric pumps. For the irrigation scheme, double rice cropping is common. Another common double cropping system is to grow field crops such as peanut, soybean, tomato and green corn, after the rice harvesting. Another source of irrigation water is a shallow well and on-farm pond. Water is applied by hand. In general, the water table depth in these areas is greater than that of the non-irrigated area. Crops commonly grown in this system are tobacco, chili and tomatoes.

Tobacco after rice

In certain areas of Roi-Et Province, tobacco is planted under the supervision of a private company after the rice is harvested in December. Tobacco is a crop whose water input must be controlled throughout the growing period, because absorption of excess water produces poor quality leaves. This makes tobacco particularly suitable in areas where water is in short supply or where water is available only during a short period after the rice harvest. The crop is hand-irrigated for the first 3–4 weeks, using water from shallow wells.

Chili after rice

In certain areas of Ubon Ratchathani Province, chili is planted in December, after harvesting the rice crop. It is hand-irrigated with water from shallow wells.

Tomato after rice

Tomato is planted under the supervision of a private company for hybrid seed production. In general, tomatoes are planted in November–December, after harvesting the rice. They are hand-irrigated using water from small farm ponds constructed in paddy fields to store water during the rainy season. This cropping pattern is practiced in certain areas of Khon Kaen Province.

Research for Development of Improved Systems

Because most of the rice production areas in Northeastern Thailand still depend on rainfall, rice-based cropping systems under rainfed conditions have been evaluated in numerous studies.

Field crops before rice (upper paddy)

The upland crops mungbean, cowpea, peanut, soybean and sorghum have been tested before rice transplanting in Khon Kaen Province. The yield of these field crops was highly variable, from field to field and from year to year, depending on rainfall distribution and drainage management in the upper paddies. The double-cropping system worked well in one year, when the first rain was light but with no drought period, but gave poor yields in another year, when drought occurred (Table 1), particularly at the flowering stage of crop growth. In addition, it gave a poor yield when the early rains were heavy, because the crops suffered from temporary waterlogging. The most reliable results were obtained by early planting (from the last week of April to the second week of May) of mungbean and cowpea, which are short-duration crops, usually maturing before the drought period and flooding events of July–August (Polthanee et al. 1982; Polthanee 1988; Vichienson et al. 1992). Efforts to develop a drainage system by ridging to eliminate flooding were not successful because most soils are sandy in texture.

Table 1. Drought period in Khon Kaen Province, 1989–94.

Year	Month	Duration
1989	13 July–4 August	3 weeks
1990	13 June–4 July	3 weeks
1991	4 June–2 July	4 weeks
1992	16 June–7 July	3 weeks
1993	30 July–22 August	2 weeks
1994	1 July–2 August	4 weeks
1995	nil	nil

In the existing double cropping that was mentioned earlier, field crops are commonly planted before rice in May. Early planting in February–April is usually not successful because the plant may die at seedling stage during the period before the wet season due to the deep soil water table in the paddy areas. In general, most of the paddy areas in Northeastern Thailand have a deep soil water table.

Field crops before rice (lowland paddy)

Upland crops such as mungbean, cowpea, soybean, peanut and sorghum were tested in farmers' fields in Khon Kaen Province. The yield of field crops planted before rice was highly variable, from field to field and from year to year, similar to the yields obtained in the upper paddies (Polthanee et al. 1982; Polthanee 1988). However, in the lowland paddies flooding occurred earlier and for longer than in upper paddies and early planting of short-duration crops such as cowpea (for green pod) and baby corn is possible.

Field crops after rice (upper and lowland paddy)

Field crops such as peanuts, mungbean, cowpea, soybean and sorghum were tested after harvesting rice both in upper and lowland paddies in farmers' fields in Khon Kaen Province. The objective was to determine how to take advantage of residual soil moisture at the end of the rainy season. Several seeding methods were tested, including sowing with and without land preparation, direct seeding in rice stubble and broadcasting seed before rice harvesting. None of the crops or seeding methods produced satisfactory yields. The seeds germinated and grew well at first, but the plants later died or produced almost no yield because of insufficient soil moisture at the end of the growing period (Polthanee et al. 1982; Polthanee 1988). Because the soil water level at the end of the wet season goes down quickly, shallow groundwater does not contribute to soil moisture in the root zone during later stages. Early planting of short-duration crops such as mungbean in October is possible after rice harvesting, because residual soil moisture seems to be sufficient for crop growth for two months as shown for castorbean in Figure 7.

Implications for Rice Cultivar Requirement

Upland crops before rice

The key to success in the use of upland crops before rice is to harvest them for vegetative parts instead of grain. This is because in Northeastern Thailand the

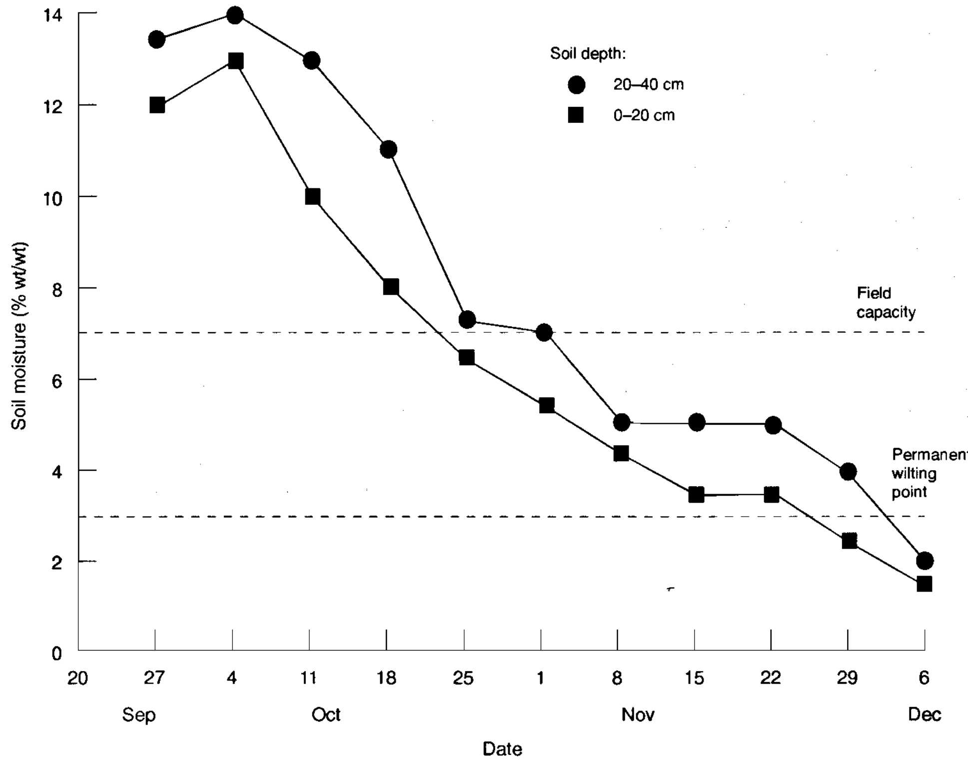

Figure 7. Soil moisture during growth of castorbean in upper paddy (farmer's field, Khon Kaen Province) (Polthanee and Ta-un 1995).

important climatological factors during the period before rice growth are drought at the vegetative stage and excessive wetness during the stage from flowering to maturity. To obtain an economic yield, the vegetative crops may need to be tolerant to waterlogging and require a reasonably long growing period.

If the crop is to be harvested late (e.g. in August), rice cultivars that can be transplanted this late but still produce high yields are therefore required.

Upland crops after rice

The important stress factors in the upland crops planted after rice are drought and high temperature. Thus, quick-maturing crops have been observed to adapt better to cropping after rice. Early planting also minimises the exposure of crops to acute stress late in the growing season. Short-duration, photoperiod insensitive rice cultivars that are harvested in October are therefore needed. Early planting of the field crop after rice may be successful by following direct-seeded rice planted early in the season. Therefore, rice cultivars that are suitable for direct seeding may be a key for successful double cropping. For example, early seedling vigour, combined with weed and drought tolerance, may enable the rice to remain competitive.

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Processes Determining Crop Yield

D.W. Puckridge*

Abstract

Yields in tropical rainfed rice fields average less than 2.4 t/ha, even though solar radiation in the wet season is adequate for yields of over 5 t/ha. Rainfed rice fields have uncertain water supply, and yields are usually far below the potential. Many breeders consider that the ideotype approach (design of specific characteristics) offers no real advantage for yield improvement, but at least a conceptual ideotype is necessary in optimising the design of phenotypes to make efficient use of the environment. The predominant yield potential improvements so far have been in the patterns of partitioning and the timing of development, not in the efficiency of the major metabolic and assimilatory processes. Convincing evidence of improvements for photosynthesis, respiration, translocation or growth rate is lacking. Increase in harvest index in cereal crops has been confined to stem shortening and to the reduction of non-ear-bearing tillers. Although the ideotype approach and selection of traits on physiological evidence are not considered to have made much progress, similar problems are apparent with empirical selection. The problem is not that either approach is wrong — it is that we do not have enough manipulative skills to lift the yield potential. Rather than abandoning either approach, more input and integration is necessary.

THIS paper gives a very brief review of some selected literature concerning our knowledge of the main processes determining crop yield, and some suggestions on how these might be related to grain production in rainfed environments. The perspectives of the single plant and the plant community are considered, along with the realisation of yield potential in the field. An outline of the main topics is given in Figure 1. Much of the content of this paper is based on the comprehensive 500-page review of over 2000 references on crop evolution, adaptation and yield by Evans (1993a). A summary of what appear to be his main conclusions is presented in Table 1.

Evans (1993a) stated that there is no indication that the genetic yield potential of any of the major crops is reaching its limit, and that it might be considered that physiological research would identify plant traits that would enable plant breeders to make more rapid progress in yield improvement.

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Yield potential, defined as the grain yield obtained when growth is not limited by water, nutrients, or pests, is determined by varietal characteristics and climatic variables such as temperature and solar radiation during the growing season. Thus, crop yield potential differs by location, and at the same location it differs by year and season (Kropff et al. 1994).

In assessing the requirements for solar radiation, Yoshida (1981) suggested that the right cultivar and good management could achieve a yield of 5–6 t/ha during the wet season. The yield potential of current high-yielding cultivars grown under the best conditions in the tropics is 10 t/ha during the dry season and 6.5 t/ha during the wet season (Khush 1995b). In the 28 years since IR8 was released, rice yield potential has remained constant (Peng et al. 1994).

Over 50% of rainfed lowland rice areas are subject to drought, or have soils with potentially major fertility constraints. Modern cultivars and technologies have to date been adopted only in the highly favourable areas with good rainfall distribution. Due to the harshness of the environment, the productivity of rainfed lowland systems remains low, with average yields of approximately 2.3 t/ha overall (Zeigler and Puckridge 1995).

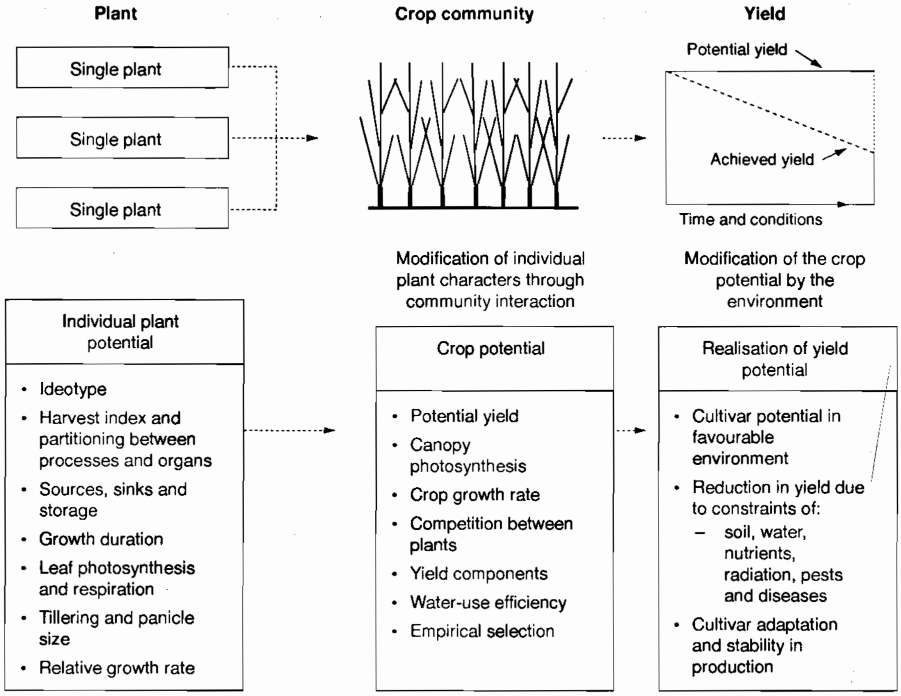

Figure 1. Topics covered in this paper and some relationships between single plants and communities and between potential yields and achieved yields.

Evans (1993a) and Bingham and Austin (1993) concluded that over the past 50 years or so, about half the increase in crop yield is attributable to plant breeding, and half to improved agronomy and management. Since 1950 in the U.K., for instance, a series of new cultivars matched by advances in agronomy (notably in the application of nitrogen (N) fertiliser, grass weed and disease control) have led to a threefold increase in the national average yield of wheat, from 2.5 to 7.5 t/ha. Bingham and Austin suggested that the yield potential of cultivars recently marketed or in national wheat trials points to plant breeding as having more to contribute to future yield increase than does agronomy, and that agronomic practices are now probably close to optimum for yield.

Marshall (1991) considered that there are two ways commercial yields can be increased by plant breeding. These are directly (by increasing yield potential above that of standard cultivars in the same environment), or indirectly (by genetically removing or overcoming biotic or abiotic constraints on crop production).

Pre-green revolution (transplanted) rice cultivars were tall and leafy with weak stems and had a harvest index (ratio of dry grain weight to total dry matter) of 0.3. They tillered profusely, grew excessively tall, lodged early, and yielded less when nitrogenous fertiliser was applied (Khush 1993). In contrast, rice cultivars such as IR8, with high yield potential and greater responsiveness to applied N, had short sturdy stems and leaves that were erect, short, narrow, thick, and dark green. Convinced of the advantages of this new plant type, rice breeders initiated crossing programs to develop short-statured cultivars (Khush 1993).

Mackill et al. (1996) suggested that the plant design, or ideotype, concept is best suited to irrigated rices, and that the traits associated with high yields under irrigated conditions are less important under rainfed lowland conditions. The rainfed rice systems share one major characteristic: uncertain moisture supply. Fields may have too much water, too little water or both within the same cropping season. This uncertainty is the basis upon which resource-poor farmers must make decisions on investment of scarce resources, and the degree of risk they are willing to take. There is a need to minimise their exposure to risk by making available cultivars with more stable and responsive yields (Zeigler and Puckridge 1995).

Table 1. Possible contribution of various factors to potential yield of cereal crops (extracted from Evans 1993a).

Potential yield

About half the increase in potential yield is attributable to ***plant breeding*** and half to improved ***agronomy*** and management.
There is no indication that the genetic yield potential of any of the major crops is reaching its limit.

Adaptation

The adaptation of crops to harsh environments has depended more on changes in the ***length and timing of their life cycles*** than on changes in ability to tolerate such environments.

Partitioning

Partitioning at the organ level has been ***central to crop improvement.*** As we approach the limits to ***harvest index***, we will need greater insight into the factors which control partitioning.

Crop growth rate (CGR)

The maximum CGR of crops ***does not seem to have been increased by selection*** so far. However, growth under unfavourable conditions and duration and rate of photosynthesis and growth after anthesis have improved.

Relative growth rate (RGR)

When comparisons are made under standard conditions, there is no evidence that crop improvement has been accompanied by an increase in RGR.

Sources and sinks

There is no clear evidence of a marked imbalance between source and sink for modern crops. Further increases in yield potential will depend on coordinated increases in both source and sink capacities.

Leaf photosynthesis

There has been no increase in maximum CO_2 exchange rate per unit of leaf area (CER) with increase in yield potential for many crops, including rice.

Canopy photosynthesis

Unlike single leaf photosynthesis canopy photosynthesis ***often bears a close relationship to yield.*** In the early stages of crop development, canopy photosynthesis is more closely related to leaf area growth than to single-leaf CER.

Respiratory losses

Growth respiration (photorespiration) is relatively independent of environmental conditions or cultivar differences, and is unlikely to be improved by plant breeding. Maintenance respiration (biomass) may have some scope for selection.

Harvest index (HI)

In rice the increase in HI from 0.36 to more than 0.5 largely accounted for the rise in yield potential. ***Increase in HI seems to have been confined to stem shortening and to the reduction of non-ear-bearing tillers.*** Other organs and reserves have not been conspicuously reduced. Many mechanisms are involved. Further rises in yield and HI are likely to require a coordinated increase in the duration of both grain growth and leaf photosynthesis.

Yield components

There are many paths to high yield. Because they are determined sequentially, the yield components often behave in a compensatory manner.

CONCLUSIONS

The predominant yield potential improvements have been in the patterns of partitioning and timing of development, not in efficiency of major metabolic and assimilatory processes. There is no convincing evidence of improvements in photosynthesis, respiration, translocation or growth rate.
Empirical selection is an extremely powerful agent of change, but ***selection by design may yet prove to be even more powerful*** when our understanding of the physiology of crop yield is more comprehensive than at present. The genetic variation in adaptive responses to soil and climatic conditions in the world's gene banks is little known relative to that in resistance to pests and diseases, but it may be the most important genetic resource of all.

In rainfed crop environments the yield potential is seldom reached. For wheat in South Australia, for example, the yield potential of the best available spring cultivars is of the order of 8 t/ha, but farm yields average less than 2 t/ha and seldom exceed half the potential yield (Marshall 1991). Therefore, cultivars considered most likely to maximise average yields and profits were those that perform better in the more favourable years.

The question then is: which plant processes or morphological traits can contribute to higher yields, and how can they be included in a plant breeding program? There are many doubts about how this can be done. Whan et al. (1993) stated that apart from the manipulation of major genes governing plant structure and phenology, physiology has had little impact on developing new cultivars because breeders have not been convinced of the value of these physiological traits to improve yield. On the other hand, Loomis (1993) suggests that plant breeders do not receive sufficient training in physiology.

Ideotypes

As early as 1968, Donald suggested that the concept of crop ideotypes cannot be tested within the framework of conventional breeding programs, and that only the conscious pursuit of ideotypes can lead to potentially high yield in novel environments. Marshall (1991) stated that the basis of Donald's philosophy was that, from known principles of physiology and agronomy, it should be possible to design a plant capable of greater production than existing types, but indicated that the development of model plants or ideotypes has been adopted by relatively few programs as a major breeding philosophy, and that most breeders have formed the view that the ideotype approach offers no advantage in terms of yield improvement — breeders may have reached this conclusion either because of perceived difficulties or because of disadvantages with the ideotype approach, or perceived advantages of alternative approaches.

Hamblin (1993) concluded that the ideotype approach has been more successful for identifying characters related to high yield in high-input, low-stress environments, and has been less successful in environments with stress, particularly those involving drought stress.

In contrast, Evans (1993b) stated that successful plant and animal breeders have always had specific features in mind when making their selections, and Loomis (1993) stated that at least a conceptual ideotype is necessary to optimise the design of phenotypes that can make efficient use of the environment.

Marshall (1991) considered that the primary practical problems in developing ideotypes are the lack of the appropriate genetic diversity, the strong interrelationships among individual traits of importance to the ideotype breeder (such as compensation among plant parts which may hinder progress in cultivar development) and the increase in the number of traits for selection. Marshall also stressed the difficulty in establishing, for any given environment, that a particular character, even a well-studied qualitative trait such as the presence or absence of awns, is unambiguously advantageous. This difficulty is greatly exaggerated for quantitatively varying traits such as leaf length, width, thickness, specific weight and angle.

Progress towards crop ideotypes is constrained by the lack of knowledge of adaptive controls of growth and development, for example, and most basic metabolic systems (e.g. photosynthesis, respiration, biosynthesis) appear to represent 'efficient evolutions' with little room for further removal of slack in the use of carbon (Loomis 1994).

Breeders 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 (Mackill et al. 1996), and breeders can select for only a very limited number of traits in any segregating population. Marshall (1991) gave an example of two parental cultivars differing by 20 loci governing traits of interest to the breeder. If breeders select for 10–15 ideotype characteristics plus the usual array of disease resistances and quality, then 20 loci are in fact a modest number. Assuming all loci are independent, then less than one plant in a million in the F_2 of a cross between such parents will carry the desirable allele at each of the 20 loci.

Nevertheless, this is not too different from standard breeding, where large populations are necessary for progress. If several traits are important, on what basis will the breeder decide which to include and how will they be incorporated in an empirical breeding program?

Since the development of the IR8 plant type, only marginal improvements in the yield potential of rice have occurred, because rice improvement efforts were directed towards incorporation of disease and insect resistance, shortening the growth duration, and improving grain quality (Khush 1995b). However, the International Rice Research Institute (IRRI) now has a specific ideotype for irrigated rice. A breeding effort to develop a 'new plant type' became a major core research project of the IRRI work plan (Peng et al. 1994). The major components desired are low tillering capacity with 3–4 panicles per plant when direct-seeded; no unproductive tillers; 200–250 grains per panicle; 90–100 cm tall; sturdy stems; vigorous root system; multiple disease and insect resistance; 110–130 days growth duration; harvest index of 0.6; and a target yield potential of 13–15 t/ha.

Harvest Index and Partitioning

Yield is a function of the total dry matter or biomass, and the harvest index (the grain to straw ratio). Therefore yield can be increased by enhancing either the total biomass production or the harvest index, or both. The harvest index of modern high-yielding rice cultivars is around 0.5, which means that the biomass comprises 50% grain and 50% straw. Under optimum tropical conditions these cultivars can produce 20 tonnes of biomass per ha; thus their yield potential is 10 t/ha. To increase the yield potential to 13 t/ha, the harvest index needs to be raised to around 0.6 and the biomass to 22 t/ha (Khush 1995b).

Harvest index (HI) is an expression of partitioning within the plant. Partitioning of assimilates can be between leaf area growth and higher carbon exchange rate (CER), between photosynthesis assimilation and respiratory loss, between sugar and starch formation, between carbohydrates and other compounds, or between the various organs of the plant. Partitioning at the organ level has been central to crop improvement (Evans 1993a).

Increase in HI seems to have been confined to stem shortening and to the reduction of non-ear-bearing tillers (Evans 1993a). Many mechanisms appear to be involved, and further rises in yield and HI are likely to require a coordinated increase in the duration of both grain growth and leaf photosynthesis. As we approach the limits to HI, we will need greater insight into the factors that control partitioning (Evans 1993a). Selection for specific changes in partitioning (larger/smaller, sooner/later) must affect the rest of the plant through feedback (Loomis 1994).

Changes in the ratio of grain to straw associated with short stature of modern wheat cultivars in the U.K. were the most significant factors for improved yields (Bingham and Austin 1993). Bingham and Austin tested four pre-1908 cultivars, which had a mean yield of 5.65 t/ha, against five modern cultivars that gave a mean yield of 9.36 t/ha, an increase of 66%. There was little difference in biomass (18.36 compared to 17.07 t/ha), so the gain in yield was almost entirely due to diversion of the plant's resources from the straw, with a large increase in HI. Fischer (1993) suggests that further reductions in stem investment for wheat may be counterproductive once the optimum plant height of 70–80 cm is achieved.

Mackill et al. (1996) suggested that many rainfed lowland farmers prefer traditional cultivars because they are taller (usually > 140 cm) than modern semi-dwarf cultivars (< 120 cm). This is contrary to the need for increasing HI. They also stated that breeders and farmers often find different plant characteristics appealing, but consider that some of the base characteristics needed in all rainfed lowland cultivars are intermediate height, sturdy culms, moderately long, erect leaves, moderate to high tillering, large panicles with many grains, seedling vigour, and early vegetative vigour. On the other hand, Surapong Sarkarung (IRRI-Bangkok, personal communication) has reported very good plant types with intermediate tillering, 6–8 productive tillers per plant when transplanted, and very dense panicles due to the introduction of new genetic backgrounds from South America.

Optimisation of partitioning is a key feature in the design of ideotypes. It is particularly important to achieve a smooth progression through developmental phases of the crop's life cycle, and it will become increasingly important to give greater attention towards fine-tuning of the fit between genotype and the environment (Loomis 1994).

Growth Duration

For most farmers growing rainfed lowland rice, growth duration (or flowering date) is the most important characteristic differentiating rice cultivars and their adaptation to particular growing conditions (Mackill et al. 1996). Most traditional cultivars in tropical and subtropical Asia mature in 160–170 days and many are photoperiod sensitive, whereas IR8 and subsequent irrigated cultivars such as IR20 and IR26 mature in about 130 days, and IR36 in 110 days (Khush 1995a). Because of higher growth rates at earlier stages, the short-duration cultivars such as IR36 are able to produce approximately the same biomass in 110–115 days as the medium-duration cultivars do in 130–135 days.

Very short-duration cultivars are not suitable for most rainfed conditions because they are sensitive to delayed transplanting; they mature during periods of heavy rainfall, which makes proper harvesting and drying difficult; they tend to be short and compete poorly with weeds; and they are not specifically adapted to the stresses that are common in rainfed lowlands, particularly drought (Mackill et al. 1996). The authors have suggested that short-duration cultivars would probably be adopted more widely in rainfed areas if efforts were stepped up to develop cultivars that are adapted to rainfed lowland conditions. Sarkarung (personal communication) reports success in producing such types by selection in situ for specific conditions.

In many irrigated areas the key to success of short-duration cultivars was the selection of genotypes with rapid vegetative vigour at early growth stages (Khush

1993). Such cultivars are more competitive with weeds, and because the field duration is 20–25 days shorter, they use less irrigation water. Per day productivity is much higher for the short-duration cultivars because they produce the same amount of grain in fewer days (Khush 1993).

Total biomass production is higher in cultivars with longer growth duration, but is accompanied by a sharp decrease in HI. Biomass is increased with greater N assimilation. However, increased biomass production in the vegetative stage from greater N uptake may not be reflected in the final biomass due to a considerable increase in respiratory losses during the ripening stage (Akita 1988, quoted by Akita 1994).

Grain-filling duration was not considered in the IRRI new plant ideotype, and thus the source of the increased assimilate for a higher yield potential is not clear (Kropff et al. 1994). The effective grain-filling period must increase from the present 25 days to 38 days to produce the required dry matter for a yield of 15 t/ha. A longer duration of green leaf area and active canopy photosynthesis is needed to meet the need of a longer period of effective grain filling. The authors state, however, that there is no evidence that direct selection for a larger panicle size will indirectly lead to a longer grain-filling duration.

The basic parameters that must be modified to achieve a major increase in yield potential of rice grown in tropical environments are: increased sink size (i.e. more spikelets/m^2), a longer period of effective grain filling, and a longer duration of green-leaf area and active canopy photosynthesis to match the increase in grain-filling duration (Kropff et al. 1994).

Photosynthesis and Respiration

Under favourable conditions, light and temperature are the main factors determining crop growth rate. A plant community with vertically oriented leaves gives better light penetration and higher carbon assimilation per unit of leaf area. Droopy or horizontal leaves increase the relative humidity and decrease the temperature inside the canopy due to reduced light penetration and air movement (Tanaka 1976 and Akiyama and Yingchol 1972, quoted by Peng et al. 1994).

Compared to other C-3 (photosynthetic pathway) species, rice has a relatively higher net photosynthesis rate per unit of leaf area, with values to 4–5 g carbon dioxide per m^2 per hour, and leaf photosynthetic rate is well correlated linearly or curvilinearly with leaf N (Yoshida 1983).

In simulations, leaf N status had a greater impact on yield potential in the dry season (DS) than in the wet season (WS). The maximum rate of carbon dioxide assimilation at high radiation levels depended on the leaf N concentration, and reasonable simulations were obtained only when the actual specific leaf N for each of the treatment seasons was also included as input. However, preliminary analyses with the ORYZA1 model indicated little gain from changing the vertical N gradient in the canopy because the extinction coefficients are similar for N and light distribution in the rice canopy (Kropff et al. 1994).

Several options have been proposed to increase the maximum rate of net assimilation by the rice plant, including modification of physiological processes such as suppression of photorespiration and reduction of maintenance respiration, although these propositions are highly speculative (Kropff et al. 1994). Loomis (1993) concluded that the basic biochemical processes, including those of photosynthesis, are generally both efficient and genetically conservative, leaving little room for improvement.

Leaf photosynthesis is the main source of carbohydrates, but Evans (1993a) notes that there is no evidence that higher-yielding cultivars were superior to wild species or old cultivars in photosynthesis rate. For crop after crop, there has been no increase in maximum CER with increase in yield potential. For many crops, including rice, the highest CERs were recorded for the wild species, and in many instances the comparisons among cultivars revealed a negative relation between CER and yield. An important paradox is that there is substantial variation in CER within most crops that is heritable and can be readily selected. The very crux of the paradox is that yield is favoured by environmental improvement of CER but not, *so far*, by genetic improvement of individual leaf rates. Increases in CER associated with higher irradiance or carbon dioxide levels generally result in increased yields, but genetic increases in CER do not.

Canopy photosynthesis, however, unlike single-leaf CER, often bears a close relationship to yield. In the early stages of crop development, canopy photosynthesis is more closely related to leaf area growth than to single-leaf CER. In later stages of crop development, varietal differences in canopy photosynthesis may reflect differences in demand rather than be the cause of differences in yield (Evans 1993a).

For several crop species, longer green leaf duration during grain filling has been a major achievement of breeders in the past decades (Evans 1990, quoted by Kropff et al. 1994). The duration of canopy photosynthetic activity can be likewise prolonged by fertiliser N application later in the growing season, and by improved crop protection against endemic late season diseases. The mechanisms that govern leaf senescence, however, are poorly understood (Kropff et al. 1994). It is also predicted for high yield levels that if the panicle was lowered to 40% of canopy height, canopy photosynthesis would improve by 25–40% (Kropff et al. 1994).

Respiratory losses account for about half the carbon fixed in photosynthesis, while photorespiration reduces the amount of carbon initially fixed by C-3 crops in photosynthesis by a further 15–20%. Many attempts have been made to reduce the photorespiration losses, but so far less effort has been given to the search for reduction in 'dark' respiration, possibly because of the view that, as the product of long evolution, respiration is already a highly efficient process. Growth respiration (photorespiration) is relatively independent of environmental conditions or cultivar differences, and is unlikely to give much scope for improvement by plant breeding (Evans 1993a).

Maintenance respiration (related to biomass) may, on the other hand, have some scope for selection, possibly at the expense of adaptation to stress (Evans 1993a). While there is evidence of genetic variation in maintenance respiration, the magnitude of such differences is small (Gifford et al. 1984, quoted by Kropff et al. 1994). One component of maintenance respiration which might be manipulated without adverse effect is the energy consumption for remobilising protein. A reduction in the energy required for remobilising proteins during leaf senescence would help maintain net assimilation and root activity during later growth stages (Akita 1994).

Growth Rates

Relative growth rate (RGR), the exponential rate of increase in the mass of plants, falls as plant size and absolute growth rate increase. While differences in RGR do occur, there is no evidence that crop improvement has been accompanied by an increase in RGR when comparisons are made between seedlings over the same size range and under standard conditions (Evans 1993a).

Crop growth rate, the increase in dry weight of the crop per unit ground area per unit time, integrates the gains by photosynthesis and the losses by respiration, the compensatory effects of leaf area and photosynthesis rate, and the trade-offs between the geometric effects of crop height, leaf inclination and shape. Crop growth rates of different genotypes can be validly compared only when crop canopies are fully intercepting radiation. Growth under unfavourable conditions has been improved, and also the duration and rate of photosynthesis and growth after anthesis, but crop growth rates do not seem to have been increased by selection so far (Evans 1993a). The maximum crop growth rate of rice is around 30–36 g/m^2 per day in the Philippines (Yoshida and Cock 1971, quoted by Peng et al. 1994).

Sources, Sinks and Storage

In crop production both a source of carbohydrates and a sink (grain) for carbohydrates are needed (Kropff et al. 1994). The source is formed by chlorophyll-containing tissues, mainly in the leaves. The amount of dry matter stored in the grains (the sink) comes from stem reserves produced in the vegetative phase, and assimilates produced in the grain-filling period. Thus the source for grain production is determined by three components: the amount of stem reserves allocated to the grains; the rate of dry-matter production in the grain-filling period; and the length of the grain-filling period.

Yield depends on how resources of carbon, water and nutrients are used over the life of the crop and thus on the order and pattern of growth of carbon sources and sinks. Loomis (1993) wrote that once carbon is partitioned in growth it generally cannot be employed again. If a first use of carbon is non-optimal in some sense (for example, for excessive leaf area), the majority of that carbon is lost from the train of yield accumulation, and water transpired in its production will not be available to support photosynthesis later in the season. Loomis suggests that where water and nutrients are non-limiting, the largest yields are generally obtained through rapid attainment of full light interception, so that the crop is source limited (sink dominated) for most of its growth cycle.

Fischer (1993) states that modern wheat cultivars appear to be sink limited with respect to grain filling and final kernel weight, having unused photosynthetic capacity, while Setter et al. (1994) suggested that, for rice, source limitation is certainly relevant in the WS, whereas a sink limitation may exist in the DS.

On the contrary, Evans (1993a) suggested that feed-forward effects of source on sink indicate that source and sink are not independent entities. Feed-back effects of storage capacity on photosynthetic rate and duration also highlight their mutual independence. The source at one time feeds forward to determine the later sink, while sink activity feeds back to modulate the photosynthetic source. Clear evidence of a marked imbalance between source and sink under conditions to which modern crops are adapted has not been found. Some spare capacity on both sides, for which there is evidence, is needed so that yields are not too sensitive to environmental conditions. Therefore, further increases in yield potential will depend on coordinated increases in both source and sink capacities.

Yoshida (1981) estimated that translocation of pre-anthesis assimilates were equivalent to 2.0 t/ha of grain when the yield was 7.8 t/ha. Setter et al. (1994) report that for rice cultivars grown at IRRI, typical values for accumulated shoot carbohydrates range from 10 to 15% of dry weight during the WS, and 15 to 25% during the DS, while in temperate climates values for total shoot carbohydrates can be 30–40% (quoting unpublished data of R.L. Williams and L. Lewin, New South Wales Agriculture, Australia), presumably due to factors such as the greater radiation per day and lower night temperatures. Rice appears to have a greater capacity to utilise accumulated carbohydrates than wheat.

Yield Components and Panicle Size

Modern high-yielding rice cultivars have many more panicles than the traditional rice cultivars they replaced. There is a limit, however, to how far panicle number can be increased. Additional tillers become unproductive and lead to excessive leaf area index and vegetative growth, and a higher percentage of unfilled grains (Peng et al. 1994). Eliminating unproductive tillers should allow more solar energy and mineral nutrients — particularly N — for growth of productive tillers, but the magnitude of the potential contribution to yield has not been quantified. Peng et al. report that in a rice crop yielding 10 t/ha of grain, up to 70% of the tillers were unproductive, but they represented only a small fraction of total primary production.

There are many paths to high yield, and because yield components are determined sequentially, they often behave in a compensatory manner (Evans 1993a). A reduction in filled spikelets per panicle with greater plant density appears to limit potential yield gains from higher panicle numbers. Hence, to achieve increased sink size, reduced panicle number in low-tillering plant types must be compensated for by a relatively greater increase in panicle size (Peng et al. 1994).

For rainfed lowland rice no firm data are available on optimum tiller number, though many widely grown rainfed lowland rice cultivars compensate for lower tiller number with large panicle size. Breeding for large panicles has thus been seen by many rainfed lowland rice breeders as a more important objective than breeding for abundant tillering (Mackill et al. 1996). The low tillering trait was hypothesised to be associated with larger panicle size by Peng et al. (1994) and became a trait selected for IRRI's new high-yielding irrigated plant type. In recent studies, heavy panicle type cultivars were found to have a higher accumulation rate of preanthesis non-structural carbohydrate (Akita 1994). Large panicle size is not necessarily associated with low tillering; the cultivar Mahsuri, for example, can have many large panicles (Surapong Sarkarung, personal communication).

Water-Use Efficiency

Drought resistance and tolerance will be considered in detail by other authors in this workshop. Productivity of a crop grown under moisture stress will be less than its productivity when it is grown with ample supplies of soil moisture; therefore, biological immunity to the effects of drought is not a possibility (Quizenberry 1982). On the other hand, a small quantity of water either saved by the plant through reduced transpiration or more efficiently used in plant photosynthesis can mean a relatively large increase in economic yield, and the amount of improvement needed in water-use efficiency does not have to be large to have a considerable influence (Quizenberry 1982).

Drought stress is less damaging during the vegetative phase than during the reproductive phase. Unlike leaf tissue, rice panicles have no mechanism for inhibiting water loss and thus for stabilising water content and water potential (Mackill et al. 1996). Flowering of rice also takes place over a very short time period, and plants have no further opportunity to compensate for reduced seed set.

Many adaptive traits have been proposed for use in breeding programs for drought-prone areas.

Unfortunately, few hard data are available about the contributions of these traits to drought resistance (Mackill et al. 1996). Comparisons are difficult. For example, the apparent differences in water-use efficiency of an upland rice over IR20 and IR36, which was a result of differences in rooting depth, disappeared when dry-matter production of the cultivars was compared on the basis of water used (Puckridge and O'Toole 1981).

Deep root systems are often mentioned as a factor in drought resistance, but as Quizenberry (1982) pointed out, unlike mechanisms that reduce water use or increase metabolic efficiency, the development of deep or extensive root systems can only occur through the use of part of the photosynthate produced by the plant, with a compensating reduction in other dry weight. A large part of the crop photosynthate goes to the root system. For example, Martin and Puckridge (1982) calculated that the total amount of fixed carbon translocated below ground by field-grown wheat over the growing period was about 30% of the total carbon fixed.

Empirical Selection

Among many reasons why the rise in yield potential of cereal crops has been sustained so far, Evans (1993b) suggests that the first is the great integrating power of empirical selection (based on observation or experiment). That is especially significant with a characteristic like yield potential, to which many physiological processes contribute and for which they must act in a balanced and coordinated way — much more than, for example, in vertical resistance to pests and diseases. The second is the reciprocation between plant breeding and agronomic innovation.

Substantial benefits may yet be gained by further research in 'defect elimination' (Marshall 1991), but although empirical selection is an extremely powerful agent of change, selection by design may yet prove to be even more powerful when our understanding of the physiology of crop yield is more comprehensive than it is at present (Evans 1993a).

Evans (1993b) believes that empirical selection for yield potential continues to be highly effective in the major crops despite the diffuse and poorly defined nature of the characteristic and the frequent claims that an entirely new approach is needed to sustain progress, but there are limitations. For example, improvement in grain yield by increasing early vigour, total biomass production and grain growth is limited because simple selection techniques are not available (Whan et al. 1993). Seed and seedling vigour can give an effective early start, particularly in competition with weeds, but do not necessarily contribute to yield in themselves. TeKrony and Egli (1991) concluded that for grain crops a yield response to seed vigour occurs only when plant densities are lower than the density required to maximise yield, or in later than normal planting.

Yield Stability and Adaptation

A cultivar usually has a stable yield when it is able to resist the environmental stresses that limit productivity (Mackill et al. 1996). Traditional rice cultivars are noted for their high yield stability, although that quality is often associated with low yield potential.

The adaptation of crops to harsher environments has depended more on changes in the length and timing of their life cycles than on changes in ability to tolerate such environments (Evans 1993a). Drought stress, for example, often has its greatest impact on yield when it occurs during meiosis and anthesis. Both *escape* (timing) from and *avoidance* (ability to maintain high turgor) of water stress involve many components and have contributed a great deal to the adaptation of crops to dry environments. It is less clear to what extent greater *tolerance* of dehydration (ability to sustain less injury when turgor is lost) has also contributed to adaptation (Evans 1993a).

The wealth of genetic variation in adaptive responses to soil and climatic conditions conserved in the world's gene banks is little known and less used relative to that in resistance to pests and diseases, but it may yet prove to be the most important genetic resource of all (Evans 1993a)

Constraints to Realising Yield Potential

A main conclusion is that production is limited by the environment. Yet we seldom quantify seasonal variation in the environment. Most models of the growth of the rice plant are for irrigated conditions, and their main inputs include radiation, development of leaf area, tillering, nutrient uptake and photosynthetic capacity to fill grains. These models are less suitable for rainfed crops because they do not predict environmental conditions, particularly random events such as drought and flood.

Modern rainfed rice cultivars have the potential to produce high yields of grain under favourable conditions. However, the realisation of that potential is often limited by constraints such as poor establishment, drought, lack of fertiliser, weeds, flood, pests and diseases. Despite this, detrimental effects in one stage of growth can be modified to a limited extent by compensation of plant parts at subsequent stages.

In order to estimate the effects of various conditions and constraints on realisation of the yield potential of rice, a very simple spreadsheet 'model' was developed. The aim was to visualise cumulative effects of different environment stresses. Inputs into the spreadsheet are estimates of the amount by which different events during the growing season are likely to change stem numbers or panicle sizes.

The spreadsheet (Table 2) starts with an estimate of potential numbers of stems and potential weight of grain per panicle, and then includes the researcher's sequential estimates of how the potential will be reduced or increased by events. Coefficients given to each 'event' (such as establishment, drought, tillering, disease, etc.) are estimates of how much the stem number or panicle weight is or is likely to be affected by that event. Note that there are no physiological inputs, and that values for coefficients are best guesses from field observations and subject to change. For example, poor soil preparation and lack of rainfall one year may result in only 70% establishment, so the coefficient is 0.7 and an initial seed rate of 400 seeds/m^2 would give only 280 plants/m^2. That number is still sufficient for the potential yield (6.0 t/ha in this example), but drought in that season may further reduce the number of stems by 40% (coefficient 0.6); in another season it may have no effect (coefficient 1.0), or an event may occur more than once in a season. In the example in Table 2, if the potential yield is to be reached, good tillering is needed in step 4 to increase the number of stems. However, the field conditions may only allow increase in stem numbers to $1.3 \times 168 = 218$, and that number will be further reduced by the natural loss of some of these tillers, possibly 40%, leaving only $218 \times 0.6 = 131$. If weed competition further decreases stem numbers by 10% (coefficient 0.9), then only 118 stems produce panicles, and the yield will be low. Similar reasoning and calculations can be applied to events that eventually affect panicle weight.

This is not a true model, but it is a useful way of recording the effect of events during the growth of the crop. It could be considered a digital diary of crop growth and interaction between plant and environment. Researchers can input values after every visit to the field, thus giving an up-to-date assessment of the expected yield for the season, and the relative influence of different events. Research can then be directed to reducing the effect of the constraints identified. The method of calculation can be used for any crop. The main point is that in many cases researchers and breeders do not have a clear record of the events during the season, and are thus unlikely to make a correct interpretation of the results of their work.

Conclusions

Optimal designs for crops and cropping systems must deal on the one hand with great complexity and on the other with the fact that, in agriculture, small differences are important: a 5% change in system performance can be of enormous benefit, yet be very difficult to measure (Loomis 1994).

Evans (1993a) concludes that the predominant yield potential improvements so far have been in the patterns of partitioning and the timing of development, not in the efficiency of the major metabolic and assimilatory processes. Convincing evidence of improvements for photosynthesis, respiration, translocation or growth rate is lacking. Crop yield is the integrated end product of many processes, and focusing on any one of these, however important, is likely to have counterintuitive effects, even when supported by quite comprehensive simulation models.

Crop physiologists have developed some strong relationships between mechanisms and adaptation to drought based on accepted approaches to plant growth and development (Quizenberry 1982), but the plant breeder has, for the most part, failed to utilise these mechanisms. The reasons given include difficulty in measuring the mechanism; lack of convincing evidence to support a relationship with increased productivity; insufficient knowledge about inheritance; poor communication with crop physiologists; and a sense of helplessness associated with the phenomenon of drought.

It can be argued that whole-plant physiology which showed the ideotype approach has failed to provide substantial on-farm benefits via clear guidelines to breeders or through other routes, but plant breeders' efforts to improve yields based on the conventional approach of 'crossing the best with the best and hoping for the best' has similarly been uninspiring (Marshall 1991). Other breeders would contend that parents are selected to complement each other, not the best with the best.

Table 2. Spreadsheet calculations of estimated yield from sequential observations in the field of factors which are expected to reduce the yield below the potential. Potential yield set at 6.0 t/ha from 200 panicles with 3 g grain per panicle, with 400 seeds sown per m^2.

Event	Component affected		Stem/panicle number		Stem/panicle weight		Estimated
	Number	Weight	Coeffic.[1]	Number	Coeffic.[1]	Weight	yield (t/ha)
Soil preparation and establishment							
Establishment (direct sown)	x	–	0.70	280[2]	–	3.00	6.00[3]
Emergence to standing water							
Drought (reduces number, weight of stems)	x	x	0.60	168	1.00	3.00	5.04
Soil fertility (affects tillering and stem size)	x	x	1.00	168	0.95	2.85	4.79
Tillers per plant	x	x	1.30	218	1.00	2.85	6.22
Natural decline in stem numbers	x	–	0.60	131	1.00	2.85	3.73
Weeds	x	x	1.00	131	0.95	2.71	3.55
Insect damage	x	x	0.90	118	0.95	2.57	3.03
Rat damage	x	–	1.00	118	1.00	2.57	3.03
Disease	x	x	1.00	118	0.95	2.44	2.88
Standing water to flowering							
Water depth	x	x	0.90	106	0.95	2.32	2.46
Weeds	x	x	1.00	106	0.95	2.21	2.34
Insect damage	x	x	0.95	101	1.00	2.21	2.22
Rat damage	x	x	1.00	101	0.95	2.10	2.11
Disease	x	x	1.00	101	0.95	1.99	2.01
Cultivar adaptation	x	x	1.10	111	0.95	1.89	2.10
Flowering to maturity							
Compensation for low panicle number	–	x	–	–	–	2.31[4]	–
Conditions during grain filling	–	x	1.00	111	0.95	2.20	2.44
Rat damage	x	x	0.95	105	0.95	2.09	2.20

x = affected; – = not applicable

[1] Coefficients: researcher inputs–number or weight of stems or panicles in the preceding row are multiplied by the coefficient
[2] Greater than 200; therefore still potential yield
[3] Potential yield
[4] (Preceding panicle weight) × (1+ 0.5–0.0025 × preceding panicle number)

Note: Cells in the spreadsheet are linked and change in any cell will affect all values below it except coefficients, which are values assigned by the researcher after observation.

Breeders seeking substantial increases in on-farm yields need to develop new physiological or genetic approaches to increasing yield potential, or make an even greater effort in overcoming constraints on crop production. The identification of genes— or, perhaps more realistically, chromosome segments—which have major effects on crop yields will also offer new opportunities to investigate the physiological basis of these major gene effects (Marshall 1991).

Loomis (1993) suggested that the real message in the failure of physiologists to find additional break-through directions for yield advance may be that none exist outside basic changes in photosynthesis. The merit of physiology is that it can explain, and its greatest failure may be that breeders are not ade-quately educated in crop physiology and ecology. He considered this problem to be complemented by plant-breeding books that omit competition, density, nutrients, morphology, physiology and plasticity from their indices, lumping such matters vaguely under 'genotype-by-environment interaction'.

It appears that the main constraint to increased yield potential under very favourable conditions is the maximum sustainable dry-matter accumulation at a rate of about 300 kg/ha per day, which is governed by the rate of net carbon dioxide assimilation (Kropff et al. 1994). Small yield gains may be possible from increased storage and remobilisation of stem carbohydrate reserves and a further push to increase the HI. Whether an increase in sink size alone will lead to an increase in yield potential remains an issue, but the existing evidence suggests it will not.

It would be useful to identify any common factors underlying the yield advantage of hybrids; even if the conclusion was that each hybrid was higher yielding because of a unique combination of traits, such studies would at least delineate some proven pathways to higher yield which are exploitable by plant breeders (Marshall 1991).

The conclusion of this author was, that although the ideotype approach and selection of traits based on physiological evidence is not considered to have made much progress, it does not mean that these methods have failed. Similar problems are apparent with empirical selection. Each breeder makes selection decisions based on personal impressions, and it is as much trouble to choose between different traits as it is to determine what is important physiologically. The problem is not that either approach is wrong; it is that we do not have enough evidence or manipulative skills to use the appropriate combination of methods to succeed in lifting the yield potential for different environments. Rather than abandoning either approach, more input and integration is necessary.

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Cultivar Improvement for Rainfed Lowland Rice in Thailand

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Abstract

The rainfed lowland rice ecosystem occupies approximately 75% of the total rice area in Thailand. Attempts to improve rice cultivars in the country started in 1910 during the reign of King Rama V, who established the first rice experimental station in 1916. The breeding objective in the early years was grain quality improvement and increasing the yield potential of local cultivars. Through evaluation and selection among collected local variations, a batch of traditional improved cultivars was first recommended in 1935. Currently, the yield constraints for rainfed lowland rice include frequent drought and flood in all regions, the inland saline and sandy soils in the northeast, acid sulfate soils in the Central Plain and coastal acid-saline soils in the south. Rice diseases such as blast and bacterial blight, and insect pests like gallmidge and stem borers, are also major problems. The current breeding objectives are to develop cultivars that are tolerant to adverse environmental conditions and resistant to disease and insects, while maintaining the superior grain characteristics of the traditional cultivars and their appropriate maturity characteristics. Breeding mainly involves hybridisation and selection. Biotechnology is used in an attempt to improve breeding techniques. Past breeding efforts have led to the development of a number of improved cultivars and today 25 cultivars are recommended for farmers in rainfed lowland regions.

BASED on an agroecological system classification, Thailand has four rice ecosystems. Seventy-seven percent of the rice area is rainfall dependent and around 6.8 million ha of rainfed rice is cultivated in the rainfed lowland, upland, deepwater and floating systems. Rainfed lowland is the major rice ecosystem in the country. It occupies more than 6.6 million ha or around 75% of the rice land, but produces only 60% of the total production because the average rainfed lowland rice yield is only 1.75 t/ha (Table 1). The Northeastern Region has the largest area of rainfed lowland rice, with 95% of 4.76 million ha of rice grown under rainfed conditions, producing around 40% of total paddy (Table 2). Rice production in the rainfed lowlands depends on rainfall (both annual total and pattern of distribution). Biotic stresses such as diseases and insects are major problems.

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Yield Constraints in Rainfed Lowland Rice

Drought

Drought is the major problem in rainfed areas. In drought-prone areas, rainfall distribution is bimodal, with a dry spell between the two peaks. Damage from drought may occur at the seedling and tillering stages, and on some occasions the damage is also severe at the reproductive stage. Drought stress is common in the Northern, Northeastern and Central Plain Regions. Although rainfall is abundant in the Southern Region, parts of the rice land, especially light soils, are normally affected by drought.

Flood

Although drought is the most severe problem, flooding can occasionally be devastating. The drought-prone area in the northeast is subjected to submergence from time to time. In the valleys and plains in the north, rice fields are usually flooded after heavy upstream rains. Overflow of the rivers causes floods on the Central Plain, sometimes submerging rice for more than 10 days. In the south, flash floods occur because of poor drainage in low-lying areas. Submergence is observed at different growth stages, but mostly during the reproductive stage.

Problem soils

The economically important soil problems in the rice areas include saline soils, acid sulfate soils and sandy soils. The inland saline soil occurs mostly in Northeastern Thailand, where irrigation is limited. The area is estimated at 2.8 million ha. Sandy soil is also scattered in the northeast; it covers about 1.0 million ha and has very low fertility. The combined effects of drought and salinity on sandy soils make rice yield in Northeastern Thailand very low.

Diseases and insects

Besides the adverse climatic conditions and problem soils, important diseases, such as blast and bacterial blight, and insect pests like rice gallmidge and stem borers are considerable yield constraints in the rainfed lowland ecosystem.

Early Breeding Efforts

Rice improvement in Thailand started during the reign of the King Rama V. The King initiated the first rice cultivar contest in 1910 during the national commercial fair in Bangkok. Such contests were adopted to promote the use of high grain quality rice cultivars through farmer selection. Rice cultivars that won at the contest were collected and tested by the then Farming Department. After that seeds were multiplied and subsequently distributed to the farmers.

The first rice experiment station, Klong Rangsit Rice Experimental Farm, presently Pathum Thani Rice Research Centre, was established in 1916 in the Thanyaburi district of Pathum Thani. As the first step of the rice improvement program, head selections and cultivar yield trials were started with emphasis on improving grain quality and yield. In addition to the normal selection by farmers, a large number of local cultivars were collected and tested. Evaluation indicated the suitability of cultivars for specific conditions. The station has developed many rice cultivars through traditional cultivar evaluation. Pin Gaew, a local selection, was one of the cultivars that won the first prize in the World Grain Exhibition Conference in Regina, Canada in 1933.

Table 1. Estimated rice area classified by ecosystem in Thailand. Main season 1991–92.

Ecosystem	Planted area (million ha)	Production (million t)	Average yield (t/ha)	Planted area (%)
Total	8.83	17.52	2.10	
Irrigated	2.03	5.62	2.84	23.0
Non-irrigated	6.79	11.89	1.87	76.9
lowland	6.64	11.62	1.75	75.3
deepwater	0.11	0.21	1.91	1.2
upland	0.04	0.06	1.59	0.4

Source: Adapted from Centre for Agricultural Statistics (1994)

Table 2. Major rice production by region, Thailand 1991–92.

Region	Planted area (million ha)	Harvested area (million ha)	Production (million t)	Average yield (t/ha)
Northeastern	4.76	4.51	7.67	1.70
Northern	1.95	1.79	4.58	2.56
Central Plain	1.64	1.59	4.33	2.73
Southern	0.48	0.46	0.94	2.03
Total	8.83	8.35	17.58	2.10

Source: Adapted from Centre for Agricultural Statistics (1994)

From the early work of the traditional cultivar development program in 1935, the Klong Rangsit Rice Experimental Farm recommended the first batch of cultivars, consisting of eight of the prize winners (Table 3). In 1936, the other three local selections were added.

Intensive rice-breeding work continued after World War II. In 1947, Thailand became a member of the Food and Agricultural Organisation (FAO) of the United Nations. With the assistance of the United States Department of Agriculture, through FAO, two eminent scientists, a plant breeder and a soil scientist, were sent to Thailand to set up the rice improvement program in 1950. The initial cultivar improvement program aimed to identify the superior cultivars from the material collected from farmers' fields. Breeding methods were concentrated on pure line selection based on the identification of high-yielding cultivars with high grain quality, long, slender grain shape and wide adaptability to local conditions.

The establishment of the Rice Department within the Ministry of Agriculture in 1954 gave a big stimulus to rice improvement. In its Breeding Division, emphasis was placed on rice cultivar improvement and seed multiplication. In 1955, the rice hybridisation and mutation breeding program was initiated, along with research on soil fertility, crop protection and farm mechanisation. Therefore, during this period, rice cultivar selection emphasised not only grain quality criteria but also adaptation to low soil fertility.

Primary Breeding Objectives

During the early phase of the rice improvement program, the main objective was to improve the cultivars that showed high yields, acceptable grain quality and wide adaptation to the environment in each region. Selection was made among the traditional cultivars and the prize winners from the rice contest, followed by the evaluation, and this showed very satisfactory results as the yield plateau was raised from 1.2 t/ha to 1.8 t/ha as a result of release of a number of outstanding cultivars.

Thai traditional cultivars are generally characterised by their profuse tillering and broad and light green leaves; they are mostly photoperiod sensitive, and are rarely responsive to nitrogen fertiliser. When tested in screenhouse or field conditions, they show different levels of resistance to major diseases and insect pests. Like most of the cultivars belonging to the indica group, Thai cultivars have long, slender, flat grain, and are typically awnless, with thin and short hairs on the glume.

Rice Research Centres and Stations

After the foundation of Klong Rangsit Rice Experimental Farm in 1916, other rice experiment stations were established to support the rice cultivars development program. Klong Luang and Huntra were built in 1922 and 1936. Sanpatong, Bangkhen, Kok Samrong, Surin and Phimai were all established at about the same time (1952–53), followed by Phan, Chum Phae and Kuangut in 1955, Chainat in 1957 and Nakorn Si Thamrat in 1959. Khon Kaen and Sakon Nakhon were set up in 1961 and Ubon Ratchathani in 1968; and some other stations have been established since that time. In 1982, six rice experiment stations were upgraded to rice research centres under the National Agriculture Research Project; they included Phrae, Phitsanulok, Pathum Thani (Rangsit), Prachin Buri, Ubon Ratchathani and Phattalung (Kuangut). At the

Table 3. Recommended rice cultivars in Thailand, 1935–36.

Cultivar name	Type and specification	Year released
Puang Ngern	Non-glutinous, early	1921
Tong Raya Dam	Non-glutinous, early, scented	1922
Khao Todlong	Non-glutinous, medium, drought tolerant	1924
Jumpah Sawn	Non-glutinous, medium, drought tolerant	1922
Pin Gaew	Non-glutinous, late	1921
Bang-pra	Non-glutinous, late, well adapted to low-lying fields	1921
Nam Dawk Mai	Non-glutinous, late, well adapted to low-lying fields	1921
Nahng Tah-ni	Non-glutinous, late, well adapted to low-lying fields	1921

Source: Adapted from Pushpavesa (1982)

present time, under the Rice Research Institute, Department of Agriculture, there are seven rice research centres (Sakon Nakhon was upgraded as the newest centre in 1996) and 20 rice experiment stations scattered in all regions.

Cultivar Development

Even though Thailand did not recommend that Thai farmers adopt the cultivar IR8 after it was released by the International Rice Research Institute (IRRI) in 1966, Thai rice breeders of the Rice Breeding Division have used IR8 widely in the national hybridisation programs. Additionally, several improved genetic materials were introduced to Thailand and used as parents in the national breeding program. Since then, many high-yielding and non-photosensitive cultivars have been developed from the crosses between Thai cultivars and IRRI's genetic materials. The breeding objectives were revised, and focused on solving lodging, diseases and insect problems in both photoperiod insensitive and photoperiod sensitive materials. The segregated progenies derived from crosses between tall, traditional, photoperiod sensitive cultivars and semidwarf, photoperiod insensitive breeding lines were screened in both wet and dry seasons. The photoperiod sensitive segregants were evaluated under rainfed conditions and the promising ones were subsequently released as listed in Table 4.

Research Projects

Rainfed Rice Improvement Pioneer Project

The Northeastern Region has the lowest rice yield in Thailand although its cultivated area is the largest. Droughts and floods cause severe damage to the rice yield in the region every year and the Thai government has, therefore, paid more attention to the rice production problems in this region. As a result of a World Bank recommendation, the Rainfed Rice Improvement Pioneer Project was launched in 1974. The aim of the project was to strengthen cultivar improvement research as well as the distribution of official certified seed to farmers. Khon Kaen Rice Experiment Station was designated as the key breeding site. Pushpavesa et al. (1986) reviewed the breeding objectives for both glutinous and non-glutinous cultivars by the time of the project as follows:

- wide adaptability for cultivation in rainfed lowlands in the northeast, including drought, flood, and salinity tolerance;
- photoperiod sensitivity, with different maturities to fit specific rainfall patterns and topography in different areas;
- plant type preferably the same as that of modern cultivars, medium to tall, and with sturdy culm; and
- combined resistance to diseases and insects, with agreeable grain appearance and good cooking quality.

The project carried on the breeding material from previous activities, which had several promising lines under development. Therefore, as the project progressed, in 1977, two mutant lines of Khao Dawk Mali (KDML) 105 were released as RD6 (KDML'65G_2U-68-254) and RD15 (KDML'65G_1U-45). Two other glutinous selections, RD8 and Niaw Ubon-1, were subsequently released from cross IR262/NSPT*2 (BKN6721-5-7-4 and BKN6721-11-3-1-3) in 1978 and 1983, respectively.

Thai-IRRI Rainfed Rice Collaborative Breeding Program

Before the Thai–International Rice Research Institute (IRRI) rainfed rice collaborative project was initiated in 1978, the Khon Kaen Rice Experiment Station had already collaborated with the IRRI Varietal Improvement Department in screening for drought resistance in rainfed rice at Khon Kaen and Chum Phae. The information on drought resistance in the breeding lines such as KDML'65G_2U-68-254, BKN6721-5-7-4, KDML'65G_1U-45 and KDML105 was used to support the recommendation of RD6, RD8 and RD15 later on. By Thai-IRRI collaboration, pedigree lines from crosses made at IRRI were grown in the northeast rice experiment stations, and IRRI breeders assisted in the selection of breeding lines on the basis of plant type and vegetative growth. The attempts seemed not as successful, as the Thai counterparts placed strong emphasis on grain quality but most of the crosses had donor parents with poor grain quality.

The collaborative effort was strengthened when a memorandum of understanding on the Thai-IRRI collaborative research and training project was signed in 1982. Thai breeders suggested the utilisation of traditional cultivars and improved hybrid progenies of Thai origin (with accepted grain quality, photoperiod sensitivity, stiff straw, good yield, and wide adaptability) as the parents for crossing with IRRI breeding lines (with disease and insect resistance and drought and submergence tolerance).

Table 4. Rice cultivars developed in Thailand, 1956–68.

Years	No. of recommended cultivars	Cultivar name	Type	Region released
1956–58	11 (from local collection and cultivar contest)	Jumpah, Puang Nahk 16, Khao Tah Haeng 17, Leuang Awn 29, Nahng Mon S-4	NG	Central Plain
		Leuang Yai 34	NG	Northern
		Meuang Pai, Gaew Khao, Lai Luang 17, Leuang Rahaeng 8, Pah 23	G	Northern
1959–61	15 with: 9 newly recommended	Khao Dawk Mali (KDML) 105	NG	Northeastern, Northern, Central Plain
		Muey Nawng 62-M, Pah Leuad 11	G	Northern
		Daw Nahng Nuan 91	G	Northeastern
		Tapow Gaew 161, Jek Cheuy 159, Pin Gaew 56, Leb Mue Nahng 111	NG	Deepwater area[1]
		Nahng Chalong	G	Deepwater area[1]
	–6 previously recommended	Leuang Yai 34, Nahng Mon S-4, Khao Tah Haeng 17, Leuang Rahaeng 8, Leuang Awn 29, Puang Nahk 16		
1962–64	16 with:9 newly recommended	Niaw Sanpatawng, Gam Pai 15	G	Northern
		Jao Leuang 11	NG	Northeastern
		Khitom Yai 98, Gam Pai 41	G	Northeastern
		Gow Ruang 88, Leuang Pratew 123	NG	Central Plain
		Leuang 152, Nahng Phayah 132	NG	Southern
	–7 previously recommended	Leuang Yai 34, Muey Nawng 62-M, KDML105, Puang Nahk 16, Tapow Gaew 161, Jek Cheuy 159, Leb Mue Nahng 111		
1965–67	14 newly recommended	Daw Hawm 26, Daw Leuang 88	G	Northern
		Dawk Mali 3, BK293, Leuang Tawng 82, Khao Pahk Maw 17, Leuang Tawng 101, Khao Pahk Maw 148, Bai Lod 104, Leuang Pratew 123, NT3986, Khao Puang 32, Leuang Tawng (Nah Prang)	NG	Central Plain
		Khao Nahng Nuey 11	NG	Deepwater area[1]
1968	6 new cultivars	Leuang Yai 148	NG	Northern
		Hahng Yi 71	G	Northeastern
		Nam Sa-gui 19	NG	Northeastern
		Puang Rai 2, Nahng Phaya 70, Pueak Nam 43	NG	Southern

G = glutinous, NG = non-glutinous

[1] Deepwater rice is grown almost exclusively in the Central Plain

Crosses were made and F_1s were grown at IRRI. F_2 populations were distributed and grown at the six experiment stations in Northeastern Thailand. Selections in different environments were made by IRRI breeders. Seeds from F_2 plants were sent to IRRI for generation advance. The F_4 seeds were sent back to Thailand and grown at the northeastern stations, carrying on to the advanced generations. The rice experiment stations conducted the observational nurseries and intra- and inter-station yield trials before nominating promising lines to regional on-farm trials.

Promising Breeding Lines

From the collaborative breeding program carrying on up to the present time, many promising lines have been identified. Some of the promising lines with specific characteristics are listed in Table 5.

Table 5. Characteristics of promising breeding lines.

Characteristic	Line
Drought-resistant	IR46331-PMI-32-2-1-1
	IR49804-UBN-7-B-1-4-1
	IR43062-PMI-B-15-1-2-2
	IR43506-UBN-520-2-1-1
Photoperiod insensitive	IR43450-SKN-506-2-2-1-1
	IR49766-KKN-54-B-B-6-1
	IR43049-CPA-510-3-3-1-1
Weakly sensitive to photoperiod	IR57514-PMI-5-B-1-2
	IR43062-PMI-B-15-1-2-2
Strongly sensitive to photoperiod	IR43506-UBN-520-2-1-1

Performance of Selected Elite Lines

The Ubon Ratchathani Rice Research Centre, with its satellite stations, has conducted the on-farm yield trials in the Northeastern Region in order to evaluate promising lines under wide environmental conditions with the aim of recommending the elite ones. During the past few years, from the regional cultivar trials, some of the elite lines have been identified as discussed below.

Early glutinous elite line

IR43070-UBN-501-2-1-1 is a glutinous selection with flowering date close to Hahng Yi 71, but it has high resistance to leaf blast and moderate resistance to brown plant hopper. IR43070-UBN-501-2-1-1 outyielded Hahng Yi 71 by 14% in the experiments, its average yield being about 2.9 t/ha.

Aromatic non-glutinous line

The selected line for KDML105 grain type, IR57576-PMI-B-2-2, has 7.5 mm grain length and a slender shape. It is clear, with 14.8% amylose content and a low gelatinisation temperature, and is scented. IR57576-PMI-B-2-2 flowers around 21 October and has an average yield, comparable to that of KDML105. It is moderately susceptible to bacterial blight.

Early, non-glutinous line with disease and insect resistance

IR57514-SRN-299-2-1-1 is a photoperiod insensitive line with 110-day maturity; IR57514-SRN-299-2-1-1 is resistant to blast and moderately resistant to bacterial blight. IR62558-SRN-17-2 is another photoperiod insensitive selection with the same maturity (110 days). This line has high resistance to blast, moderate resistance to bacterial blight and moderate resistance to brown plant hopper.

Both early lines have long, slender grains with little chalkiness; IR57514-SRN-299-2-1-1 has 25% amylose content while IR62558-SRN-17-2 has 22% amylose. In farmers' fields they yielded, on average, about 3.0 t/ha.

Cultivars Currently Recommended

There are 25 rice cultivars recommended for rainfed lowland areas in different regions. Some cultivars, such as KDML105, are recommended for all regions if they are suitable for the conditions. RD6, a waxy rice, is recommended for both the Northern and Northeastern Regions. These cultivars can be grouped according to the recommended region as follows:

- Upper Northern
  RD6, Muey Nawng 62-M, Niaw Sanpatawng, KDML105 and Leuang Yai 148
- Lower Northern
  Leuang Pratew 123, Khao Pahk Maw 148, RD27, KDML105 and Phitsanulok 60-1
- Northeastern
  RD6, RD8, RD15, KDML105, Nam Sa-gui 19, Khao Tah Haeng 17, Khao Pahk Maw 148, Chum Phae 60, Niaw Sanpatawng, Niaw Ubon-1 and Hahng Yi 71
- Central Plain
  Gow Ruang 88, Khao Tah Haeng 17, Khao Pahk Maw 148, Pathum Thani 60, Nahng Mon S-4, Leuang Pratew 123 and RD27
- Southern
  RD13, Gaen Jan, Phattalung 60, Nahng Phayah 132, Pueak Nam 43 and Puang Rai 2

Disease and insect resistance in popular recommended cultivars are shown in Table 6.

The efforts of Thai rice breeders and strong government support for the rice improvement program has provided Thailand with an abundance of rice cultivars possessing the desirable grain characteristics of superior grain quality, appropriate agronomic traits and some major disease and insect resistance. However, rice production in areas such as the Northeastern Region, or drought- and flood-prone areas,

Table 6. Harvest date, plant height and disease and insect resistance in recommended rainfed lowland rice cultivars in Thailand[1].

Cultivar name	Harvest date	Height (cm)	Disease and insect reactions[2]						Year released
			BL	BB	RTV	GSV	BPH	GLH	
RD6	Nov 21	150	MR	S	S	S	S	S	1977
RD8	Nov 23	150	MR	S	MR	S	S	S	1978
RD15	Nov 10	130	S	S	S	S	S	S	1977
RD27	Dec 10	160	MR	–	–	–	–	–	1981
NUBN-1	Nov 15	145	MR	S	MR	S	S	S	1983
PSL60-1	Dec 10	150	S	MR	S	MS	S	S	1987
PTT60	Nov 25	160	S	S	S	S	S	S	1987
PTL60	Feb 13	155	S	R	S	S	S	S	1987

[1] MR = moderately resistant; MS = moderately susceptible; S = susceptible; R = resistant; – = not known
[2] BL=blast, BB=bacterial blight; RTV= rice tungro virus; GSV= grassy stunt virus; BPH=brown plant hopper; GLH=green leaf hopper
Source: Adapted from Somrith (1995)

still needs to be improved and the objectives of the breeding program have been revised, along with the national policy guidelines on rice improvement, to meet the demand for both domestic consumption and the world market.

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Germplasm Development for Rainfed Lowland Ecosystems: Breeding Strategies for Rice in Drought-Prone Environments

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Abstract

More than 50% of the approximately 40 million ha of rainfed lowland rice areas worldwide are affected by water deficit at some growth stage. The majority of these areas are found in Northeastern Thailand, eastern India, Bangladesh, and Indonesia. About 10 million ha in Thailand and India are grown to improved traditional cultivars.

A new approach has been used to develop breeding strategies in this subecosystem, involving: (i) decentralisation of the breeding activities to key sites representative of drought-prone environments; (ii) identification of component traits contributing to drought resistance; (iii) development of anther culture derived doubled-haploid populations for molecular mapping of genes responsible for drought resistance; and (iv) development of field techniques for mass screening of rice cultivars for drought resistance.

Attempts have been made to increase productivity in these water-limiting rice environments by designing new plant types that can raise the harvest index to 0.4. The other requirements, such as appropriate photoperiod sensitivity and resistance to major pests (blast, bacterial blight, green leaf hoppers, gallmidge), have also been incorporated.

The importance of the environmental conditions that influence the performance of cultivars has also been recognised and a diversified set of rice cultivars has been developed for testing in different key sites. The main objectives of this study were: (i) to characterise the cultivar responses under different environmental conditions; (ii) to group the environments; (iii) to identify traits that are less influenced by environment; (iv) to determine the efficiency of selection; and (v) to establish selection criteria for the rainfed lowlands.

WORLDWIDE, more than 50% of the total 40 million ha rainfed lowland rice areas experience water shortage at some stage during the growing season; the duration and intensity of stress vary from place to place. The majority of these rainfed lowland rice areas can be found in the major rice-producing countries such as Thailand, India, Bangladesh, Cambodia, Indonesia and the Lao People's Democratic Republic (Lao PDR), with the largest proportion in Northeastern Thailand and eastern India, together covering more than 12 million ha.

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At present, only improved traditional cultivars are commercially grown by farmers. Important cultivars that are well adapted to the water-deficit conditions include KDML105 and RD6 for Northeastern Thailand, and Rajshree and Safri 17 for eastern India, but the cultivars KDML105 and RD6 are no longer suitable, due to decreasing levels of rainfall and its uneven distribution. Little is known about the mechanisms of drought resistance in these cultivars.

On the other hand, in eastern India, where drought occurrence is frequent during the reproductive stage, the current cultivars match the rainfall pattern well. Their shortcomings are, however, susceptibility to diseases and lodging.

Strategies for Breeding Program

Appropriate site

Three key sites that are representative of the major rainfed lowland's drought-prone environments have been chosen and characterised for climate, soil condition and cropping pattern. These sites differ greatly in the duration and intensity of drought occurrence. The screening and evaluation sites are described below.

Thailand — Ubon Rice Research Centre (URRC), Ubon Ratchathani

This centre is located in Northeastern Thailand, where 5 million ha of rice is grown annually. These rainfed lowland areas are frequently subject to water shortage, which may come in July (seedling–tillering stage) and mid-October (flowering–grain-filling stage). The latter is considered a very critical stage as it contributes to severe yield losses. URRC is mainly characterised by acidic sandy soils and erratic rainfall distribution.

India — Indira Gandhi Agricultural University, Raipur, Madhya Pradesh

The central plain of eastern Madhya Pradesh is a major rainfed rice area, covering about 2.5 million ha. In general, soils are fertile and are heavy clay types. The research station at Raipur is characterised by favourable rainfall in the early Kharif (wet) season and irregular distribution toward the grain-filling period (terminal drought).

Bangladesh — Bangladesh Rice Research Institute, Rajshahi

The evaluation site at Rajshahi is located in farmers' fields of the Barinct tracts areas with fertile, predominantly heavy-textured soil types. Drought may occur during the vegetative and reproductive stages but, due to good water-holding capacity of the clay types, yield loss has been minimal.

Characterisation of parents

The majority of traditional and landrace cultivars have been cultivated by farmers for many generations under the different environmental conditions in the rainfed lowlands. Therefore, it is expected that these cultivars have been adapted to the principal constraints of those environments, including climate, soils and biotic factors. Also, they are considered to be invaluable sources of genetic diversity. The main task of the rainfed lowland breeding program is to evaluate and characterise the major traditional and exotic cultivars and use them as parents. These cultivars have traditionally been recognised for their competitiveness and resistance to adverse conditions. Therefore, in designing the ideal plant types for different target drought-prone environments, these indigenous types have served as a model. Incorporation of resistance or tolerance to other abiotic and biotic stresses such as drought, nutritional toxicity, blast and green leaf hoppers has to be made from other sources, including the improved breeding lines (Table 1).

Table 1. Summary of the characteristics of selected traditional and improved rice cultivars that are used as parents for breeding in drought-prone environments.

Cultivar	Important traits
Traditional	
Safri 17	Early maturing (125–130 days)
Rajshree	Early, good in low fertility soils
NSG19	High OA, good recovery from drought
KDML105	Tolerance to low pH soils and good grain quality
Banla Phda	Adapted to low N and P conditions
Improved	
Abhaya	Blast, GLH, GM resistance
CT9993	Deep roots, blast resistance
IR58821-23-B	Strong root penetration
IR62266-42-6-2	High OA
IR57514-PMI-8-B	Seedling drought tolerance

OA= osmotic adjustment; GLH= green leaf hopper; GM= gallmidge

Identification of component traits related to drought resistance

Drought stress is a symptom displayed by the rice plant in response to water deficit. However, under field conditions, these symptoms are expressed in combination with stresses induced by other factors such as temperature and/or nutrients. In rice, the empirical selection employed by breeders to select material adapted to drought conditions has been quite successful as many traditional cultivars (e.g. NSG19, Safri 17) and improved breeding lines (e.g. IR57515-PMI-8-1-1-SRN-1-1, IR54071-UBN-1-1-3-1-2, and

IR57514-PMI-8-B-2-2) are currently being grown by farmers and tested under field conditions, respectively. However, little is understood about the mechanisms responsible for resistance. Using a group of rice cultivars adapted to the rainfed condition, M. Ludlow (CSIRO Division of Tropical Crops and Pastures, Brisbane, Australia; unpublished data) identified osmotic adjustment (OA), dehydration recovery and root depth as the major traits that are associated with drought resistance.

In 1992, a group of the breeding lines was evaluated for agronomic performance under rainfed lowland conditions at Ubon. The selected lines were further examined for OA, rooting depth and root penetration ability. The brief characteristics of each parent are given in Table 2. The line CT9993-5-10-1-M originated from the International Centre for Tropical Agriculture and is a japonica upland type but is well adapted to rainfed lowland conditions. In addition to having an extensive, deep root system, this breeding line is highly responsive to anther culture techniques. The International Rice Research Institute breeding lines, including IR58821-23-B-1-2-1, IR52561-UBN-1-1-2 and IR62266-42-6-2, are semidwarf plant types but nevertheless adapt well to drought-prone conditions. On the other hand, KDML105 is widely grown in the acidic, drought-stricken Northeastern Region of Thailand, covering more than 2 million ha. IR42 is an irrigated cultivar but adapted well in the shallow rainfed lowlands of eastern India.

The anther culture derived doubled-haploid (DH) lines, intended primarily to be mapping populations to identify the genes controlling the drought traits possessed by the selected parents, were developed from the F_1 hybrids of crosses involving different combinations (Table 3). Based on the DNA polymorphism survey, the cross of CT9993-5-10-1-M and IR62266-42-6-2 gave high polymorphism (58%) between the parents, indicating their divergent origin (Table 4).

Phenology requirement

One of the breeding strategies for drought-prone environments is to develop rice cultivars that fit well into the different rainfall patterns of the target environments. The aim of this strategy is for the rice plant to reach maturity before severe water shortage occurs. This may be a good tactic in areas where the rain distribution is reliable, but it may not work well in those areas with intermittent drought due to variable rainfall.

In the multilocational testing of rice cultivars in the northeast of Thailand coordinated by the Australian Centre for International Agricultural Research, the breeding line IR57514-PMI-5-B-1-2 gave high grain yield because its phenology is suited to the rainfall of the northeast (ACIAR 1995). In the northeast this cultivar matures about 10–14 days earlier than KDML105.

Evaluation of the segregating populations

One of the most critical stages in the breeding process is the ability to select materials that adapt to target environments. Our approach is to expose the early generation material, starting from F_2 populations, to conditions representative of major drought-prone areas. We do this for two to three generations before subjecting the nearly fixed lines to systematic drought testing. The selected material then includes the required plant types and other desirable agronomic traits, as well as the adaptability.

Because the rainfed lowland farmers are mostly resource poor, rice is grown largely on marginal land using low input management (e.g. low fertiliser rate, low seeding rate). In the breeding nurseries, therefore, a similar practice is employed in order to select the lines that adapt well and are productive under the local growing conditions. The failure of the breeding lines to perform well in unfavourable environments

Table 2. Major component traits of the parental lines that are used in drought resistance studies.

Cultivar/line	Component traits conferring drought resistance			
	Root depth	Penetration	Osmotic adjustment	Ecotype
CT9993	deep	high	low	Upland, tropical japonica
IR58821	deep	high	low	Rainfed lowland, indica
IR52561	shallow	low	low	Rainfed lowland, indica
IR62266	shallow	low	high	Rainfed lowland, indica
KDML105	shallow	low	low	Rainfed lowland, indica
IR42	shallow	high	low	Irrigated, indica

can be due to the selection of early generation material under more favourable conditions (Ceccarelli et al. 1996).

Table 3. Maximum, minimum and mean of the root-pulling force of the anther culture derived doubled-haploid lines (CT9993/IR62266) and parents evaluated under field conditions. Ubon, wet season 1996.

Doubled-haploid lines (DHL)/cultivar[1]	Pulling force (kg)
DHL with maximum pulling force	102
DHL with minimum pulling force	28
Mean	57
CT9993 (deep-rooted parent)	75
IR62266 (shallow-rooted parent)	45
LSD (5%)	18.0
CV (%)	23.0
Standard error of mean	0.98
Significance	$P < 0.01$

[1] Total number of doubled-haploid lines was 244

Plant type requirements for drought-prone areas

Numerous experiments previously conducted under drought conditions have indicated that semidwarf plant types were not suitable for moisture-limiting environments because of low biomass production and the semidwarf types suffered markedly when soil moisture fluctuated. It has been demonstrated, however, that the intermediate and semi-tall types (130–150 cm) with stiff straw grew better. In a study aimed at increasing the productivity of rainfed lowland rice, Khush and Sarkarung (1996) described the major traits of the new plant types that are required for different subecosystems. In addition to incorporating resistance or tolerance to major biotic and abiotic factors, the harvest index has to be increased to 0.4 in order to produce a significant yield increase. This can be achieved by selecting plants of intermediate height (110–130 cm) that have stiff straw, erect upper leaves, no unproductive tillers, and 5–7 panicles with 200–250 grains per panicle. For drought-prone conditions under which plant growth and development could be severely altered by the interruption of water supply, high plasticity of the rice plant during the time of stress needs to be emphasised. Plasticity in this context refers to the ability of the rice plant to maintain turgor during prolonged dry spells, and to be able to recover quickly. Plant height provides a degree of plasticity in response to moisture availability. The variety NSG19, known for its ability to withstand drought under rainfed lowland conditions, could be used as a plant model, although some of its traits would have to be modified. Besides appropriate plant height, other important traits need to be incorporated in order to ensure stability and to avoid complete crop failure. Priority traits are tolerance of drought and low pH and salinity, as well as resistance to major diseases (blast and bacterial blight) and insects (green leaf hopper, gallmidge, stem borer, brown plant hoppers).

Development of field screening techniques for drought resistance

Field screening techniques aimed at mass screening of rice lines for drought resistance during the dry season have been developed at Ubon, using a sprinkler irrigation system. Our main objective was to develop a methodology that can be used to visually

Table 4. Summary of the polymorphism survey of the parental lines.

Line/cross	Target traits	Polymorphic probes	
		Number	%
Overall		49	76.5
CT9993-5-10-1-M/IR62266-42-6-2	low OA* vs high OA	37	57.8
CT9993-5-10-1-M/IR52561-UBN-1-1-2	deep root vs shallow root	33	51.5
IR58821-23-B-1-2/CT9993-5-10-1-M	deep root vs deep root	30	46.8
IR42/IR52561-UBN-1-1-2	strong penetration vs weak penetration	25	39.0
IR58821-23-B-1-2-1/IR52561-UBN-1-1-2	strong penetration vs weak penetration	20	31.4

* OA = osmotic adjustment
Source: Redrawn from Shashidhar et al. (1994)

differentiate the responses of the rice plant to water deficit at the vegetative stage. At a later stage of this project, however, the vegetative drought reaction of different groups will be examined at the reproductive stage in order to determine if responses at these two growth stages are correlated. Due to soil heterogeneity, the experimental field was puddled and levelled to improve uniformity of the soil. Agricultural lime and farmyard manure were also applied to minimise the acidity effects.

This facility will serve as a service centre for screening of rice cultivars developed by national scientists and international agricultural research centres and as a database unit for drought research on rice.

Evaluation of doubled-haploid lines for drought resistance and major root traits

In the 1995–96 dry season, the DH populations (CT9993/IR62266) originally intended for the molecular mapping of the genes controlling root depth, mass and thickness traits and physiology traits (the ability to osmotically adjust) were evaluated for drought responses. The 220 DH lines were direct-sown on hills with spacing at 15 × 20 cm. The parents, CT9993 (a deep-root, low OA line) and IR62266 (a shallow-root, high OA line), and control cultivars NSG19 (a drought-resistant cultivar) and IR20 (a drought-susceptible cultivar) were also included. There were four replications. At 21 days after seeding plants were thinned to one per hill. The field was irrigated with 5–10 cm standing water 30 days after seeding for 7–10 days and allowed to dry for another 7–10 days in order to simulate the growing conditions of the rainfed lowlands of Northeastern Thailand, where drought can frequently occur about 30–40 days after seeding.

The water was drained when the plants reached 60 days and the first drought score was taken when the susceptible control (IR20) displayed symptoms; drought score was based on the severity of leaves showing tip drying, lower leaf senescence and leaf yellowing. A reading scale of 1–9 was employed: 1 represents highly resistant; 9, highly susceptible. The reaction of DH lines to different moisture stresses was compared with that of the parents and control cultivars. The readings were recorded at four different times (at times of mild, moderate, severe and very severe stress) based on the plant responses to water deficit. Figure 1 shows the responses of DHs after moderate and severe stress. Clear genetic differences were evident among the lines. The scores were roughly divided into three groups, resistant (1–3), intermediate (4–6) and susceptible (7–9), with the majority falling into the intermediate group. Under conditions of moderate stress, based on the drought score of the susceptible control cultivar IR20, the majority of DH lines showed an intermediate drought score (4–6). On the other hand, CT9993, the deep-rooted parent, had a score of 5 as compared with the shallow-rooted parent, IR62266, which displayed severe growth reduction but did not show intense drying of the leaves; the drought score was therefore similar to the line CT9993. It was discovered, however, that leaf senescence and tip drying on CT9993 was largely caused by bacterial blight disease.

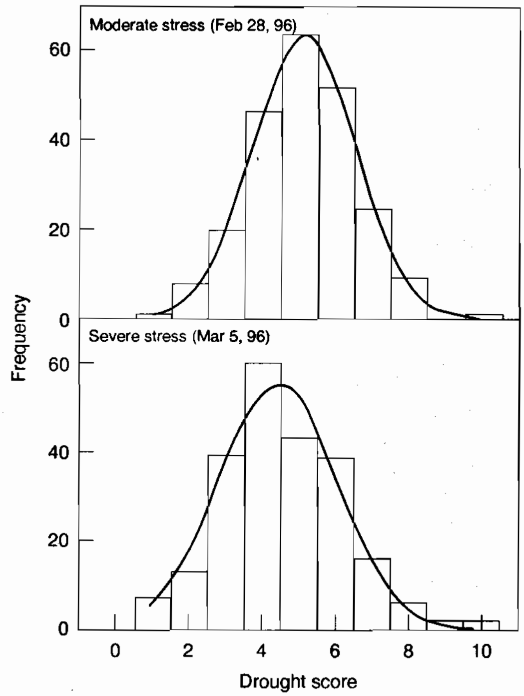

Figure 1. Drought-score distribution of doubled-haploid lines (CT9993/IR62266) after exposure to moderate and severe water deficit. Drought score was based on senescence of lower leaves, tip drying and leaf yellowing, using a score of 1–9 (where 1 represents the most resistant and 9 is the most susceptible).

The same DH populations (CT9993/IR62266), including the parents (CT9993 and IR62266) and control cultivars (NSG19 and IR20), were evaluated in the 1996 wet season for major root traits (root depth, root thickness and root mass) as well as for important agronomic characteristics (leaf canopy arrangement, tillering, plant height, 50% flowering and grain yield). Each entry was dry-seeded on hills at a spacing of 10 × 10 cm, with four replications. At 21 days after seeding plants were thinned to one per hill. The experimental plots were maintained with irrigated conditions for 60 days after seeding and thereafter under field conditions in order to allow maximum root expression. The strength of the root system was measured using pulling equipment that registers in kilograms the resistance of the roots to uprooting of the rice plant (IRRI 1984); the deeper and bigger the roots, the greater the force required, irrespective of plant height and tiller number.

Table 3 shows preliminary findings for the maximum, minimum and mean of the pulling force of the DH lines evaluated under field conditions in comparison with the parents and control cultivars. In this experiment, many DH lines displayed high root pulling resistance (this being equal to or higher than that of the deep-rooted parent, CT9993, or the drought-resistant control, NSG19). In addition, a group of DHs in this population showed the least resistance. The maximum pulling force was 102 kg and minimum pulling force was 28 kg (Table 3). Previous work on the inheritance of the root pulling resistance conducted by Ekanayake et al. (1985) indicated that the high pulling resistance is controlled by dominant and additive genes and that plants with high root pulling resistance have the ability to maintain higher leaf water potentials under severe drought stress.

Multilocation testing

The nature of drought varies from location to location in regard to timing and intensity. It is therefore important to characterise environments for both genotypic performance and environmental conditions. A set of rice cultivars with known drought-response characteristics is being developed and tested at different drought-prone sites.

At present a group of breeding lines adapted to the drought-prone condition at Ubon, as well as the control cultivars (e.g. KDML105, NSG19, Mahsuri, Sabita, and Safri 17) are being evaluated under drought conditions in northeast Thailand, Bangladesh, eastern India, Indonesia, and the Philippines to study the interactive effects of the environment and genotype expression. The main objectives of this genotype-by-environment interaction research are: (i) to characterise cultivar responses under different environments; (ii) to identify traits that are less influenced by the environments to be used as the selection criteria; (iii) to determine the improvements made in the selection; and (iv) to identify groups of environments.

Strategies for Biotechnology Application

As mentioned earlier, drought is a complex syndrome arising from the interaction of soil, moisture and ambient temperature, the combined effects of which result in rice plants displaying less than optimum growth. Many factors are known to be responsible for plant expression. Foremost of all are the root systems (depth, mass, thickness), the ability to adjust osmotically, the recovery ability and the dehydration tolerance. These component traits and characters are extremely difficult to evaluate under field conditions but fortunately they appear to be genetically controlled.

In collaboration with Texas Tech University, The University of Queensland and the Ubon Rice Research Centre, populations of doubled-haploids and recombinant inbreds have been developed from crosses involving diverse parents possessing these traits (Table 4). Using molecular marker technology, these materials will be used as the mapping populations to establish linkages between genes controlling the traits of interest and molecular markers. Once the molecular markers that have close linkage with the required genes are identified, they can be used in the breeding program to facilitate selection of the desired traits, preferably in the segregating populations of F_2 and F_3. With the availability of this technology, the selection and identification of traits contributing to drought resistance will be more efficient and consistent.

Conclusion

A concerted effort is being implemented for drought research. This includes breeding strategies involving key evaluation sites; selection and characterisation of parents; strategic research on component traits; establishment of drought-screening techniques; and multilocation testing. More progress on the selection of drought-resistant and drought-tolerant genotypes would be made if appropriate molecular markers that are closely linked to the traits contributing to drought resistance could be identified and marker-aided selection developed and effectively used in the breeding program.

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Rice Improvement for Rainfed Lowland Ecosystems: Breeding Methods and Practices in Eastern India

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Abstract

About 17 million hectares of rainfed lowland rice area in India are mainly concentrated in eastern India. Low yields, averaging 1.5 t/ha, are mainly due to lack of appropriate cultivars to cope with risks such as floods and droughts. Earlier attempts to improve rainfed lowland rice were on reselections from landraces and introductions, and only to a limited extent from on-station hybridisation, selection and testing. Considering the limited scope for yield increase in irrigated areas, the rainfed lowlands have recently received special emphasis, and accordingly well-organised efforts are under way to develop cultivars suited to varying situations in eastern India. Specific breeding methods and practices suited to different agroecological niches are being followed by different centres. A shuttle breeding program in collaboration with the International Rice Research Institute has been initiated to supplement the breeding efforts. Some of these methods and their relative usefulness, including that of the modified pedigree method, modified bulk method and culling combined with pedigree selection, are discussed.

RAINFED lowland rices experience drought, flooding and intermittent submergence at different stages of crop growth depending upon land and rainfall characteristics; this affects rice yields substantially (Singh and Singh 1996). The rainfed lowlands account for about 25% of the world's rice area, but yield only about 17% of total rice production (IRRI 1992). In India, about 17 million ha are planted to rainfed lowland rice each year. These areas are in eastern Uttar Pradesh, Bihar, eastern Madhya Pradesh, Orissa, West Bengal and Assam, where average grain yields are 1.5 t/ha (Singh et al. in press).

The lower yields are partly due to inadequate tolerance of cultivars to hydrological and biotic stresses, poor response to inputs, and basically low yield potentials. Soil-related stresses, such as zinc and phosphorus deficiencies, salinity, iron toxicity and peat soils, also contribute to lower yields in some places (Singh et al. 1994). Though it has not been feasible to develop genotypes with multiple stress tolerance, several genotypes have been noted to have a fairly high level of tolerance to some of the important stresses. Efforts to develop rice genotypes for the adverse environments in eastern India have been limited to research stations and have not captured the realities of on-farm situations (Maurya et al. 1988). Breeders, therefore, have only partially succeeded in developing genotypes that combine resistance with tolerance to major biotic and abiotic stresses. The cultivars under cultivation in rainfed lowland areas, unlike those in other ecosystems, are mainly the traditional low-yielding cultivars. In order to address these problems, a wide range of breeding methods is currently being used for cultivar improvement to suit adverse situations. This paper reviews these methods and describes them in the context of eastern India.

Problems and Breeding Objectives

Factors affecting rice yield in eastern India include flash flooding during early growth, prolonged water stagnation, low soil fertility and low light intensity.

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The declining temperature during flowering, coupled with droughts during the reproductive stage, further reduces the yield level. Poor crop stand, delayed seeding or transplanting, high grain sterility, weed infestation (especially in direct-seeded conditions), damage due to stem borer, bacterial blight and brown spot, and poor nutrient management of the soil have been identified as the major production constraints in rainfed lowland areas.

As evident from the details in Table 1, photoperiod sensitivity, waterlogging and bacterial leaf blight (BLB) are issues common across the states; submergence is a problem in six states, stem borer in five states, drought at reproductive stage and gallmidge (GM) in four states. Drought at vegetative stage and problem soils occur only in some specific areas. However, based on the expert knowledge and the extent of areas and crop loss estimates, drought at reproductive stage is the most important problem in eastern India as a whole, followed by photoperiod sensitivity, submergence and waterlogging, BLB and GM. Keeping these problems in mind, breeding objectives in each state have been developed.

Breeding Methods and Practices

Rainfed lowland rice breeding programs

In India, many rainfed lowland rice breeding programs began by selecting superior lines within local landraces. In this method, the best performer's panicles are harvested and bulked, which improves the uniformity and increases yield to some extent. Table 2 lists the cultivars developed through this method in India. These cultivars are tall and photoperiod sensitive, and have varying degrees of submergence tolerance. Some of these cultivars, such as Sabita in West Bengal, T100 and Madhukar in Uttar Pradesh, and Rajshree in Bihar, have been quite popular with farmers. FR13A is one of the most submergence-tolerant cultivars known. However, it is a poor combiner and has inferior grain quality (Malik et al. 1995).

Cultivar introduction has been an age-old practice. Cultivars are introduced from one country to another and tested for their suitability and direct release. Mahsuri is one such example; it was introduced to India and other countries from Malaysia and became popular with farmers in eastern India because of its moderate non-lodging habit and good grain quality (Rao Balakrishna and Biswas 1979). Sometimes, photoperiod sensitivity can be a problem when a variety is introduced from one country to another (Ahmad 1979; Salam and Mackill 1993). Our experience is that the Indian rainfed lowland cultivars flower early in Thailand, when floodwater may still be rising, while Thai cultivars flower late under Indian conditions due to their shorter critical daylength. The breeder should keep this in mind when introducing a cultivar to a new area.

Pedigree, bulk and modified bulk-pedigree, described in the following section, are the most common breeding methods used for rainfed lowland conditions (Maurya and Mall 1986; Mackill et al. 1996). Although the list of cross-bred cultivars released in India using these methods is quite large (Table 3), only a few could really find favour with the farmers in the complex rice-growing rainfed environments. The low adaptability is believed to be due to the fact that the segregating materials were grown and tested at the research station without being subjected to the rigours of on-farm environmental stresses (Maurya et al. 1988; Goet 1989; Thakur 1995).

Often, hybridisation causes adapted gene complexes to be broken up, and thus makes it difficult to recover the desirable characteristics of the adapted parents. Mutation breeding offers promise when one trait or a few traits are to be improved. Traits such as plant height, grain quality, duration and photoperiod sensitivity could be improved by mutation. In India, the two widely accepted rainfed lowland cultivars, Biraj and Jagannath, are the short mutants developed from OC1393 and T141, respectively, and are suitable for use in 5–30 cm of standing water (Rao Balakrishna and Biswas 1979).

The rapid generation advance technique with single-seed descent is a tool to increase the efficiency of breeding. It is a method to reduce to as low as three months the growth duration of the rice crosses that could otherwise be harvested only once in a year due to photoperiod sensitivity (Ikehasi and HilleRisLambers 1979; Ikehasi and Nieto 1980). At present, this facility exists at the International Rice Research Institute (IRRI), where breeders from various centres in India, e.g. Ghaghraghat, send their crosses for advancing generations. In the past, hundreds of crosses have been handled by rapid generation advance at IRRI to improve the breeding materials of eastern India dealing with photoperiod sensitive cultivars. The facility to do this is now being created at the Central Rice Research Institute (CRRI), at Cuttack in India.

Table 1. Major constraints identified at different sites in eastern India.

Centre	Submergence	Drought[1]		Photoperiod sensitivity	Water-logging	Problem soil	BLB	GM	GLH/BPH	Stem borer	Others	
		Veg.	Repr.								Shoot blight	Shoot rot
CRRI, Cuttack	X	X	–	X	X	–	X	X	–	X	X	
Masodha, Uttar Pradesh	X	–	X	X	X	Sodicity	X	–	–	X	X	
Pusa, Bihar	X	X	–	X	X	Zn deficiency	–	–	–	–	X	
Patna, Bihar	–	–	X	X	X	–	X	–	X	–	–	
Raipur, Madhya Pradesh	–	–	X	X	–	–	X	X	X	X	X	
Chinsurah, West Bengal	X	–	–	X	X	–	X	–	X	–	X	
Titabar, Assam	X	–	X	X	X	Fe toxicity	X	X	–	X	X	
Ranital, Orissa	X	–	–	X	X	–	X	–	–	–	Seed discoloration	
Bhubaneswar, Orissa	–	X	–	X	X	X	X	X	–	X	Sheath blight and seed discoloration	
Location	6	3	4	9	8	3	8	4	3	5	8	
Priority[2]	7	5	9	8	7	4	5	4	3	6	4	

x = constraint occurs; – = constraint does not occur
BLB = bacterial leaf blight; GM = gallmidge; GLH = green leaf hopper; BPH = brown plant hopper
[1] Drought can occur during the vegetative or reproductive stages of growth
[2] Based on expert knowledge and extent of area and crop loss estimates where: 1 = least; 9 = highest

Table 2. Rainfed lowland rice cultivars developed through selection in eastern India.

States	Cultivars
Bihar	BR8, BR9, BR34, Sugandha, Rajshree, T141
Madhya Pradesh	Safri 17, Laloo 14, Kranti, Pragati
Orissa	BAM6, BAM9, FR13A, FR43B, SR26B, T90, T141, T1242
Uttar Pradesh	T100, Type 9, Madhukar, Chakia 59
West Bengal	Tilakachari, Sabita, Amulya, Matangini, Nalini

Table 3. Cross-bred cultivars developed for rainfed lowland ecosystems in India.

States	Cultivars
Assam	Manoharsali, TTB 4/7, KMJ1-17-2, KMJ1-19-2, Mahsuri, Pankaj, Bahadur
Andhra Pradesh	Tella Hansa, MTU3626, Surekha, AKP70-73, BPI1235, MTU4407, MTU7029, RPW6-17
Bihar	Rajendra dhan, Panidhan 2, Radha, Shakuntala, Mahsuri
Karnataka	Vikram, Phalguna
Madhya Pradesh	Anupama, Jagitri, Garima, Samridhi
Maharastra	Karjat 184, Ratnagiri, Karjat 14-7, Ratnagiri 68, Sakoli 17, Sindewali 75.
Orissa	Savitri, Gayatri, Tulasi, Panidhan
Uttar Pradesh	Mahsuri, Jal Lahari

Anther culture, somaclonal variation and mutant isolation are being explored for increasing stress tolerance of otherwise high-yielding cultivars (Martinez 1990; Narsimman and Rangasamy 1993). Anther culture could be particularly useful for breeding improved photoperiod sensitive rices as it reduces the time required to develop homozygous lines after a cross (Mackill et al. 1996). Although use of anther culture as a routine technique is limited by low response of indica rices, efforts made to breed rice cultivars at the Indian Agricultural Research Institute, CRRI, the Directorate of Rice Research (DRR) and some state agricultural universities resulted in hundreds of doubled-haploids from indica × indica and indica × japonica hybrids. These lines are being field-tested (Raina 1989; Bong 1991; Sharma et al. in press).

The use of molecular markers, such as restriction fragment length polymorphism, to identify the segments of chromosomes associated with traits of agronomic importance, is rapidly advancing towards routine application in rice improvement. In India, systematic rice biotechnology work was initiated in 1993 under the Asian Rice Biotechnology Network. Accomplishments since then include molecular characterisation of the population structure of bacterial blight and blast and DNA fingerprinting of the Indian isolates of Xoo. From the first phase of collaboration between IRRI and CRRI, the program has now been expanded to other centres — DRR, Indira Gandhi Krishi Vishwa Vidylaya and Punjab Agricultural University — to work on gallmidge resistance and quantitative trait loci for drought tolerance and blast resistance.

Current approaches

To breed rice cultivars to cope with the specific problems of the rainfed lowland rice-growing areas in the region, plant breeders have adopted their own breeding methodology, guided by financial constraints, infrastructure facilities and ecogeographical features. However, there is no information available on the relative efficiency or any genetic comparison of these methods. Despite this limitation, and the lack of any supporting data on output, an attempt has been made to analyse the merits and demerits of these methods.

The modified pedigree method (single-panicle selection) adopted by breeders at Narendra Deva University of Agriculture and Technology (NDUAT), Faizabad, Uttar Pradesh, is able to handle larger population sizes in the F_2 and subsequent generations up to F_4. Selection in F_5 and F_6 is made among the progeny of the selected individuals from F_4. This maintains sufficient genetic variability to allow selection of desirable genotypes. In later generations (F_5 onward), when there are fewer promising lines to be handled, the precision increases and the cost is lower. The uniform progeny from the F_5 and F_6 generations are tested on the farmers' fields under their own management. Some of the selections, with yields ranging from 4 to 6 t/ha, are currently in the advanced trials of All India Coordinated Testing (Mishra et al. 1996).

In view of the poor adaptability of the on-station selected genotypes in the heterogeneous and uncertain on-farm conditions, the breeders at Rajendra Agricultural University (RAU), Pusa (Bihar) developed a strategy that includes early generation testing of segregating materials under on-farm situations, followed by on-station evaluation and release (Thakur 1995). Thus, the modified bulk method at RAU handles bulk populations up to the F_4 generation at farmers' fields, under direct-seeded conditions, followed by single-panicle selection in the F_4 and F_5 generations and testing at the research station. The main drawback of this method appears to be increased plant competition in the direct-seeded early generations. Thus, there is a risk of losing otherwise genetically superior but competitively poor genotypes. Vaidehi was released after testing its performance under on-farm conditions (Thakur 1994).

Breeders at Assam Agricultural University, Titabar, Assam include photoperiod sensitivity and delayed transplanting (60-day-old seedlings) in their selection criteria. By combining culling of plants flowering earlier than 10 October in F_2 and pedigree selection from F_3 onwards, the method becomes quite cost-effective because of non-maintenance of the culled material and provides full opportunity to exercise selection from among individual plant progeny. The selected material is planted under both normal and late conditions, as the objective is to select genotypes that will perform well in both situations (Ahmed 1996).

The pedigree method adopted by CRRI at Cuttack involves both spaced transplanting and direct seeding in alternate generations. Direct seeding is a common practice in rainfed lowland areas in some states (Orissa, West Bengal, Madhya Pradesh), and transplanting is practiced in other places (Bihar, eastern Uttar Pradesh).

Sometimes, circumstances force the farmers to direct-seed or transplant. For example, in Orissa, the early heavy rains in May 1995 compelled the farmers to transplant rainfed lowland rices, instead of direct-seeding as usual. For better stability, it is desirable that the breeding material is subjected to both direct seeding and transplanting (Roy et al. 1996). In the F_3 and F_4 generations, stringent selection for submergence tolerance is also practiced. The chances of reducing genetic variability appear to be increased by this method, due to the exposure of the segregating populations to both direct-seeding and transplanting stresses. No cultivar has so far been released following this approach, as a breeding program was started only a few years ago. However, some promising materials are at an advanced stage of testing. It should be emphasised that earlier selection was by transplanting, but the fixed lines that led to the identification of Utkalprabha and Panidhan cultivars were subjected to direct seeding before final selection, which was found useful as these cultivars do well under both conditions.

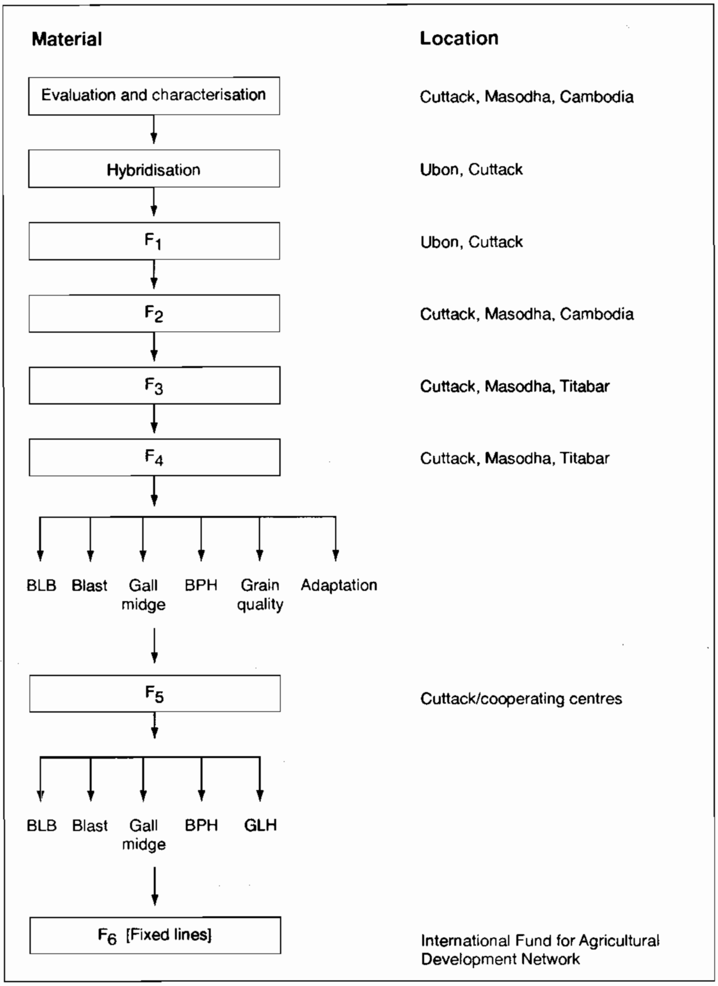
It should be once again emphasised that in the absence of supporting empirical data, the comparative superiority or inferiority of these methods cannot be judged.

Shuttle breeding program

In an attempt to improve yield potential of rice cultivars for the rainfed lowland conditions of eastern India, a shuttle breeding program was established in 1992 in collaboration with the Rainfed Lowland Rice Research Consortium coordinated by IRRI (Sarkarung 1995). Research is currently being conducted in six states: Orissa, Uttar Pradesh, Madhya Pradesh, West Bengal, Assam and Bihar. This program has the following objectives:

- to make available diversified sets of donors and improved breeding lines suitable for the rainfed lowlands;
- to provide the segregating material with broad genetic background for effective selection under location-specific environments; and
- to evaluate elite breeding lines developed by the participating centres and IRRI, specifically for submergence tolerance, thermo-insensitivity and yield potential in eastern India.

With the above objectives, the locally adapted traditional and improved cultivars originating from each centre were characterised and used in the crossing program. CRRI and IRRI are responsible for parental characterisation and planting of genetic materials with diverse background. Other centres in Masodha (NDUAT) and Cambodia also participate in characterisation to determine the performance of genetic materials in the broader environment (e.g. temperature, photoperiod, soils, etc.). The breeding materials (F_2 onwards) with a wide genetic base (mostly received from IRRI) are initially evaluated at CRRI and the lines selected by cooperating breeders are tested by satellite stations, which include Masodha, Raipur, Chinsura, Titabar, Pusa and Patna. The scheme of flow of genetic materials is shown in Figure 1. During the 1994 wet season, 2343 breeding lines were evaluated by these centres (Roy et al. 1996). In addition, a total of 12 000 breeding lines originating from 500 crosses and the doubled-haploid lines have been tested in eastern India for adaptation and suitability.



BLB=bacterial leaf blight; BPH=brown plant hopper; GLH=green leaf hopper

Figure 1. Flow of genetic material in shuttle breeding program (adapted from Sarkarung 1995).

Furthermore, under the shuttle program, a set of traditional and improved rice cultivars adapted to the region were evaluated at each key site in order to determine the degree of photoperiod sensitivity.

Based on the cultivar responses to daylength, three specific photoperiod sensitive groups were identified for the eastern India lowlands (Table 4). It was observed that the best entries for Orissa and West Bengal, flowering in the first week of November, were too late for Assam and Madhya Pradesh. Similarly, the best entries for Assam and Madhya Pradesh were too early for Orissa and West Bengal, as they were damaged due to late cyclones and water stagnation in the fields. Hence, use of specific donors and selection pressure for development of cultivars flowering at a particular time (photoperiod sensitive group), are the important breeding strategies for rainfed lowlands.

The program has also helped identify additional sources of tolerance and resistance to submergence, cold, salinity, GM, BLB, blast and delayed transplanting. A number of the breeding lines that combine tolerance to major stresses are currently being field-tested by farmers through an International Fund for Agricultural Development supported network on rainfed rice research and development project for eastern India (Singh et al. in press).

Table 4. Photoperiod sensitive groups identified for the eastern Indian lowlands.

Group	Optimum flowering time	Centres	States
Group I	1st week October	Raipur	Madhya Pradesh
		Titabar	Assam
Group II	3rd week October	Pusa and Patna	Bihar
		Masodha	Uttar Pradesh
Group III	1st week November	Cuttack and Ranital	Orissa
		Chinsurah	West Bengal

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Drought Problems in Rainfed Lowland Rice in the Philippines

R.T. Cruz* and J.F. Fabiosa*

Abstract

Rainfed lowland rice is grown in 14 regions of the Philippines, and constitutes about 44% of the total rice area and 88% of the total rainfed rice area. Because of the increasing demand for rice by the increasing population and the decrease in rice production due to decrease in the area devoted to rice, any yield improvement (above Philippine averages of 1.6–2.3 t/ha) will be significant. In order to improve yields in the rainfed lowland, current information is needed on agronomic practice, drought occurrence and yields, and drought-associated problems in key rice-producing areas.

A survey of many farmers from the provinces in the different regions in the Philippines showed that during the wet season (July–December) a greater proportion of the rice area was seeded to modern varieties and higher rates of fertiliser were used. Some areas were seeded more during the dry season (January–June) because the wet season could start early or precipitation was close to the minimum requirement. In addition solar radiation is high and typhoon damage is less at that time. Average drought indices and grain yields of modern varieties for a 120-day growing period during the wet season were 56.5% and 2.3 t/ha for Tarlac (Region III), 65.0% and 2.0 t/ha for Cagayan (Region II) and 42.5% and 2.0 t/ha for Camarines Sur (Region V). The survey showed that rainfed lowland rice farmers in Region III provinces considered drought, typhoon and pests to be the major problems. Some farmers considered salinity, acidity and soil mechanical impedance to be drought-associated problems.

RAINFED lowland rice in the Philippines is usually transplanted in levelled, bunded fields and shallowly flooded with rainwater. Rice yields are low in the rainfed lowland because of drought and drought-associated problems (BSWM 1989; Widawsky and O'Toole 1990; Ingram 1995; Mackill et al. 1996). Despite the low yields in the rainfed lowland, most research is directed to irrigated environments because research workers and resources are scarce and the potential for increasing rice production is uncertain in the rainfed lowland (Mackill et al. 1996). However, research into rainfed lowland rice would produce higher rates of return than research on irrigated rice (Barker et al. 1985). Any yield improvement in rainfed lowland rice would be a great help in meeting the demand of the increasing population, especially as there have been some decreases in rice production due to a reduction in the area devoted to rice. Hence, current information is needed on agronomic practices, occurrence of drought and its associated problems, and rice yields in farmers' fields at the provincial level in key rice-producing areas in the Philippines, in the effort to improve yields in the rainfed lowland.

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Distribution of Rainfed Lowland Rice in the Philippines

Rainfed lowland rice (RLR) is grown in 14 regions of the Philippines (Fig. 1). It constitutes about 44% of the total rice area (irrigated, rainfed lowland and upland) and 88% of the total rainfed rice area in the Philippines. Irrigated rice has a total area of 1.56 million ha, RLR a total area of 1.39 million ha, and upland rice a total area of 0.19 million ha. Regions I

(Ilocos), III (Central Luzon), IV (Southern Tagalog) and VI (Western Visayas) have an average RLR area of 206 011 ha. Regions II (Cagayan), VIII (Eastern Visayas), XI (Southern Mindanao), and XII (Central Mindanao) have an average RLR area of 89 105 ha. Regions V (Bicol) and VII (Central Visayas) have an average RLR area of 60 519 hectares. Regions IX (Western Mindanao), X (Northern Mindanao) and the Cordilleras have an average RLR area of 31 369 ha.

Agronomic Practices and Rice Yields

Seasonal data from 1970 to 1994 in rainfed and irrigated conditions show that grain yields of modern varieties are higher than yields of traditional varieties (Fig. 2). Yields of modern and traditional varieties in rainfed conditions were about 1 t/ha lower than yields in irrigated conditions. This could be attributed to the lower amount of fertiliser used in rainfed conditions,

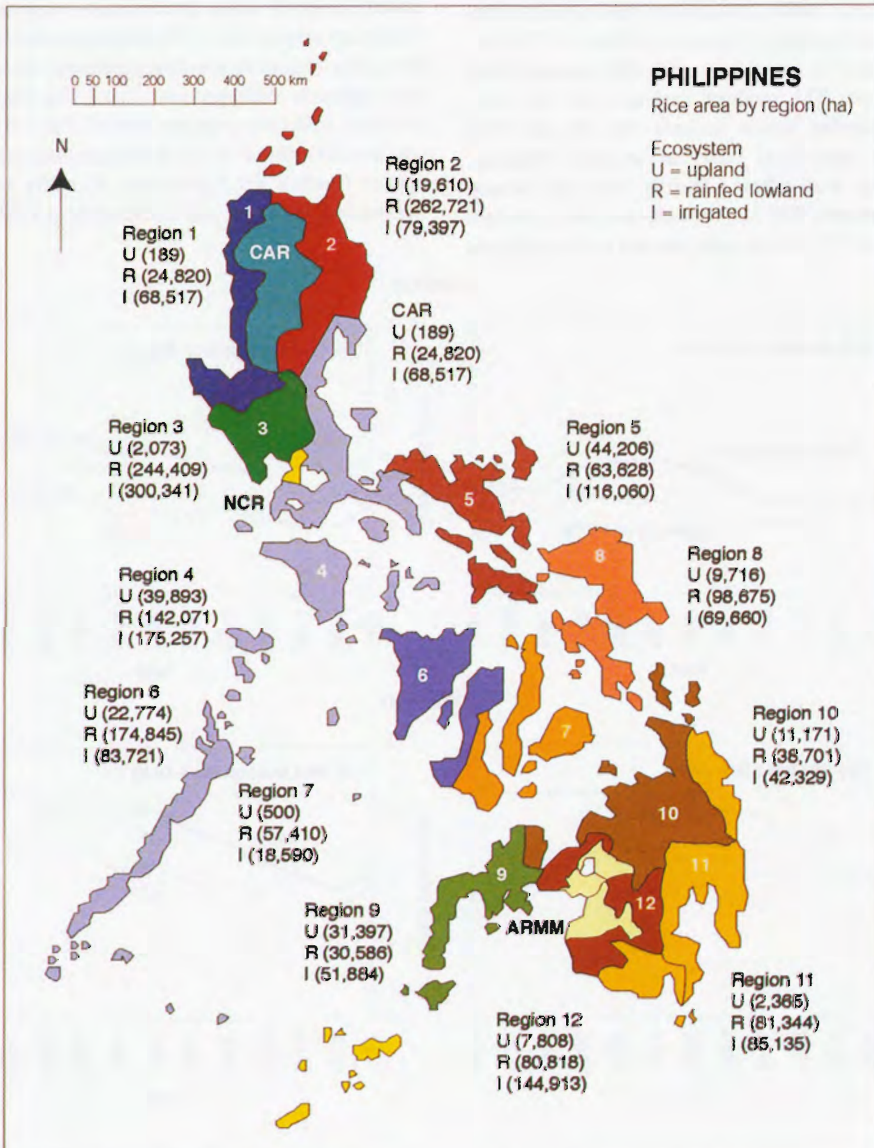

Figure 1. Total rice area in the different regions and ecosystems in the Philippines (BSWM 1993; PhilRice-BAS 1995).

where there was greater risk of exposure to drought stress (PhilRice-BAS 1995). Yields of both modern and traditional varieties increased with time. However, the rate of increase in grain yield, especially from 1976–84, was greater in irrigated conditions (Fig. 2). The country's surplus rice production at this time was due to massive government intervention through supervised credit, fertiliser subsidy and greater use of technology (Balisacan 1990).

The results of a survey of the major rainfed rice-producing areas in the Philippines seeded to modern and traditional varieties is shown in Table 1. The survey was based on interviews with 400 farmers from each province. The modern varieties are the high-yielding varieties which include the IR and PSB series. The traditional varieties include Wagwag, Sinandoming and others. During the wet season (July–December), 731 750 ha were seeded to modern varieties and 122 800 ha were planted with traditional varieties. During the dry season (January–June) 349 770 ha were planted with modern varieties and 45 660 ha were planted with traditional varieties. Relatively more areas were planted during periods of high rainfall, but in Regions II, VII, VIII and XI (see Table 1 for a list of the provinces in each region) more areas were planted during the dry season than in the wet season. It is possible that farmers in some of the provinces in the region have opted for dry-season planting because of a window when the wet season could have started early or when precipitation was close to the minimum requirement. The farmers were also aware that solar radiation was higher during the dry season and typhoon damage was less. The frequency of typhoon occurrence ranges from 0.3 to 1.5 during the dry season and 1.5 to 3.5 during the wet season (Philippine Council for Agriculture, Forestry and Natural Resources Research and Development 1990).

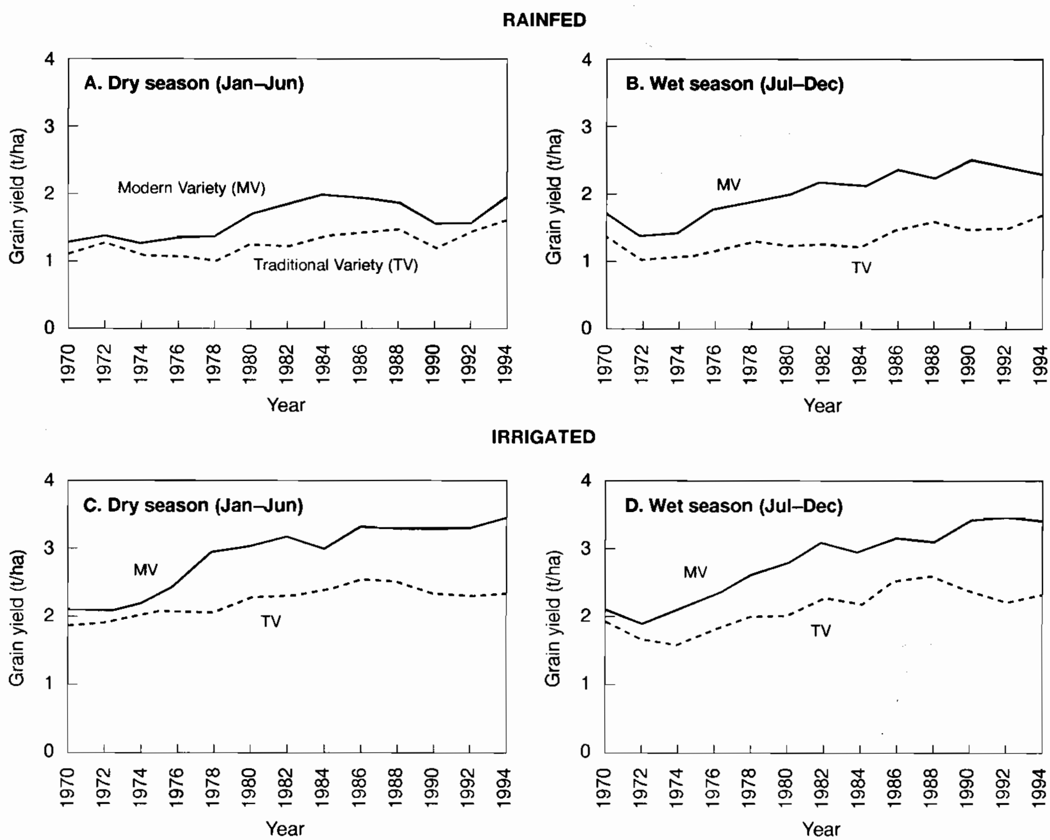

Figure 2. Average grain yields for dry (A) and wet (B) seasons under rainfed conditions; and dry (C) and wet (D) seasons under irrigated conditions in the Philippines (1970–94). Modern varieties include IR and PSB series; traditional varieties include Wagwag, Sinandoming, Biniding and others.

Table 1. Rainfed areas (ha) planted to modern and traditional rice varieties in regions of the Philippines, 1995.

Region	Dry season January–June		Wet season July–December	
	Modern	Traditional	Modern	Traditional
I	–	–	142460	3730
II	34530	2530	23760	4970
III	570	–	114910	900
IV	50310	500	84040	13840
V	33510	1740	68220	3890
VI	106450	740	147690	5080
VII	32930	3370	30560	2450
VIII	33640	13080	13220	1290
IX	6040	1760	21770	4930
X	16930	6090	36700	10500
XI	15700	7410	11520	2190
XII	4110	500	21820	4610
XIII	14630	7580	14470	63710
CAR	420	150	610	710
Total	349770	45660	731750	122800

Provinces. Region I: Ilocos Norte, Ilocos Sur, La Union and Pangasinan; **Region II**: Cagayan, Isabela, Nueva Vizcaya and Quirino; **Region III**: Tarlac, Nueva Ecija, Pampanga, Bataan and Bulacan; **Region IV**: Aurora, Laguna, Quezon, Palawan, Mindoro Occidental and Mindoro Oriental; **Region V**: Camarines Norte, Camarines Sur, Albay, Sorsogon and Masbate; **Region VI**: Aklan, Iloilo, Capiz, Antique and Negros Occidental; **Region VII**: Negros Oriental and Bohol; **Region VIII**: Northern Samar and Leyte; **Region IX**: Zamboanga del Sur; **Region X**: North Cotabato, Bukidnon, Agusan del Norte, Agusan del Sur, Surigao del Norte; **Region XI**: South Cotabato, Davao del Sur, Davao Oriental and Surigao del Sur; **Region XII**: Sultan Kudarat, Lanao del Norte; **Region XIII**: Maguindanao, Lanao del Sur; **Cordillera Administrative Region (CAR)**: Ifugao and Kalinga-Apayao. **Region XIII** is under the Autonomous Region of Muslim Mindanao (ARMM).

Source: PhilRice–BAS (1995)

Drought Index in Selected Major Rice-Producing Provinces

Available data on key variables in major rice-producing provinces allow the occurrence of drought in rainfed environments to be quantitatively characterised using a drought index. The procedure for estimating exposure to drought risk ('drought index' or 'DI') is to incorporate into one index number the pertinent variables that influence drought risk, such as rainfall levels and variability, minimum rainfall requirements of rice in the rainfed ecosystem, and timing of planting by farmers. A normal probability density function of rainfall by month was estimated in each province using rainfall data from the Rice Weather Database of the International Rice Research Institute (IRRI), i.e.

$$r(x;\mu,\sigma)=\frac{1}{\sigma\sqrt{2\pi}}e^{\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2} \quad (1)$$

To fully describe this probability density function, a mean and standard deviation were computed for each month. The probability of drought in each month is estimated as the probability of rainfall levels falling below the minimum requirement of 200 mm. Based on the agroclimatic classification system for rice, it can be assumed that the average amount of 200 mm is sufficient for rice, considering the expected rates of evapotranspiration, seepage and percolation (Oldeman 1980; Huke 1982). Therefore:

$$\Pr_{ij}\left(x=200,\mu_{ij},\sigma_{ij}\right)=\int_0^{200}\frac{1}{\sigma_{ij}\sqrt{2\pi}}e^{\frac{1}{2}\left(\frac{x-\mu_{ij}}{\sigma_{ij}}\right)^2} \quad (2)$$

where the ith index represents the province and jth index represents the month.

The DI is the average probability of drought for the entire growing period of the rice crop, which is assumed to be four months:

$$DI_{ij} = \overline{\Pr}_{ij} = \frac{\sum_{k=1}^{4} \Pr_{i(j+k)}}{4} \qquad (3)$$

Of the 13 provinces examined, three distinct patterns of rainfall, drought index and timing of planting emerge (Fig. 3). The first group has a rainfall pattern with distinct wet and dry seasons where rainfall levels in the wet season are three times higher than in the dry season. This category includes the provinces of Tarlac (Fig. 3a), Nueva Ecija, Pangasinan, and Ilocos Norte. Tarlac, the representative province in this group, has a total rainfall of 438 mm in the dry season and 1352 mm in the wet season. As a result, the drought indices by month vary widely from a maximum of 100 to a minimum of 29. Farmers in these provinces have adopted a planting pattern that capitalises on the period when rainfall is adequate to meet the minimum water requirement of the rice crop during its entire growth period.

The second pattern includes the provinces of Camarines Sur (Fig. 3b), Zamboanga, Negros Occidental, and Iloilo. In these provinces, some planting activity occurs even during the dry season. This could be because available rainfall, though not in excess of the minimum rainfall requirement, is at levels that can support the crop. It could also be a strategy to avoid the typhoon months of August–December, and at the same time capture the higher radiation during the dry season. The third pattern includes the provinces of Benguet, Cagayan (Fig. 3c), and Laguna, where substantial planting occurs in the dry season despite low rainfall levels. Average drought indices and grain yields of modern varieties during the wet season for a 120-day growing period were 56.5% and 2.3 t/ha, respectively, for Tarlac; 42.5% and 2.0 t/ha for Camarines Sur; and 65.0% and 2.0 t/ha for Cagayan. Yield differences during the wet season could also be attributed to typhoon damage (PhilRice-BAS 1995).

Investment in irrigation is still the main strategy to improve the productivity of existing rainfed farms. The level of irrigation investment has declined substantially in this decade. But with the projected higher

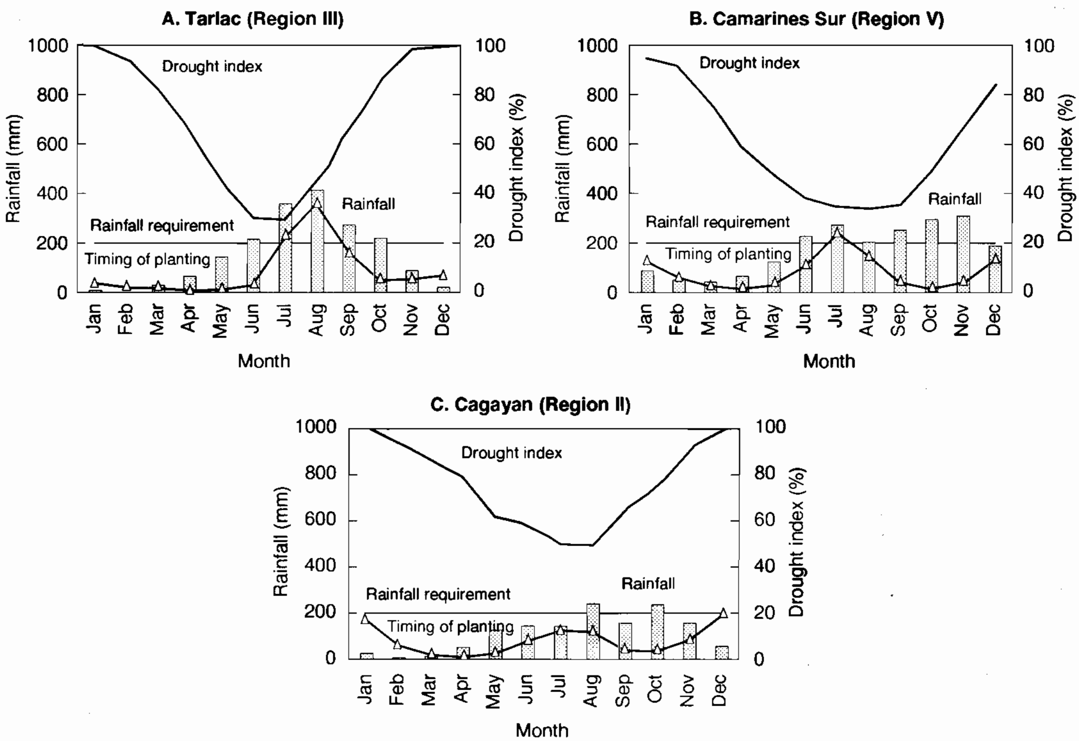

Figure 3. Rainfall, time of planting and drought indices (DI) for the provinces of (A) Tarlac, (B) Camarines Sur and (C) Cagayan.

world rice price under the general agreement on tariffs and trade (GATT), the economic returns of this type of investment are projected to increase. In addition, because rice production in rainfed ecosystems is restricted to very narrow time limits, reliable and timely weather forecasts will be a significant advantage to farmers.

Drought-Associated Problems in Rainfed Lowland Rice

The primary factor limiting rice yields in the rainfed lowlands is drought, which is reflected both in the extent of crop losses due to drought and in the priority given to this problem in breeding programs (Widawsky and O'Toole 1990). The combined effect of drought at anthesis and seedling stages caused more yield losses than those caused by weeds. Other causes of yield losses were submergence, lodging, blast, yellow stem borer, zinc deficiency and bacterial blight. A survey in rainfed lowland rice fields in the provinces of Bulacan, Tarlac and Nueva Ecija (W. Collado and R. Cruz, PhilRice 1996; unpublished data) indicated that farmers perceived three major problems: drought, typhoon and pests (Table 2). Few farmers indicated problems from salinity, acidity or soil mechanical impedance. Some farmers indicated that soils from their farms needed analysis. Some indicated that the interpretation and corresponding recommendations of soil analysis should be relayed to them quickly. Note that the provinces of Bulacan, Tarlac and Nueva Ecija have employed transplanting and wet direct-seeding methods (Table 2). While wet direct-seeding (broadcasting pregerminated seeds onto wet, puddled and levelled soil) could reduce labour costs during seedling establishment, it requires a high seeding rate and can result in poor crop stand due to bird, rat and snail damage, poor root anchorage and exposure to moisture stress (Cruz et al. 1995). To improve crop stand, anaerobic seeding technology (i.e. broadcasting pregerminated seeds into the soil immediately after the final harrowing and land levelling) is being tested in farmers' fields in Nueva Ecija. Machines which can reduce seeding rates and give good crop stand are also being tested.

In a large monitoring study in rainfed lowland rice fields in several municipalities in San Jose, Nueva Ecija, Sanchez et al. (1995) reported that the major rice diseases were blast, sheath blight, leaf spot and rice tungro virus. Major pests were stem borers (*Scirpophaga*) and weeds *Echinocloa glaberescens*. Bonman et al. (1988) indicated that water deficit at the vegetative stage increased the severity of both leaf and neck blast (*Pyricularia oryzae* Cav.) in dry-season upland rice (Cv. C22). The greatest disease development occurred in drought-stressed plots after irrigation, due to increased host-plant susceptibility.

When rice breeders of South and Southeast Asia were asked to rank the weaknesses of rainfed lowland varieties currently grown in their localities, lack of disease and insect resistance emerged as the most significant shortcoming, followed by lack of drought and flood tolerance, low yield potential, low tolerance for problem soils, weak straw, response to

Table 2. Common problems perceived by rainfed lowland rice farmers in several municipalities in Region III (see Table 1) provinces of Bulacan, Tarlac and Nueva Ecija, Philippines.

Province/municipality	Crop establishment	Soil type	Problems perceived
Bulacan			
San Rafael	WDSR > TPR	Medium to heavy clay	Drought, typhoon and pests
San Ildelfonso	TPR > WDSR	Light to medium clay	Drought, typhoon and pests
Tarlac			
Victoria	TPR, WDSR	Heavy clay	Drought, typhoon and pests
Nueva Ecija			
Guimba	TPR > WDSR	Medium to heavy clay	Drought, typhoon and pests
Cuyapo	TPR, WDSR	Heavy clay	Drought, typhoon and pests

TPR = transplanted rice; WDSR = wet direct-seeded rice
Note: Salinity, acidity, and soil mechanical impedance were considered as drought-associated problems by few farmers
Source: Collado and Cruz (unpublished data 1996)

inputs and grain quality (Mackill 1986). For rainfed lowland rice breeding programs, the most relevant accessions are those that tolerate drought, submergence and adverse soils (Mackill et al. 1996). Many agricultural scientists have sought to overcome the drought 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. The rationale is that rice is a semiaquatic species and therefore has not developed many of the adaptations like deep rooting habit and thick epicuticular wax that have evolved in upland crops such as wheat, sorghum and maize. However, it would be impossible to provide sufficient irrigation to large rainfed areas, and thus rice breeders are now challenged to improve varietal resistance (Mackill et al. 1996). We suggest that, to be more effective, drought and drought-resistance problems should be approached by a team of plant breeders, plant physiologists, agronomists, soil physicists, meteorologists, socioeconomists, and farmers. Farmers have wide experience in coping with drought-related stresses in the environment and with socioeconomic problems. Hence, research on rainfed lowland rice drought resistance and its management must be built upon the practice and knowledge of farmers.

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Modelling Approach for Estimation of Rice Yield Reduction Due to Drought in Thailand

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Abstract

A rice simulation model was used to estimate yield reduction due to drought in rainfed lowlands using data from experiments conducted for three years at nine locations in Northern and Northeastern Thailand. Actual grain yield was well estimated by the simulations ($r = 0.89$, $n = 27$). Irrigated conditions were simulated for each location and large differences in grain yield existed. These differences were attributed largely to differences in radiation-use efficiency, which reflects soil fertility, seeding date and seedling age at transplanting. Estimated yield loss due to drought after transplanting using 20 years rainfall data ranged between 11 and 58%, depending on location. The large yield reductions at some locations were attributed to low rainfall after transplanting, partly due to late seeding. Estimates of free water at these locations also indicated that a low water table at transplanting reduced yield. The simulation model is a useful tool, complementing experimental work, in rainfed lowland rice research.

Drought in Rainfed Lowland Rice in Thailand

RAINFED lowland rice culture occupies 6.7 million ha of a total rice area of 9.6 million ha in Thailand of which 3.7 million ha of rainfed lowland rice is grown in the Northeastern Region. Drought is considered the major problem affecting yield of rainfed lowland rice, particularly in the northeast, due mainly to rainfall distribution and soil type (Fukai et al. 1995), which will influence retention of standing water. Drought may develop at any stage of plant growth, and has been classified into early-season drought, affecting transplanting; intermittent drought during crop growth; and late-season drought, which develops at the end of the rainy season before crop maturation (Jearakongman et al. 1995). Large yield reductions are observed (Garrity and O'Toole 1994; Lilley and Fukai 1994) when rice is subjected to drought during the reproductive stage. However, drought in the vegetative stage does not cause such large yield reductions (Lilley and Fukai 1994).

Normally farmers transplant rice seedlings during July–August. However, drought at this time is a major problem (Fukai et al. 1995) and causes delay in transplanting, with subsequent use of old seedlings, which can result in yield loss. Immark et al. (these proceedings) noted that, depending on photoperiod sensitivity, a delay of 20 days in transplanting can result in 5–9 day delay in flowering and this may expose the crop to a late-season drought. In some years drought may cause complete crop failure.

The rainfed lowland ecosystem is characterised by uncertain moisture supply, with high year-to-year variation in amount and distribution. Fukui (1982) reported that drought is one of the most significant causes of year-to-year fluctuations of rice production in Thailand. Hossain (1995) suggested that appropriate crop models are needed to simulate growth for variable environments and examine the effects of variable weather on yields.

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Modelling Approach for Estimation of Yield Variation

A crop model quantifies plant growth processes and their responses to environmental factors. Models can be used to assist in the extrapolation of research results of field experiments in time and space and to assess the potential of new technologies. Wopereris et al. (1995) noted that a number of rice simulation models have been used successfully in the past to evaluate the diverse and variable rainfed lowland ecosystems.

The rice model used in the present study was originally designed for upland conditions (Boonjung et al. 1993) and it has been further developed for rainfed lowland conditions for the photosensitive cultivar KDML105, using data from six environments in Northeastern Thailand (Fukai et al. 1995). Unlike other rice models, for example, RICEMOD and CERES-Rice, which are based on comprehensive physiological processes, this model is based on well-specified field data under particular growing conditions and is considered a simplified process model.

The aim of this study was to investigate yield variability and yield loss due to drought for rainfed lowland rice in Northern and Northeastern Thailand using 20 years of rainfall data. The sensitivity of the model was investigated, and the model was used to estimate differences between potential yield under irrigated conditions and yield estimates for rainfed lowland conditions.

A Rice Model for the Rainfed Lowland Ecosystem

A simulation model for rainfed lowland rice was developed for the photoperiod sensitive cultivar KDML105, widely grown in Northeastern Thailand (Fukai et al. 1995). The model describes crop growth processes on a daily basis and consists of a number of major submodels. It estimates phenological development, taking into account photoperiod sensitivity, length of basic vegetative phase, date of seeding and available water content. A water-balance submodel estimates soil–water content and free water level above or below the paddy soil surface for each day after transplanting to maturity. Crop growth rate (CGR) is calculated from incident solar radiation, the proportion of radiation intercepted by the canopy, and radiation use efficiency (RUE) when water is not limiting. When plants are water stressed due to low soil–water content, CGR is calculated as a product of transpiration and transpiration efficiency. Assimilate partitioning depends on phenological stage. Yield components are determined by CGR at various growth stages and independently of CGR when water stress develops at anthesis and early grain filling. A full description of the model has been given by Fukai et al. (1995).

Model Inputs

A simulation study was conducted that utilised inputs from multienvironment experiments conducted over three years at nine locations (1992–94) in Northern and Northeastern Thailand (see map on page x, Introduction):

- Sanpatong (SPT)
- Phrae (PRE)
- Phitsanulok (PSL)
- Chum Phae (CPA)
- Khon Kaen (KKN)
- Ubon Ratchathani (UBN)
- Sakon Nakhon (SKN)
- Surin (SRN)
- Phimai (PMI)

Input parameters (Table 1) required to run the model are seeding and transplanting dates; seedling age and level of free water at transplanting; weather conditions, daily rainfall, pan evaporation, solar radiation and temperature; and soil conditions, water-holding capacity in the top 50 cm layer, deep percolation rate and estimates of soil fertility level which are incorporated in RUE values (Fukai et al. 1995). The percolation rates were estimated each week at each location by monitoring the free water level above or below the soil surface within a 50-cm long PVC pipe inserted into the paddy. RUE was calculated from an independent data set for four locations (CPA, KKN, SRN and PMI); the average from these (2.5 g/megajoule [MJ]) was then used for SPT, PRE and PSL. The RUE was reduced by 20% for UBN and SKN, which have poor soil fertility.

Comparison with Experimental Results

Simulations were conducted using actual input data for seeding date, seedling age at transplanting, free-water level at transplanting, and available soil–water content estimates for each of nine locations over three years (1992–94). Rainfall data were available for each location.

Table 1. The parameter values of nine locations, 1992–94.

Parameters	Location								
	SPT	PRE	PSL	CPA	KKN	UBN	SKN	SRN	PMI
Seeding date[1]									
1992	17 Jul	16 Jul	20 Jul	13 Jul	20 Jun	23 Jul	13 Jul	31 Jul	15 Jul
1993	20 Jul	8 Jul	16 Jul	9 Jul	25 Jun	16 Jul	8 Jun	21 Jun	13 Jul
1994	19 Jul	8 Jul	12 Jul	8 Jul	1 Jul	11 Jul	16 Jun	1 Jul	12 Jul
Seedling age[2] (days)									
1992	35	27	25	29	25	42	30	31	30
1993	31	38	42	38	41	40	30	29	28
1994	37	25	28	25	46	36	26	31	35
Free water[3] (mm)									
1992	–1000	50	50	10	50	10	50	50	10
1993	–1000	50	50	–1000	–200	10	50	0	–200
1994	–1000	50	10	–1000	–200	10	50	0	–100
Percolation rate (mm/day)	1.5	1	1	1.5	2	6	4.5	0	1.5
RUE[4] (g/MJ)	2.5	2.5	2.5	2.5	2.4	2.0	2.0	2.5	2.7
AWC_{max}[5] (mm)	75	75	75	75	75	55	75	75	75

[1] Seeding date was the actual seeding date used in the experiments
[2] Seedling age was at transplanting
[3] Free water was the estimated free water level above or below the soil surface in the paddy at the time of transplanting
[4] RUE = radiation-use efficiency (reflects soil fertility differences)
[5] AWC_{max} = maximum available water content (was assumed to be lower for UBN due to the sandy nature of the soil)
Note: Experiments were conducted for three years and these values were used to run simulations

At SPT, the 50 mm irrigation applied once in 1993 and in 1994 was added to the rainfall input just before the anthesis stage. In some locations, daily data on pan evaporation and solar radiation were not available. The pan evaporation data from adjacent locations were used when the data were not available for a particular location. For 1992 simulations, 1992 SPT solar radiation data were used, while for 1993 and 1994, 1993 SPT solar radiation data were used for all simulations.

The actual grain yields obtained in the experiments were reasonably well estimated by the model, with a correlation coefficient of 0.89 (Fig. 1). The 3-year average for actual and simulated yields for each location is given in Table 2. The actual yield ranged from 0.86 t/ha at UBN to 3.72 t/ha at SPT. The simulated yield ranged from 0.78 t/ha at UBN to 3.89 t/ha at SRN. For both the actual and simulated yields, UBN and CPA were the lowest-yielding locations, the simulations indicating a 68% and 58% yield reduction due to drought, respectively. Similarly, on average, in both actual and simulated yields the three highest-yielding sites were SPT, SRN and PSL; however some re-ranking did occur.

Location Differences in Yield under Irrigated Conditions

The 1993 actual parameter values were utilised to run each simulation for irrigated conditions (Table 2). For all locations the same irrigation (including rainfall) input was used, in which 50 mm was applied every five days. Total irrigation input varied due to seeding date differences, but on average each simulation received 1200 mm. According to the simulations, this was sufficient to cause no water stress throughout growth.

Large variation in irrigated yield was obtained from the nine locations, ranging from 2.46 t/ha at UBN to 5.23 t/ha at PMI. The irrigated yields were also quite high at SRN (4.86 t/ha) and PSL (4.67 t/ha), while SKN (3.40 t/ha) and CPA (3.44 t/ha) were relatively low yielding. To investigate why different simulated yields were obtained at the different locations under irrigated conditions, the 1993 inputs at UBN were adjusted one by one to the inputs used at SRN in the same year (Table 3).

Table 2. Simulated and actual yields of KDML105 at nine locations in Northern and Northeastern Thailand.

Actual and simulated yields (t/ha)	Location									
	SPT	PRE	PSL	CPA	KKN	UBN	SKN	SRN	PMI	Mean
Irrigated yield (1993) — simulated	4.05	3.85	4.67	3.44	3.82	2.46	3.40	4.86	5.23	3.98
3–year average (1992–94)										
Rainfall (mm)	452[2]	277	422	428	405	563	744	420	348	443
Yield — simulated	3.37	3.23	3.58	1.45	2.93	0.78	2.30	3.89	2.99	2.72
Yield reduction[1] (%)	17	16	23	58	23	68	32	20	43	33
Yield — actual	3.72	3.11	3.47	1.74	3.00	0.86	2.30	3.66	2.60	2.72
20–year average (1975–94)										
Rainfall (mm)	423	361	446	434	521	506	846	687	412	515
Yield — simulated	2.73	3.02	3.23	1.86	3.23	1.03	2.32	4.33	2.47	2.67
Yield reduction[1] (%)	33	22	31	46	15	58	32	11	53	34

[1] Compared to irrigated yield — simulated
[2] Excluding 50 mm irrigation in 1993 and 1994

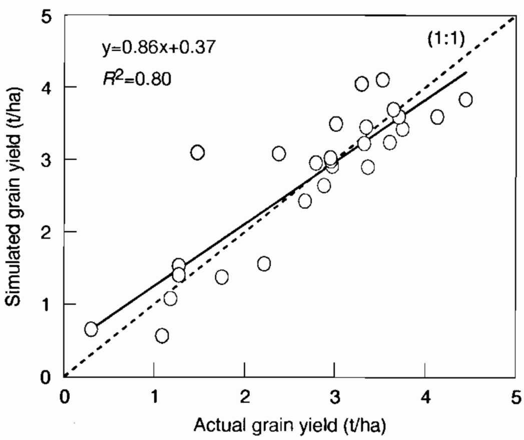

Figure 1. Relationship between simulated and actual grain yield obtained over three years (1992–94) at nine locations in Northern and Northeastern Thailand.

Table 3. Simulated yield under irrigated conditions with UBN inputs and after modifying parameter values of inputs to those used at SRN.

Inputs	Changes	Yield (t/ha)	%Yield increase
(1) UBN inputs (1993)	–	2.46	0
(2) RUE	increased 0.5 g/MJ	3.93	60
(3) seeding date	25 days earlier	2.74	11
(4) seedling age at transplanting	11 days younger	2.56	4
(2)+(3)	RUE and sowing date	4.35	77
(2)+(3)+(4)	RUE, sowing and seedling age	4.88	98

RUE = radiation-use efficiency (reflects soil fertility differences)

With an increase in RUE from 2.0 g/MJ to 2.5 g/MJ, plants at UBN were estimated to produce more total dry matter, which led to a 60% increase in grain yield. Similarly, when seeding was conducted 25 days earlier, on June 21 instead of July 16, simulated yield at UBN increased by 11%. Seedling age at transplanting was adjusted and this contributed to a 4% yield increase. When these three factors were combined, a 98% increase was observed, and this yield was similar to that obtained at SRN. It is noted that the resultant yield indicates an interaction effect is present as the increase from the combined effect was larger than the sum of the individual increases. Thus, in terms of the model, low yields under irrigated conditions were attributed to low RUE, delayed seeding date and increased seedling age.

Estimation of Yield Loss Using Rainfall Data for Twenty Years

The simulation model was run for 20 years at each of nine locations using actual rainfall data from 1975 to 1994 to estimate the yield loss due to drought. For these simulations the parameter values (for example, seeding date and seedling age, level of free water, etc.) came from the actual 1993 data for each location (Table 1).

The average rainfall received and estimated grain yield for the 20 simulations at each location is shown in Table 2. As expected, yields were reduced in comparison with the irrigated simulations, by 11% to 58% depending on location. A 34% yield reduction was observed across all locations. For the 20-year average UBN, PMI and CPA had the largest yield reductions, of 58%, 53% and 46%, while SRN and KKN had the lowest, 11% and 15%, respectively.

The large reductions in grain yield observed at some locations can be attributed to lower rainfall after transplanting, partly due to late seeding, in combination with low water tables at these locations; this occurred, for example, at KKN relative to CPA, which are reasonably close geographically. When simulations were conducted at CPA using KKN inputs for seeding date and free water level, the average grain yield for three years (1992–94) was 2.85 t/ha, very close to that of KKN (2.93 t/ha).

The absolute difference in rainfall is not the only important factor; the timing of rainfall in relation to the developmental phase of the crop is also important. Fukai and Cooper (1995) highlighted the importance of matching crop phenology to the target environment. The simulation model takes this into account, and Table 4 indicates the frequency of occurrence of drought at the different growth stages at UBN, with drought defined here as at least two consecutive days when the fraction of extractable soil water drops below 0.75.

Table 4. Total rainfall from transplanting to maturity, simulated grain yield and drought development between growth stages[1] for simulations at UBN, 1975–94.

Years	Rainfall (mm)	Growth stages[1]			Simulated yield (t/ha)
		PI–A	A–MGF	MGF–M	
1975	666			*	1.89
1976	569		*	*	1.22
1977	374	*	*	*	0.48
1978	449	*	*	*	0.78
1979	307	*	*	*	0.11
1980	636		*	*	1.94
1981	302	*	*	*	0.76
1982	600		*	*	1.74
1983	467		*	*	1.37
1984	709			*	2.05
1985	513	*	*	*	0.77
1986	533		*	*	0.93
1987	595		*	*	1.46
1988	368	*	*	*	0.43
1989	432	*	*	*	0.57
1990	547	*	*	*	1.00
1991	597		*	*	1.12
1992	475		*	*	0.97
1993	389	*	*	*	0.58
1994	596	*	*	*	0.53
Average	506	(50%)	(90%)	(100%)	1.03

[1] PI = panicle initiation; A = anthesis; MGF = mid-grain filling; M = maturity
*Initiation of stress (drought)

In 20 years of simulation, drought did not develop between transplanting and panicle initiation; however, drought developed in 50% of the years between panicle initiation and anthesis; 90% between anthesis and mid-grain filling; and every year between mid-grain filling and maturity. In general, low yields were achieved in low-rainfall years (e.g. 1979), and high yields in high-rainfall years (e.g. 1984). However, in some years (e.g. 1994), stress developed at a critical stage and yield was low despite high total rainfall.

For most locations the average percentage yield reduction obtained from the 3-year (1992–94) and 20-year (1975–94) simulations were similar (Table 2). Differences reflected differences in rainfall, with the 3-year simulation involving lower rainfall, particularly in 1993. At a number of locations, a 10–12% difference existed between the two estimated yield reductions (e.g. UBN, CPA and PMI). However, the 3-year average for PMI was less than the 20-year average, while for UBN and CPA it was higher. These results highlight the importance of simulation modelling as a tool in scientific research, as experiments conducted for a 3-year period may not accurately represent the long-term average.

The yield loss estimates for KDML105 are due to drought that develops after transplanting. Transplanting failure or use of old seedlings was prevented in the experiments by using irrigation water at transplanting. Thus, the effect of drought on grain yield would be greater than that estimated here when yield loss due to lack of water at transplanting is included. Also, the yield loss would be greater if cultivars were used which mature later than KDML105, and would be smaller if they matured earlier than KDML105 (Satit Rajatasereekal et al., this volume).

Comparison of Yields at Ubon Ratchathani and Sakon Nakhon with Twenty Years of Rainfall Data

The patterns of average monthly rainfall at UBN and SKN for 20 years were similar (Fig. 2) but SKN had higher rainfall from June to August, while UBN had greater rainfall between September and November. At both locations rainfall decreased from September through December.

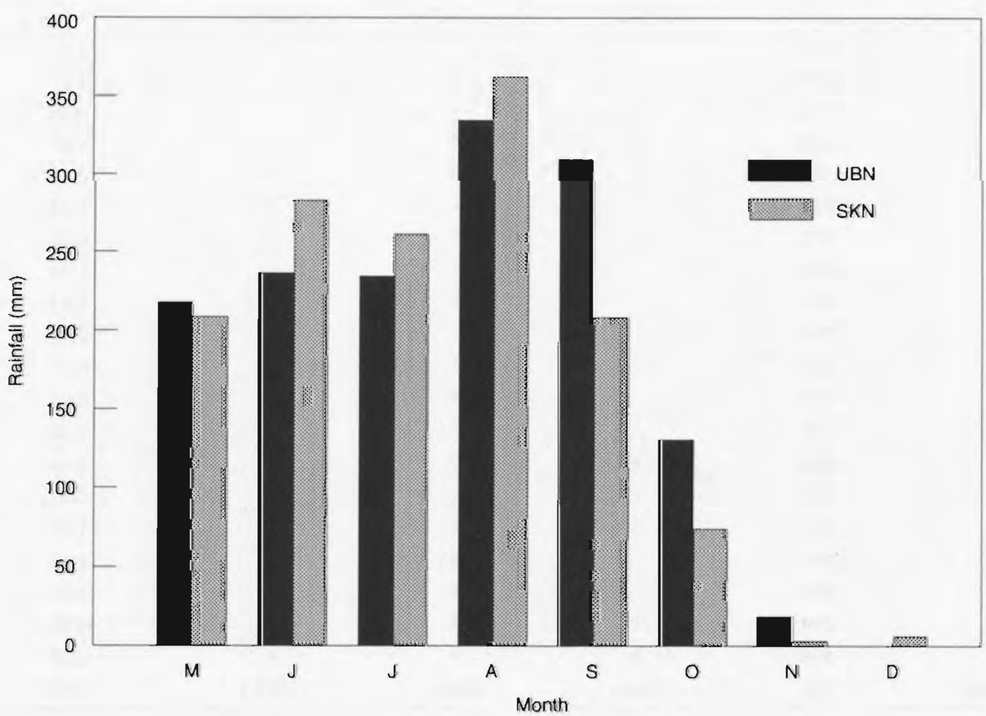

Figure 2. Average monthly rainfall (20 years) at UBN and SKN.

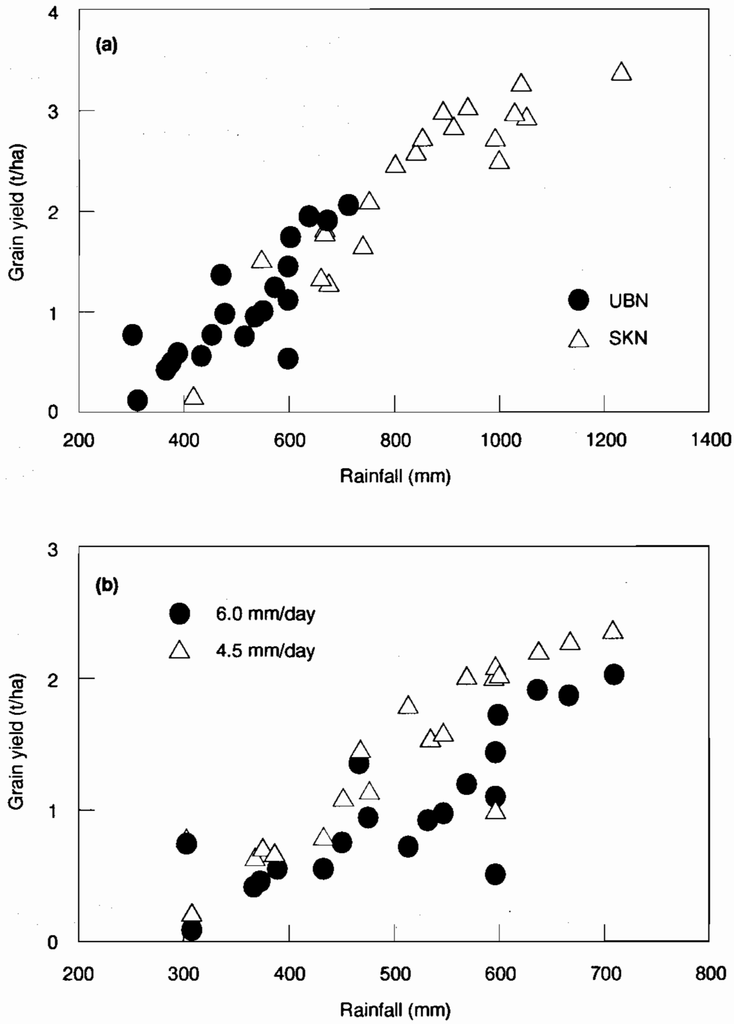

Figure 3. Relationship between rainfall and simulated grain yield between 1975 and 1994 (a) at UBN and SKN and (b) at UBN as affected by percolation rates (6.0 and 4.5 mm/day).

The association between yearly rainfall after transplanting to maturity and simulated yield for 20 years at UBN and SKN indicated that yields at SKN were generally higher than at UBN (Fig. 3a). This is in part due to the fact that plants at SKN were seeded 38 days earlier than at UBN and were therefore exposed to more rainfall, a finding supported by Somdej Immark et al. (this volume). The grain yields at SKN ranged between 0.13 t/ha and 3.37 t/ha, with rainfall ranging from 412 to 1229 mm, while at UBN grain yields were 0.11–2.05 t/ha, with rainfall ranging from 302 to 709 mm. One possible reason for the lower yield at UBN was the higher percolation rate of the soil at that site. This was tested by running the simulation for 20 years with the percolation rate reduced from 6 to 4.5 mm/day, as at SKN (Fig. 3b). For a given rainfall, grain yield increased with reduced percolation rate.

To demonstrate the effect of seeding date, simulations using 1993 input data for UBN (Fig. 4a) and SKN (Fig. 4b) were conducted with four seeding dates: 8 June (seeding date at SKN), 20 June, 3 July and 16 July (seeding date at UBN). As seeding date was delayed at both locations, the probability of obtaining a high grain yield was reduced, the effect being greater at UBN than SKN.

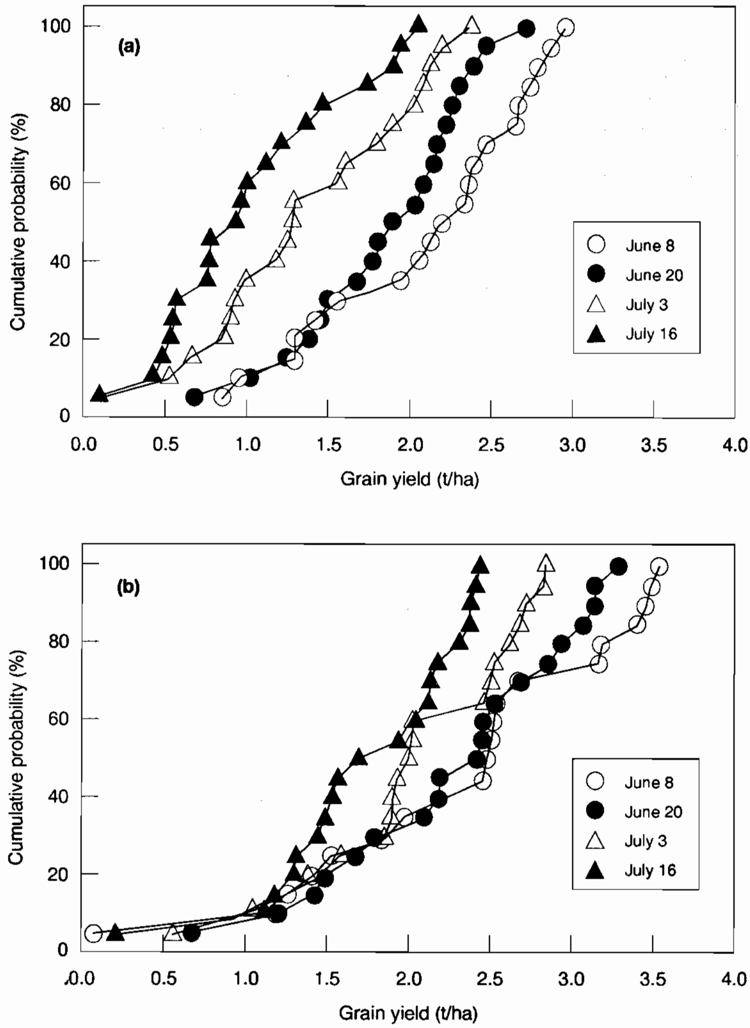

Figure 4. Cumulative probability of grain yield at (a) UBN and (b) SKN, for different seeding dates.

Conclusion

Simulation yields using the model were well correlated with actual data. The results of 20 years simulation at nine locations has suggested that rainfall distribution from transplanting to maturity was a major determinant of grain yield. As well as rainfall differing due to location and year-to-year variability, rainfall after transplanting varied due to seeding date and seedling age. Other factors, such as percolation rate and soil fertility, also affected simulated yield. Early sowing, young seedling age, low percolation rate and high soil fertility are factors which contribute to increased yield according to the simulations. Overall, the simulation model was considered a useful tool, complementing experimental work, in rainfed lowland rice research.

Acknowledgment

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Drought Problems and Genotype Requirements for Rainfed Lowland Rice in Lao PDR

Phoumey Inthapanya*, Sipaseuth*, Vorachit Sihathep*, Monthathip Chanphengsay* and Shu Fukai†

Abstract

Thirty-nine cultivars mostly adapted for the rainfed lowland ecosystem were compared in Vientiane in the upper central region and Champassak in the southern region in three wet seasons to determine the extent of the drought problem and genotype requirements for rainfed lowland rice in Lao PDR.

In Vientiane, total rainfall during the wet seasons was less than in Champassak and rain generally stopped earlier, causing standing water in the paddies to disappear earlier. Under this condition of late-season drought, medium–late flowering cultivars, including some popular Thai cultivars, did not perform well. In contrast, early–maturing cultivars, which were mostly photoperiod insensitive or only mildly sensitive and flowered in late September to early October, generally produced higher yield. On the other hand, a higher total amount of rainfall and late-season rainfalls in Champassak allowed medium–late flowering cultivars to produce yields similar to those of earlier-flowering cultivars. There was a significant cultivar-by-location interaction for yield, suggesting that different cultivars are required for the southern and the upper central regions. Matching phenology development with water availability in the paddies is required for high yield. Among 15 early–medium flowering cultivars that were not affected by late-season drought in either location, semidwarf cultivars with a larger number of panicles tended to produce higher yield, although the cultivar differences were not significant ($P < 0.05$) in any experiment. The improved Lao cultivar Thadokkham 1 and Thai line IR57514-PMI-5-B-1-2 performed well in all the experiments.

RAINFED lowland rice accounts for 64% of the rice-growing area and 74% of rice production in the Lao People's Democratic Republic (Lao PDR). Average annual rainfall in much of the rainfed lowland area ranges between 1200 and 1500 mm, 70% of which falls during the period June–September. Drought occurs frequently in this rice ecosystem in the Lao PDR, and is considered to be the major constraint for rice production in most rainfed lowland regions of the country (Phoudalay Lathvilayvong et al., this volume). Thus, agronomic practices to minimise drought effects and development of cultivars that yield well even under water-limiting conditions are required for enhanced rice production for Lao PDR as well as for other countries. The main rainfed lowland rice area in Lao PDR extends from Vientiane Province in the upper central region to Champassak Province in the south. Rainfall patterns and soil type vary within the area (Phoudalay Lathvilayvong et al., this volume), and hence drought development patterns and cultivar requirements are expected to differ in different regions.

Cultivars currently grown in the rainfed lowland ecosystem in Lao PDR are almost exclusively glutinous endosperm types, with more than 85% of the area being sown to traditional, photoperiod sensitive cultivars. Each farmer commonly grows 2–4 cultivars of different maturity types. A plant improvement program for rainfed lowland rice has commenced recently in Lao PDR. The program has released three cultivars that are generally adapted to the Lao conditions. They are semidwarf statured and photoperiod insensitive, and mature in 130–140 days after sowing

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(Inthapanya et al. 1995). The Lao improvement program relies heavily on Thai germplasm, particularly glutinous endosperm types. Hence it is useful to compare improved and traditional cultivars grown in Thailand and those that grow well in Lao PDR, so that the types of Thai materials likely to be useful for introduction or used as parents for crossing in Lao PDR can be determined.

The objectives of this work were:

- to determine drought development patterns and cultivar requirements for the two locations in the rainfed lowland area in Lao PDR;
- to compare improved Lao cultivars with improved and traditional Thai cultivars under various growing conditions; and
- to identify plant types that are associated with high-yielding cultivars for the rainfed lowland ecosystem.

Materials and Methods

Wet-season experiments were conducted at the National Agricultural Research Centre, Vientiane Municipality in the upper central region, and Phon Ngam Station, Champassak Province in the southern part of the Lao PDR in 1993–1995. Each experiment involved 39 cultivars, including four Lao cultivars (Thadokkham 1, Phon Ngam 1, Leuang and Khao Takhiad), with three replications. Each plot was 1.5 × 5 m. The other 35 cultivars were mostly from Thailand, including some improved cultivars.

The seeds were sown on 17, 29 and 22 June in Vientiane and 18, 13 and 14 June in Champassak in 1993, 1994 and 1995, respectively. Seedlings at the age of 26–35 days old were transplanted at three seedlings per hill. There were 16 hills per m^2. In the Vientiane 1993 experiment, it was necessary to irrigate the paddy for transplanting, but no irrigation was used in any other experiment. Basal fertiliser at the rate of 24 nitrogen (N), 30 P_2O_5 and 20 K_2O kg/ha was applied at transplanting, and top-dressing of 16 kg N/ha was applied about 20 days after transplanting, except in Champassak in 1994, when top-dressing of 36 kg N/ha was applied 35 days after transplanting. The Vientiane 1993 experiment followed a crop of soybean and the Champassak 1994 experiment was in the plot of seed multiplication where fertiliser was applied in the previous season. All other experiments followed the unfertilised rice crop grown in the previous wet season. Some chemical and physical properties of the sandy loam soils used in the experiments are shown in Table 1.

Table 1. Some chemical and physical properties of the soil at Vientiane (1994) and at Champassak (1993).

	Vientiane	Champassak
pH (H_2O)	5.4	5.5
Organic matter (%)	0.77	1.31
Total nitrogen (%)	0.056	0.072
Available phosphorus (ppm)	5.85	1.25
Available potassium (K_2O mg/100 g soil)	1.8	3.0
Soil texture		
Sand (%)	58.9	53.4
Silt (%)	27.3	37.2
Clay (%)	13.8	9.3

Dates of panicle initiation and 75% flowering were recorded. Free water level in the paddy was determined using 50-cm long PVC tubes that were embedded in the ground. At maturity the plants in the central 4 m × 1 m area were harvested, and grain yield (at 14% moisture content) and yield components were determined.

Results

In Vientiane in 1993, rainfall was generally favourable until September but was very low in October (Table 2). High rainfall at the end of July and early August, immediately after transplanting, caused some flooding damage in Vientiane both in 1994 and 1995. Rainfall was generally higher in Champassak than in Vientiane except in August 1995, when it was less than half the average monthly rainfall.

In Vientiane, standing water disappeared from the paddies in late September–early October in both 1993 and 1995, and cultivars that flowered after late October produced very low yields (Fig. 1). The second order polynomial regression was used to describe the relationship between grain yield and flowering date for all experiments. For Vientiane, the optimum flowering time estimated from the regression was late September in 1993 and 1995, and mid-October in 1994, when sowing was delayed and standing water lasted until the end of October. For Champassak, the estimated optimum time was early October in all years. It was 10–22 days before the date when standing water disappeared in all experiments. Grain yields of early–medium flowering cultivars that were not affected by drought were the highest in Vientiane in 1993, followed by Champassak in 1994 and 1995, and the lowest in Champassak in 1993 and Vientiane in 1994 and 1995. Combined analysis of variance for the six experiments

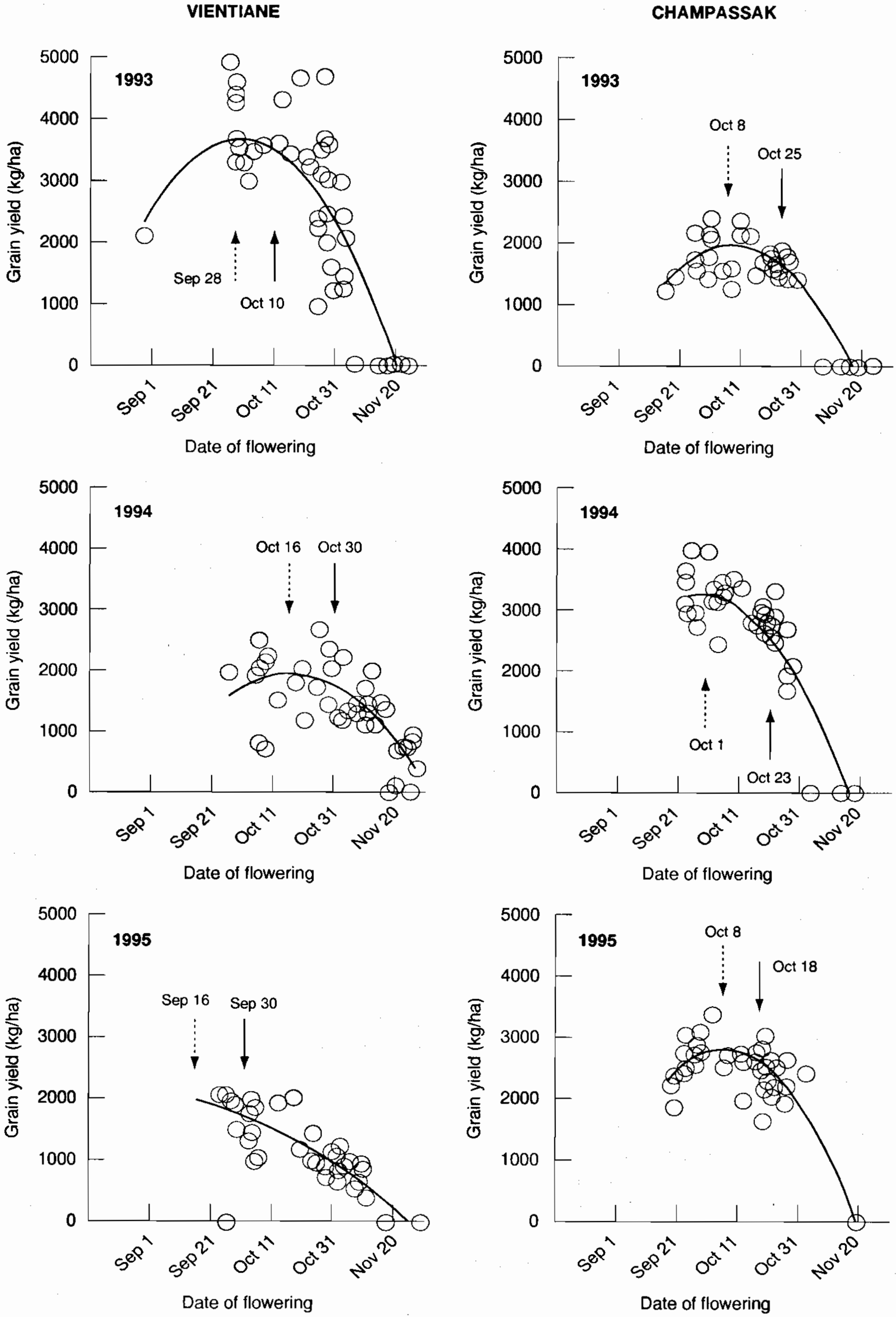

Figure 1. Relationships between grain yield and flowering date of 39 cultivars grown under rainfed lowland conditions in Vientiane and Champassak, Lao PDR, 1993–95. The date and arrow indicate the time of disappearance of standing water from the paddies (solid arrow), and optimum flowering date (dotted arrow).

Table 2. Monthly rainfall (mm) at Vientiane and Champassak (May–November, 1993–95) and the average for the last 20 years.

	Vientiane				Champassak			
	1993	1994	1995	20-year mean	1993	1994	1995	20-year mean
May	199	273	228	270	142	254	169	201
June	448	470	360	284	147	360	321	325
July	315	193	765	264	180	516	636	376
August	221	400	750	297	336	538	181	501
September	475	304	211	290	393	697	194	297
October	7	102	93	99	94	98	93	117
November	0	0	0	14	7	24	35	18

shows a strong effect of cultivar ($P < 0.01$) and also of cultivar, location and year interaction ($P < 0.01$).

Phenology effect on grain yield was examined further by grouping 39 cultivars into seven phenology groups according to the mean flowering date of each cultivar. Cultivar names and mean time taken to flowering for each phenology group are listed in Table 3. It is noted that the four Lao cultivars belong to early, early–medium and medium phenology groups. The two most common cultivars for the rainfed lowland ecosystem in Thailand (RD6 and KDML105) belong to the medium–late group, and most traditional Thai cultivars flower later.

In Vientiane, group mean yield was highest in the early group in all three years. Yields of the medium and early–medium groups were not much different from the yield of the early group, whereas the three late groups produced much lower yields (Fig. 2). In Champassak, the yield was highest in the medium group in all three years, followed by early–medium and early groups, but the yield reductions in the medium–late and late groups were rather small.

Since the early, early–medium and medium groups were little affected by drought in any experiment, all 15 cultivars in these groups were compared in an attempt to identify characteristics that were associated with high-yielding cultivars under favourable conditions. Analysis of variance for grain yield of the 15 cultivars in the six environments showed no significant cultivar effect. There was a significant cultivar-by-location interaction effect ($P < 0.05$), but no significant cultivar–soil fertility level interaction — high fertility (Vientiane 1993, Champassak 1994 and 1995) vs low fertility (Vientiane 1994 and 1995 and Champassak 1993). A reason for the cultivar-by-location interaction is that the genotypic variation in yield was smaller in Champassak than in Vientiane (Fig. 3). While two cultivars (Thadokkham 1 and IR57514-PMI-5-B-1-2) did well and Leuang Bun-

Table 3. A list of cultivars in each phenology group.

Group	Mean time to flowering (days)	Cultivars
Very early (1)	91	Lemont
Early (3)	100	RD23, Khao Takhiad*, IR43450-SKN-506-2-2-1-1
Early–medium (8)	106–115	Phon Ngam 1*, NSG19, Leuang*, RD10, Leuang Bun-ma, IR20, IR49766-KKN-54-B-B-6-1, IR43049-CPA-510-3-3-1-1
Medium (4)	118–123	Khao Strok, Thadokkham 1*, IR57514-PMI-5-B-1-2, IR43062-PMI-B-15-1-2-2
Medium–late (9)	126–132	RD6, KDML105, Lum Narai, Puang Sawan, E-Nawn, Leuang Samer, IR52532-SKN-23-B-1-2, IR57546-PMI-1-B-2-2, IR43506-UBN-520-2-1-1
Late (7)	133-138	KPM148, Chiangsaen, Khao Luang, Jumpah Tawng, Tah Tae, E-Pad, BKKBR82027-NSR-8-1
Very late (7)	145–155	LPT123, Leum Dern, Leuang Dawk Koon, Khao Yai, Daeng Noi, Chabah Sarahn, Taw Chaw Daw

*Lao cultivars

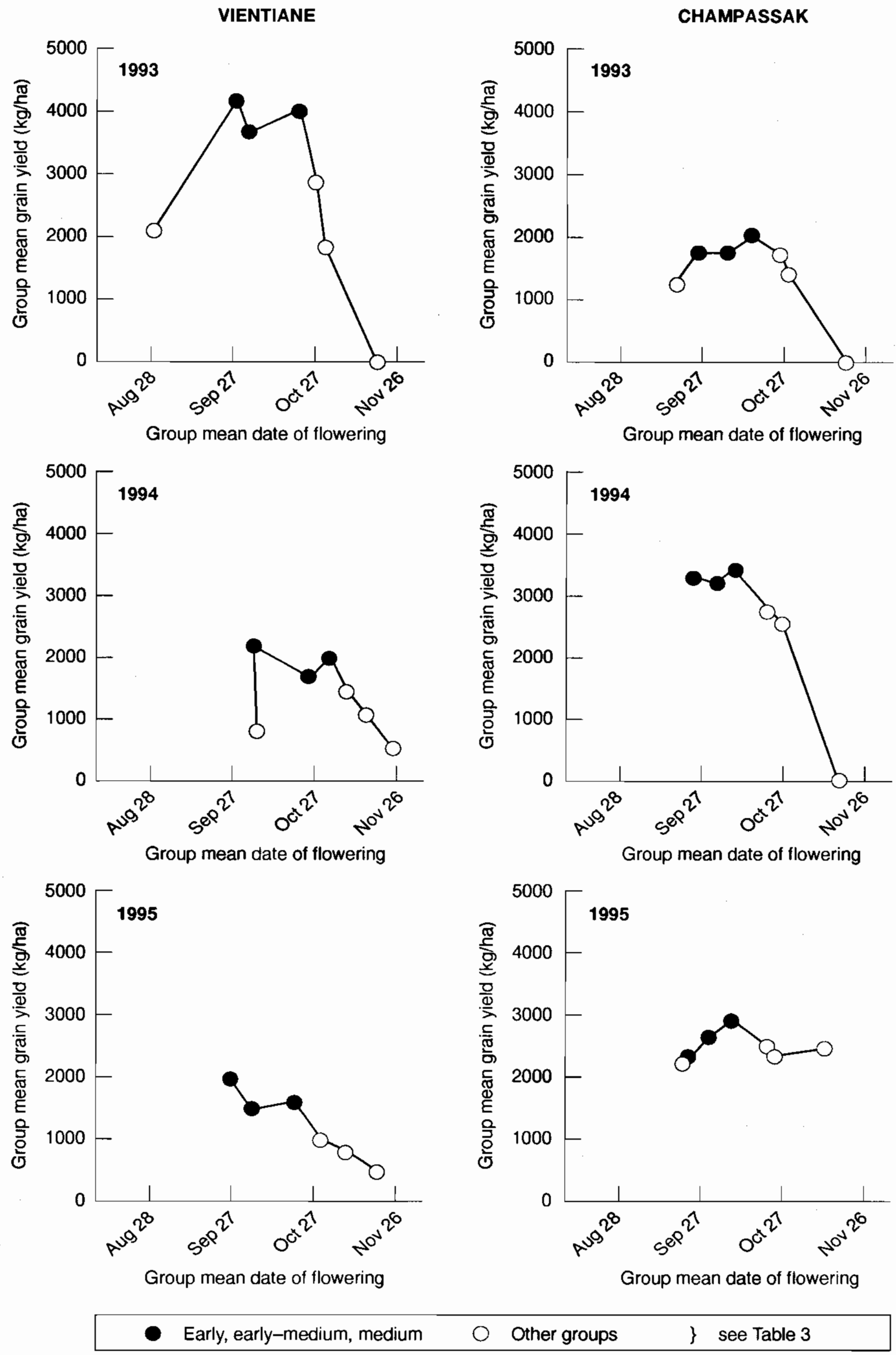

Figure 2. Mean grain yields of seven phenology groups under rainfed lowland conditions in Vientiane and Champassak, Lao PDR, 1993–95.

ma poorly in both locations, yields of other cultivars varied greatly in Vientiane but not in Champassak.

Among the 15 cultivars in these groups, grain yield tended to be correlated positively with panicle number per m^2 and negatively with plant height, but the correlation coefficients were not significant in any experiment. When all the six experiments were combined, there was a significant correlation (R^2 = 0.24) between grain yield and panicle number per m^2. Grain number per panicle, unfilled grain proportion, flowering time and the duration between panicle initiation and flowering were not correlated with grain yield.

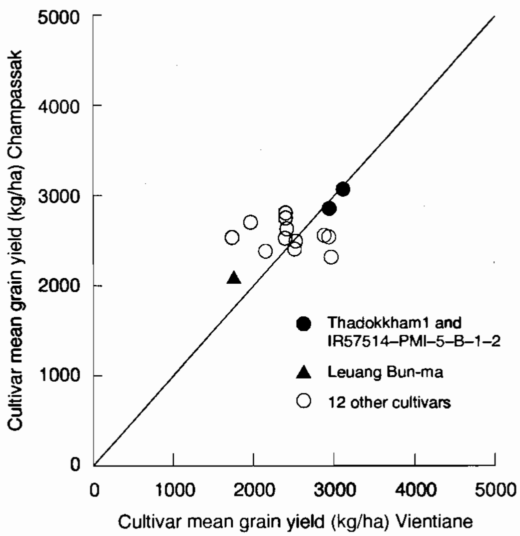

Figure 3. Relationship between cultivar mean grain yields for 15 cultivars in Champassak and Vientiane, 1993–95.

For the medium–late group there were nine cultivars, including RD6 and KDML105. Analysis of variance for grain yield showed no cultivar effect when combined for six experiments, but there was a significant cultivar–year–location interaction effect (P < 0.05). Analysis of variance for each experiment showed no significant variation among the nine cultivars in any location except Vientiane in 1993 when the medium–late maturing cultivars grown under high soil fertility experienced drought during the period from flowering to grain filling. High-yielding cultivars were E-Nawn and IR52532-SKN-23-B-1-2, whereas Leuang Samer produced a low yield. No significant correlations were found between grain yield and any yield component determined.

Discussion

The results of the experiments suggest that the two locations, Vientiane in the upper central region, and Champassak in the southern region, require different types of cultivars, due mostly to the differences in rainfall pattern. Paddies in the southern region with higher rainfall would be able to retain standing water for a longer period, and later-maturing cultivars can be used in addition to early–medium flowering cultivars. Thus for the crops sown in mid-June, cultivars that flower in 100–120 days after sowing in late September to mid-October are preferred in the Vientiane region, whereas for the southern region, cultivars flowering in 130 days after sowing up to late October may be acceptable. The early–medium flowering groups with flowering in 100–120 days after sowing should be the focus of plant breeding programs for rainfed lowland rice in the country, but for the southern region the material in the same phenology group as RD6 and KDML105 could be introduced from Thailand or other countries for testing in the Lao breeding program.

All 15 cultivars classified as early, early–medium and medium flowering are either photoperiod insensitive or mildly sensitive (Somdej Immark et al., this volume). Conversely, all cultivars except one in the medium–late, late and very late phenology groups are strongly photoperiod sensitive. This suggests that the Lao program may be most efficient by concentrating on photoperiod insensitive or mildly sensitive materials, particularly for areas with a high probability of late-season drought. Some local Lao traditional cultivars flower in September (Inthapanya et al. 1995), and these materials or photoperiod insensitive lines could be used for crossing to produce high-yielding, early-flowering cultivars. High yield potential under favourable conditions appears important for rainfed lowland rice in Thailand and Lao PDR (Satit Rajatasereekul et al., this volume), and high tillering and semidwarf stature may be important characteristics (Jearakongman et al. 1995), as also suggested in this study.

It should be noted, however, that development of late-season drought depends on not only rainfall but also deep percolation rate and lateral water movement in individual paddies. Thus cultivar requirement would depend on soil type, and earlier-flowering cultivars are required for paddies with sandy soils and high percolation rate, as was demonstrated by Fukai (1996) for

Northeastern Thailand using a simulation model. The present work suggests the strong dependence of phenology requirement on the date of disappearance of standing water. If the approximate date of disappearance of standing water is known for individual paddies, then cultivars may be chosen and planted in such a way that standing water would disappear from the paddies in mid-grain filling. There would be seasonal variation in rainfall and hence date of disappearance of standing water, and this variation should be taken into account when choosing cultivars. Jearakongman et al. (1995) have also shown from rainfed lowland experiments in Northeastern Thailand that yield declines rapidly as flowering takes place after disappearance of standing water late in the season. These experimental results support a general contention by Fukai and Cooper (1995) that the most important cultivar requirement for rainfed lowland rice is matching phenology with the water environment of the paddy concerned.

The results of the Vientiane 1993 experiment show that there was genotypic variation in grain yield within a phenology group (medium–late flowering) when drought developed in the latter part of growth cycle. In five other experiments where water stress did not develop or was only mild, there was no genotypic variation within the group. This suggests existence of drought-tolerance mechanisms in some cultivars. Jearakongman et al. (1995) found a drought-tolerant cultivar to be able to retain more green leaves and increase plant dry mass during a dry period when susceptible cultivars stopped growing and lost green leaves. Wonprasaid et al. (1996) found significant genotypic variation in grain yield under water-limiting conditions in rainfed lowland rice at Ubon Ratchathani, Thailand, when a high rate of farmyard manure was applied, but not under non-fertilised conditions. This suggests that the significant yield variation obtained in the group in Vientiane in 1993 was associated with the high soil fertility conditions and the variation was likely to be smaller under the lower soil fertility conditions of farmers' fields. It appears therefore important to determine genotypic variation against late-season drought under soil fertility appropriate for the target environments of a breeding program.

This work has shown common occurrence of late-season drought in the upper central region. Early-season drought could also develop, as was also shown in the Vientiane 1993 experiment, when transplanting could not take place due to the lack of standing water in the paddies. Without irrigation water in most farmers' fields, transplanting would have been delayed, and the use of old seedlings could have reduced yield potential. While monthly rainfall is generally high in July, there could be a period of low rainfall, resulting in a lack of standing water. In areas where there is a high probability of having no standing water at the appropriate time of transplanting, direct seeding may be an alternative to reduce the effect of drought.

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Phenology Determination in Rice

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Abstract

Durations of phenophases in rice show a wide range of diversity, depending on genotype and environment, and have a significant influence on growth and yield. In this paper, rice phenological responses to temperature, daylength and other minor determinants are briefly reviewed to give a base for modelling phenological development. Contrary to the traditional approach (in which the whole process of rice phenological development toward maturity has been analysed by dividing it into three phases: vegetative, reproductive and grain-filling), this paper considers a further subdivision of the vegetative and reproductive phases to give four preflowering development phases that take account of the photoperiod sensitive stage of rice development. These are: a juvenile (photoperiod insensitive) and a photoperiod inductive phase for panicle initiation; and photoperiod sensitive and insensitive phases for panicle development. A model simulating rice phenology and incorporating temperature and daylength effects on development in each phenophase is explained with discussion of its validity and usefulness.

PHENOLOGY is one of the most important features in determining the adaptability of a crop to its environment. For stabilisation and maximisation of crop production, crop phenology has to be adjusted carefully to the environment so that the crop can complete its life cycle within the available growing season, and to allow full and safe utilisation of environmental resources. Identification of the most suitable crop genotype in terms of timing of anthesis in a given environment usually requires field trials of cultivars × cropping season experiments for several years. Crop simulation models, in which crop ontogenic processes are properly incorporated, can be a powerful alternative tool (Horie 1994).

In the present paper, genetic and environmental variations of rice growth durations are first shown for cultivars well adapted to each agroecological zone (AEZ) in Japan (Ozawa 1962), with the emphasis on environmental adaptability (see Fig. 1 and Table 1). Flowering responses in rice to temperature, daylength and other minor determinants are summarised and, finally, a model for predicting phenological development is explained and applied to rice cultivars, including typical ones in the respective AEZs in Japan. Genetic variations in rice flowering responses to the environment are clarified by analysis of model parameters for phenologically different cultivars.

Phenological Development in Rice

There are three distinctive developmental phases in rice: vegetative (emergence to panicle initiation), reproductive (panicle initiation to heading) and grain-filling (heading to maturity). Table 2 shows the duration and the environmental variation of these three developmental phases in japonica-type rice cultivars calculated using phenology data obtained under different environments at five locations typical of the different AEZs in Japan (Fig. 1 and Table 1). Cultivars adapted to the northern AEZs have shorter growth durations than those adapted to the southern AEZs when grown in the same environments. This is an indispensable adaptation allowing the short-duration cultivars to complete their life cycles within the cool and short summer of the northern part of Japan and the late-maturing cultivars to have a vegetative growth duration long enough to promote high productivity in the south.

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Table 1. Agroecological zones in Japan and their characteristics.

Zone	Name of zone	Warmth index[1] (°C/month)	Annual precipitation (mm)	Frostless period (days)	Snow cover period (days)	Moisture type[2]
I	Tempoku	50–55	800–1000	120–140	120–140	Dry-S/moist-W
II	East Hokkaido	45–50	c. 1000	120–140	c. 100	Moist-S/moist-W
III	Central Hokkaido	60–70	c. 1200	140–160	c. 140	Dry-S/moist-W
IV	South Hokkaido	65–75	1200–1400	160–180	70–90	Moist-S/moist-W
V	East Tohoku	75–85	c. 1200	150–170	< 50	Moist-S/moist-W
VI	West Tohoku	80–90	1600–2000	c. 180	100–120	Moist-S/wet-W
VII	Kanto	90–110	1300–1600	180–220	< 25	Moist-S/moist-W
VIII	Tozan	c. 90	c. 1300	160–180	c. 40	Moist-S/moist-W
IX	Hokuriku	100–110	2400–2800	c. 200	100–140	Dry-S/wet-W
X	Sanin	c. 110	c. 1800	200–220	c. 50	Dry-S/wet-W
XI	Tokai	c. 120	c. 2000	220–240	0	Moist-S/moist-W
XII	Setouchi	110–120	1200-1400	200–240	0	Dry-S/dry-W
XIII	Kyushu	120–130	1600–1800	c. 220	0	Moist-S/dry-W
XIV	Nankai	130–140	2400–3000	240–280	0	Wet-S/moist-W

[1] Warmth index is sum of monthly mean temperature above 5°C
[2] Moisture type denotes pattern of annual moisture distribution. S and W stand for summer and winter, respectively
Source: Adapted from Ozawa (1962)

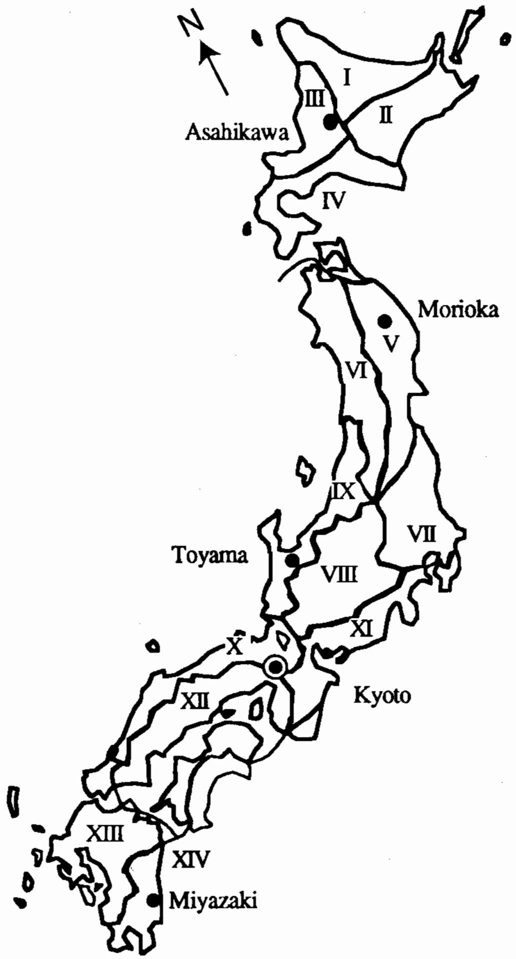

Figure 1. Agroecological zones (I–XIV; see Table 1) in Japan (Ozawa 1962), and five locations (●) where crop-locational experiments (Table 2) were carried out.

Genotypic and environmental variations in the duration of postanthesis development are relatively small, and thus the time to maturity of a cultivar is mainly governed by the preanthesis development (Table 2). The number of days to heading is mainly controlled by the duration of vegetative growth. This does not necessarily mean that the time required for inflorescence development is fixed, as is supposed in many studies. For this reason, we have focused on preanthesis development, especially flower initiation, to study the phenological requirement in rice cultivars in a target area.

Temperature and Daylength Effects on Flowering

Temperature and daylength are the two main determinants that govern flowering time in plants (Garner and Allard 1920). Rice cultivars are short-day or day-neutral plants. A wide range of variations are observed in the flowering response of rice to photoperiod (Vergara and Chang 1985). Some cultivars have critical daylengths above which they will never flower (qualitative photoperiodic response), while others can reach flowering at any daylengths, with the variation of days to flowering depending on the daylength (quantitative photoperiodic response). The response patterns to photoperiod are well characterised by the maximum optimum daylength, critical daylength, slope of the response curve, and maximum and minimum developmental rate. The temperature effects on phenological development are twofold: one is as a general promoter of development through activation of enzymatic processes, except in the supraoptimal range; and the other is as a modifier of photoperiodism (Horie 1994).

Figure 2 gives examples of the temperature and daylength effects on flowering in rice, shown as the relationship between days to panicle initiation, and average temperature and daylength until panicle initiation. Days to panicle initiation decreased with a rise in temperature, except for Koshihikari rice at daylengths longer than 15 hours. The delay of development with temperature rise under the longer daylength in Koshihikari was due to the small shift of critical daylength by temperature (Haniu and Chujo 1987). However, such a response was not observed in IR36 rice, which has much weaker photoperiodicity than Koshihikari. Thus, we can omit the role of temperature as a modifier of photoperiodism for simulating phenology in field-grown rice (excluding cases in which a strongly photoperiod sensitive cultivar is grown under unusually long day conditions).

Supraoptimum temperatures delay flowering at any daylengths (Haniu et al. 1983; Nakagawa et al. 1993) and considerable varietal difference in the optimum temperature has been reported (Yin et al. 1996). The optimum temperature for flowering is higher during the day than during the night (Haniu et al. 1983; Yin et al. 1996). Base temperatures for development towards panicle initiation were estimated to be 9–10°C for two japonica cultivars and 14°C for IR36, an indica type (Nakagawa and Horie 1995).

Table 2. Means and standard deviations of days from emergence to panicle initiation (E–PI), panicle initiation to heading (PI–H), and heading to maturity (H–M) for rice cultivars well adapted to each agroecological zone (AEZ) in Japan.

Cultivar	Main producing area (AEZ)	E–PI		PI–H		H–M	
		mean±sd	(n)	mean±sd	(n)	mean±sd	(n)
Tomohikari	III, IV	37.9±18.5	(16)	41.1±6.7	(16)	40.1±8.9	(16)
Yukihikari	III, IV	41.4±18.2	(16)	40.3±5.5	(16)	39.2±6.9	(16)
Akihikari	VI, V	60.4±17.3	(16)	33.1±4.0	(16)	38.5±6.4	(13)
Fukuhikari	VI, V	64.5±19.2	(16)	32.8±4.4	(16)	38.5±8.2	(13)
Sasanishiki	VI, V	66.9±18.8	(16)	33.6±4.3	(16)	41.3±5.7	(11)
Koshihikari	VII, VIII, IX	71.1±22.6	(16)	34.3±4.4	(15)	36.5±4.1	(10)
Tomihikari	VII, VIII, IX	73.5±20.2	(16)	36.5±6.7	(15)	39.4±3.3	(10)
Nipponbare	X, XI, XII	77.8±21.7	(16)	35.1±5.7	(15)	41.0±6.8	(10)
Koganebare	XIII, XIV	79.1±22.0	(16)	34.6±5.6	(15)	41.0±6.1	(10)
Minaminishiki	XIII, XIV	86.2±18.7	(16)	36.6±8.1	(14)	46.2±5.0	(10)

Note: Means and standard deviation values were calculated by use of the data (Horie 1990) obtained at different growing seasons at five locations (Fig. 1) in Japan.

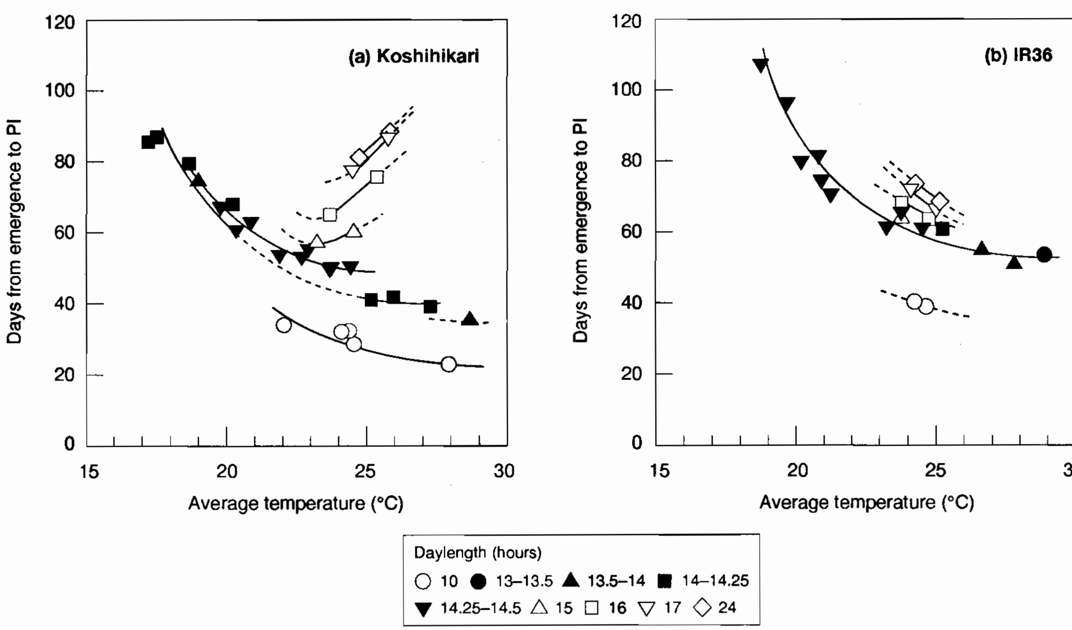

Figure 2. Relationship between days from emergence to panicle initiation (PI), and average temperature and daylength over the growth season for rice cultivars: (a) Koshihikari; and (b) IR36. Open symbols denote the data obtained at constant daylengths (Nakagawa and Horie 1989), and closed symbols under field conditions (Nakagawa and Horie 1995).

Each of the vegetative and reproductive phases of rice development can be subdivided into two phases by considering the photoperiod sensitive period. We have therefore distinguished four phases of preflowering development: the juvenile phase (photoperiod insensitive) and the photoperiod inductive phase for panicle initiation; and the photoperiod sensitive and insensitive phases for panicle development. Vergara and Chang (1985) described the juvenile phase as the basic vegetative phase (BVP). This term is well known but sometimes confusing, because some other researchers define BVP as minimum days to panicle initiation or heading.

Mimoto et al. (1989) transferred 13 cultivars of japonica rice from a long-day (20-hour) to a short-day (10-hour) photoperiod on different days after emergence under a constant temperature and observed the date of panicle initiation. The duration of the juvenile phase is clearly detected as the initial period in which days to panicle initiation is unaffected by the days of the short-day treatments. After this juvenile phase, the days to panicle initiation increased linearly with the delay of the short-day treatment. Similar results were obtained by Nakagawa and Horie (1988) and Yin et al. (1997) for both japonica and indica rice cultivars. The linearity of the relationship between days to panicle initiation and day of transfer implies that the effect of photoperiod on photoinductive responses is cumulative and that photoperiod sensitivity is not affected by plant age (Horie 1994). The slope of the line (P) relates the development rate at a short daylength (V_S) to that at a long daylength (V_L) as (Nakagawa and Horie 1988; Horie 1994),

$$V_L = (1 - P)V_S \quad (1)$$

The slope P, which takes a value in the range 0–1, is a good indicator for photoperiod sensitivity of cultivars. Cultivars with $P = 1$ are qualitative short-day type, and those with $P = 0$ are day-neutral type.

After panicle initiation, cultivars which have weak or no photoperiod sensitivity before panicle initiation lose photoperiod sensitivity, while those with strong photoperiod sensitivity ($P > 0.7$) still need short day cycles for panicle development (Nakagawa and Horie 1989). Three groups of genotypes exist with respect to photoperiod sensitivity for initiation and subsequent development of panicles: insensitive before and after initiation, sensitive before initiation and insensitive after initiation, and sensitive before and after initiation. Nipponbare, a cultivar of the third group, loses the photoperiod sensitivity about 10 days before heading (Nakagawa and Horie 1989).

Other Determinants for Flowering

Plant nutrition, environmental stresses such as water deficit and atmospheric carbon dioxide (CO_2) concentration can also modify the phenological development towards flowering in rice. Water deficit delays panicle initiation and prolongs the reproductive phase (Tsuda 1986). The delay of heading date induced by water stress in the panicle formation stage was proportional to cumulative water stress, which was expressed by the summation of daily difference in predawn leaf water potential between irrigated and stressed treatments (Tsuda 1991).

It is important to assess the effects of atmospheric CO_2 concentration on various plant processes, because CO_2 concentration is now increasing rapidly. Doubling CO_2 concentration promotes phenological development towards heading in rice (Nakagawa et al. 1993). The promotion rate by doubling CO_2 in Akihikari rice was about 4% at temperatures below optimum, and increased with temperature rise due to the upward shift of the optimum temperature for development (Nakagawa et al. 1993). The mechanism by which elevated CO_2 promotes development is still unknown, but may involve a rise in leaf temperature induced by partial stomatal closure, dilution of nitrogen content, and hormonal regulation such as ethylene.

Modelling of Phenological Development

Many models have been proposed for predicting phenological development for many crops (Loomis and Connor 1992; Horie 1994). The crop phenological model, combined with a growth model, can be a powerful tool for a better understanding of crop responses to environments, and hence optimising management of crops to maximise and stabilise yield (Horie 1994). A model for predicting the rice phenological development is explained here, basically according to Horie and Nakagawa (1990).

Rice development stage is quantified by a continuous variable termed development index (DVI) as in de Wit et al. (1970). DVI is defined to be, for example, 0, 1, 2 and 3 at emergence, panicle initiation, heading and maturity, respectively. The value of DVI at any moment is given by integrating the development rate with respect to time:

$$\mathrm{DVI} = \sum_{i=0}^{t} \mathrm{DVR}i \quad (2)$$

where: DVRi is the development rate at the ith day.

Temperature (T) and daylength (L) responses of DVR in the preanthesis phase can be given by the following equation, as employed by many researchers:

$$DVR = 1 / G f(T) h(L) \tag{3}$$

where: G is the minimum number of days required for the completion of one phenophase under optimum T and L, and $f(T)$ and $h(L)$ are the functions giving the temperature and daylength effects on development.

Introduction of the G parameter makes the ranges of $f(T)$ and $h(L)$ 0 to 1, respectively. To subdivide each of the vegetative and reproductive phases according to the photoperiod sensitive period, the value of DVI at which the rice plant becomes sensitive to photoperiod in the vegetative phase (DVI_s), or becomes insensitive (DVI_e) in the reproductive phase is introduced as a parameter:

$$DVR = \begin{cases} 1/G\, f(T), & \begin{pmatrix} DVI < DVI_s \textit{ for vegetative phase} \\ DVI \geq DVI_e \textit{ for reproductive phase} \end{pmatrix} \\ 1/G\, f(T) h(L), & \begin{pmatrix} DVI \geq DVI_s \textit{ for vegetative phase} \\ DVI < DVI_e \textit{ for reproductive phase} \end{pmatrix} \end{cases} \tag{4}$$

For the function $f(T)$, the logistic equation (5) can be successfully applied to the preflowering development process if the supraoptimum temperature range can be omitted from the analysis (Horie and Nakagawa 1990).

$$f(T) = 1 / \left[1 + \exp\{ -A(T - Th) \} \right] \tag{5}$$

A new function is introduced here to explain the flowering responses to a wider range of daylengths, combining equation (1) and the beta-function proposed by Yin and Kropff (1996).

This is shown in equation (6), below, where: P is the daylength sensitivity factor explained in the previous section, Lo is the optimum daylength, Lc is the critical daylength, and α is the parameter that characterises the curvature of the response.

The parameters of the model were estimated using the panicle initiation dates of 14 rice cultivars obtained under different environments at Kyoto in Japan, including field experiments and constant daylength treatments (10–24 hours) as shown in Figure 2, and transfer experiments between two different daylengths (Nakagawa and Horie 1988). The simplex method was applied for parameter estimation. This model explained observed days to panicle initiation with a high level of accuracy (R^2 = 0.984–0.999, SE= 1.6–2.8 days for 14 cultivars). The results for the development of three representative cultivars are shown in Figure 3a. Application of the model for rice development during the reproductive phase also gave a high accuracy of estimation (Fig. 3b). The DVI values obtained from the model corresponded well to morphological development stage (Nakagawa and Horie 1995). The four-stage model presented here for predicting the heading date was compared with one- and two-stage models, which have the same structure as the four-stage model but with different types of phasic division. The one-stage model assumes a constant DVR response to environment over the entire development phase till heading, and the two-stage model assumes two DVR responses to environment that are different before and after panicle initiation. The one-, two- and four-stage models explained the heading dates of Nipponbare grown under a wide range of environments with standard errors of 5.2, 4.5 and 3.5 days, respectively, indicating that the rational division of the phenophase increases the accuracy of the model.

For the grain-filling stage, the DVR response can be represented as a function of temperature alone, by setting $h(L)$ = 1 in equation (3). This temperature-dependent model explained the numbers of days from heading to maturity of rice cultivars fairly well, although its accuracy was inferior to that for panicle initiation and heading date (Horie 1990).

$$h(L) = \begin{cases} \left[1 - P + P \left[(L/Lo)\{(Lc - L)/(Lc - Lo)\}^{(Lc-Lo)/Lo} \right]^{\alpha} \right], & (L \leq Lc) \\ 1 - P, & (L > Lc) \end{cases} \tag{6}$$

As the model has been shown in the present analysis to have a high level of validity and accuracy it can also be used to quantitatively describe the genetic variations in crop phenological responses to environments. The P and G parameters of the model for typical rice cultivars from the respective AEZs in Japan, as well as IR36 and Milyang 23, were therefore plotted as P–G plains (Fig. 4). Cultivars in Hokkaido (III, IV) have small G and P values; those in the Tohoku area (VI, V) have large G and medium P values. P and G values of cultivars in the central and southern parts of Japan increase and decrease, respectively, with decrease in latitude in the main rice-producing area. It is, therefore, suggested that the early maturation of northern Japanese rice cultivars arose mainly through a weakening of photoperiodicity (decreasing P values) as the rice-producing area

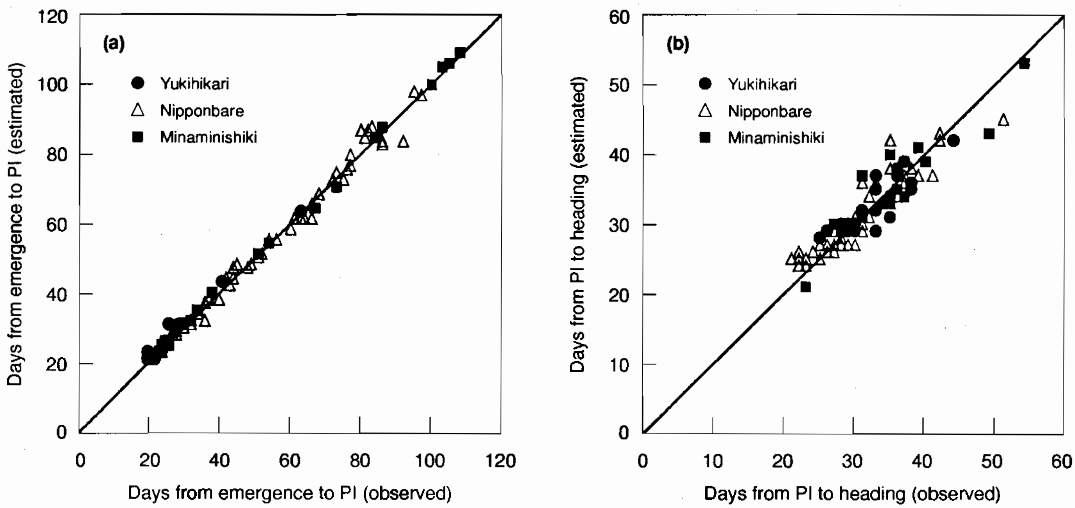

Figure 3. Relationship between estimated and observed numbers of (a) days from emergence to panicle initiation (PI), and (b) days from PI to heading, of three rice cultivars grown in different environments, including field experiments at Kyoto (Nakagawa and Horie 1995), constant daylength treatments (Nakagawa and Horie 1989), and transfer experiments between two constant daylengths (Nakagawa and Horie 1988).

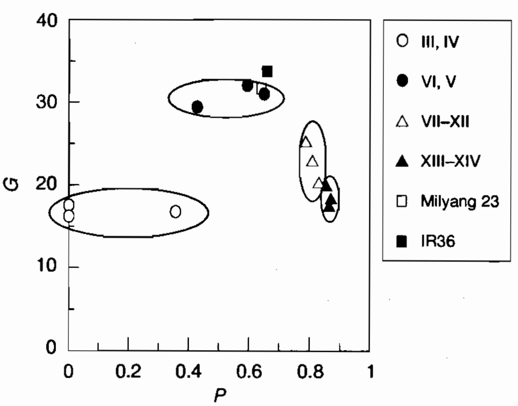

Figure 4. Variations in the values of development parameters P and G for the rice cultivars Milyang 23 and IR36, and 12 Japanese cultivars adapted to particular agroecological zones.

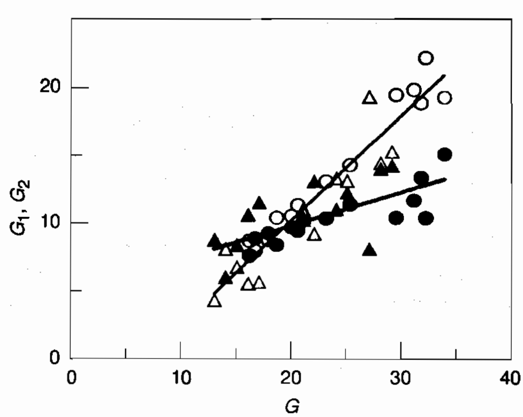

Figure 5. Relationship between parameter G and the minimum durations of juvenile (G_1, open symbols) and photoperiod inductive phases (G_2, closed symbols) for rice cultivars. Circles denote the results for 14 rice cultivars in the present paper, and triangles the values derived from Mimoto et al. (1989).

spread from the southern to the northern part of Japan, and that G is a subsidiary modifier for earliness. Figure 5 shows the relationship between G and minimum numbers of days for juvenile and photoperiod inductive phases (G_1 and G_2, respectively) for 14 cultivars from this analysis and 13 cultivars after Mimoto et al. (1989), in which G, G_1 and G_2 were directly obtained from the data of the transfer experiment. G varied from 14 to 34 days. This varietal difference in G was strongly correlated with G_1, ranging from 4 to 20 days. G_2 was a relatively stable trait which seems to have a different genetic background from the juvenile phase, but also showed some varietal differences.

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Determination of Phenology Development in Rainfed Lowland Rice in Thailand and Lao PDR

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Abstract

Flowering time of rice is an important determinant of yield in the rainfed lowland ecosystem. It is strongly determined by sowing time in photoperiod insensitive cultivars, but is less affected in photoperiod sensitive cultivars. The response of flowering time to sowing time of 35 cultivars was examined using data obtained in 12 locations in Thailand and Lao PDR in three seasons.

Most traditional Thai cultivars used in the experiment were strongly photoperiod sensitive, flowering in late October–mid-November, although late sowing delayed date of flowering slightly. Several cultivars were mildly photoperiod sensitive while others were almost insensitive. Photoperiod insensitive and mildly sensitive cultivars generally flowered earlier than strongly sensitive cultivars, particularly when sown early in the season. However, these cultivars were more affected by the seedling age at transplanting. Regression analysis indicates delay in flowering of 5–9 days when transplanting is delayed by 20 days.

In another experiment, over 1100 F_7 recombinant inbred lines from seven biparental crosses were tested for flowering time and photoperiod sensitivity. Flowering date differed greatly among lines but was not related to photoperiod sensitivity, indicating that cultivars with a particular flowering time can be developed from crosses with various photoperiod sensitivities.

RAINFED lowland rice in Thailand and the Lao People's Democratic Republic (Lao PDR) commonly experiences drought during some stages of its growth. Lao farmers consider this to be the most important factor affecting rice production (Lathvilayvong et al., this volume). One way of increasing rice yield in the rainfed lowland ecosystem is to develop drought-resistant cultivars. Of many traits that have been suggested to be useful for drought resistance, the most important is considered to be the correct phenology to match the water availability for rainfed lowland rice (Fukai and Cooper 1995). Late-season drought is common in rainfed lowland areas of Thailand and yields of late-maturing cultivars are affected very severely, whereas early-flowering cultivars may escape the drought. Using several cultivars of different phenology groups in several locations in northeast Thailand, Jearakongman et al. (1995) found a large reduction in yield of rainfed lowland rice when standing water disappeared before flowering. It is therefore important to choose cultivars that flower before the disappearance of standing water towards the end of the wet season.

Rice is a short-day crop but cultivars differ greatly in photoperiod sensitivity (IRRI 1976). Traditional cultivars in Thailand and Lao PDR are photoperiod sensitive, and flowering generally coincides with the end of the rainy season, although cultivars released recently in Lao PDR are photoperiod insensitive (Pushpavesa and Jackson 1979; Inthapanya et al. 1995). Between these two extreme types, there are some cultivars that are only mildly sensitive to photoperiod. Factors other than photoperiod sensitivity are known to affect phenology of rice. For example, water stress and nutrient deficiency delay flowering (Lilley and Fukai 1994; Wonprasaid et al. 1996). Delay in transplanting, and hence the use of old seedlings for transplanting, also delays flowering (Joseph 1991).

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The objectives of this study were to determine the variation in photoperiod sensitivity among rice cultivars that are commonly used in the rainfed lowland ecosystems of Thailand and Lao PDR, and assess how strongly the date of flowering is determined by photoperiod sensitivity. This information should help plant breeders to develop strategies for selection of germplasm that is phenologically adapted to the rainfed lowland environments of these countries.

Materials and Methods

Multilocation trials

Wet season experiments were conducted under rainfed lowland conditions at 10 locations (Ubon Ratchathani, Sakon Nakhon, Surin, Phimai, Khon Kaen, Chum Phae, Kok Samrong, Phitsanulok, Phrae and Sanpatong) in the north and northeast of Thailand in 1992–94 and two locations in Lao PDR (Vientiane and Champassak) in 1993–95 (see map on page x). The most northern location was Sanpatong (latitude 18°16' N) and the most southern location was Phimai (15°10' N). Mean daily temperature was close to 30°C in the early part of the wet season, gradually decreasing to below 25°C towards maturity in November. Variation in daily temperature among the 12 locations was generally small. At Ubon Ratchathani the daylength decreased from 13.0 hours in June to 11.3 hours in December (Pushpavesa and Jackson 1979). Each experiment consisted of 35 cultivars with three replicates in a randomised complete block design. The cultivars were mostly from Thailand, except Lemont, which is a United States cultivar. Some cultivars are adapted for irrigated lowland conditions (IR20, RD23), but most are grown commonly in rainfed lowland conditions. The majority of cultivars are traditionally grown in specific areas of Thailand, but a number of improved cultivars and advanced lines were included. KDML105 and RD6, grown widely in Thailand, are improved cultivars selected from traditional types.

The seeds were sown between 8 June and 26 August, and seedlings were transplanted after 20–46 days, except on one occasion (Kok Samrong in 1993), where direct seeding was adopted because of lack of standing water at the time of transplanting. In 1993 there was widespread drought throughout the region at the time of transplanting in late July–early August, and many experiments were irrigated for transplanting. In Sanpatong, paddies were irrigated for transplanting in all years and also at booting stage, with development of drought in 1993 and 1994. In all experiments there were three seedlings per hill and 16 hills per m^2. Each plot was 1.5×5 m. Fertiliser rate varied slightly among experiments, but common rates for nitrogen (N), phosphorus (P) and potassium (K) were 18 (N), 36 (P) and 36 (K) kg/ha applied as basal fertiliser at transplanting and 18 kg N/ha applied 20–30 days later.

Date of 75% flowering was recorded for each cultivar. Following the procedure of Katayama (1963), photoperiod sensitivity index was calculated from the regression coefficient of a linear relationship between days to flowering and seeding date (Julian days) for all 35 cultivars. Cultivars with a sensitivity coefficient of zero are completely insensitive and would require the same number of days to flowering, whereas those with a coefficient of 1.0 are strongly sensitive and would flower on the same date, regardless of the time of sowing.

Trial using recombinant inbred lines

An experiment was conducted at Phitsanulok, Upper Central Plain, Thailand in 1995, to examine the relationship between photoperiod sensitivity and date of flowering using 1105 F_7 recombinant inbred lines (RILs) from seven crosses (see Table 1).

Table 1. Crosses used for production of recombinant inbred lines (RILs) for examination of the relationship between photoperiod sensitivity and date of flowering, Thailand 1995.

Population	Parents	Number of F_7 RILs
IR66321	IR43506-UBN-520-1-3-1-1/IR43342-10-1-1-3-3	138
IR66322	IR43506-UBN-520-1-3-1-1/IR49804-UBN-7-B-1-4-1	198
IR66327	IR46331-PMI-32-2-1-1/IR53466-B-118-B-B-20	99
IR66331	IR46331-PMI-32-2-1-1/NR15013-40-10-7	97
IR66364	KDML105/IR51952-B-12-1-1-1	191
IR66368	RD6/IR46331-PMI-32-2-1-1	199
IR66369	RD6/IR49804-UBN-7-B-1-4-1	183
Total		1105

The seeds were sown on 3 April and 4 July. Parents of these crosses were included (except NR15013-40-10-7) in only the July sowing for estimation of flowering date. Photoperiod sensitivity for the parents was estimated by sowing them in April and July in 1996. In 1995, there was only one replication in the April sowing, whereas there were two in the July sowing in a randomised complete block design. Each plot occupied two 3 m rows. Young seedlings were transplanted at 1 seedling/hill with spacing of 20 × 25 cm. The date when 50% of the plants flowered was observed.

Results and Discussion

Multilocation trials

The results of all 36 experiments were combined to examine relationships between sowing time and flowering time. The number of days taken from sowing to flowering was reduced as sowing was delayed, but cultivars differed in their responses. Three contrasting examples of cultivars (RD23, NSG19 and KDML105) are shown in Figure 1. Flowering of RD23 occurred 85–105 days after sowing in most experiments and thus was only slightly affected by sowing date, although variation along the regression was rather large. Another early-flowering cultivar (NSG19) was more responsive to sowing date than RD23, and 80 days delay in sowing from early June to late August hastened flowering by almost 40 days. The popular cultivar KDML105 flowered much later than RD23 and NSG19 when they were sown in June, but the differences were reduced greatly when sown in late July. When sown at the most common time of early to mid-July, KDML105 took about 105 days to flowering, whereas sowing in mid-June resulted in flowering about 130 days after sowing.

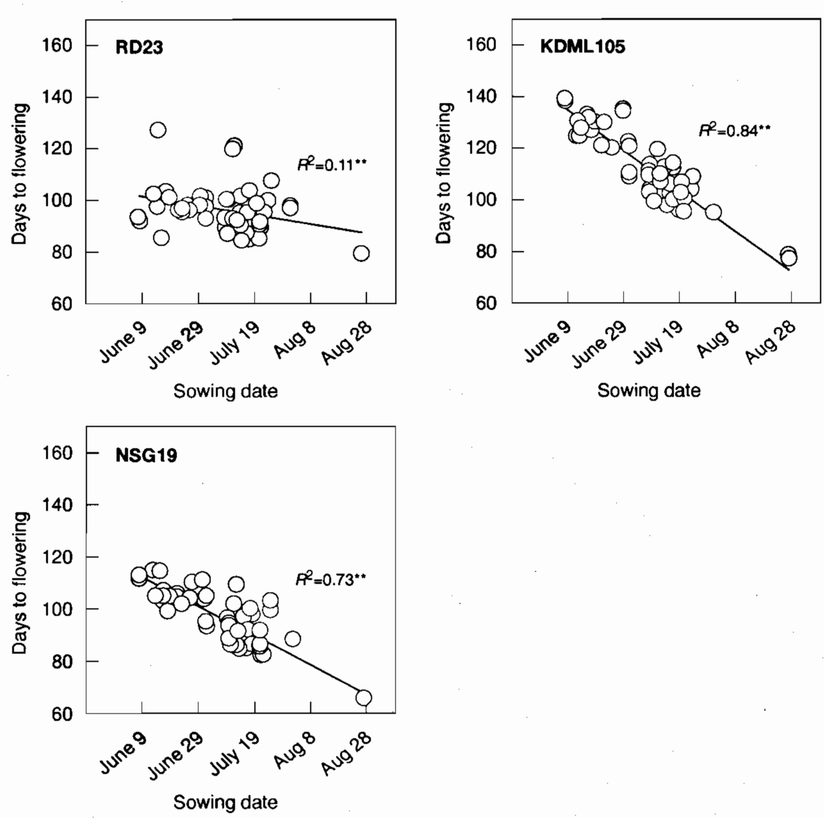

Figure 1. Relationship between days to flowering and sowing date of three rice cultivars (RD23, KDML105 and NSG19) under rainfed lowland conditions. Different sowing dates were obtained in 3-year experiments in each of 12 locations in Thailand and Lao PDR (** = $P < 0.01$).

These differences in response to sowing date appeared to be due mostly to differences in photoperiod sensitivity, with photoperiod sensitive cultivars flowering in a shorter time as daylength was getting shorter with delayed sowing. On the other hand, photoperiod insensitive cultivars would be little affected by changes in daylength caused by differences in sowing time. The photoperiod sensitivity coefficients for RD23, NSG19 and KDML105 were 0.14, 0.59 and 0.77, respectively. NSG19 has been identified to be a weakly photoperiod sensitive cultivar in previous studies (Poonyarit et al. 1989).

Photoperiod sensitivity coefficients varied between 0.08 and 0.90 among 35 cultivars, and generally were associated with mean days to flowering of the cultivar ($R^2 = 0.62$, $P < 0.01$; see Fig. 2). Cultivars with large sensitivity coefficients took a long time to flower, whereas insensitive cultivars generally flowered early. The 35 cultivars were grouped into five groups according to the photoperiod sensitivity (Table 2). Groups 1 and 2 with small coefficients (0–0.3) are considered to be insensitive. Group 1 consists of only Lemont, which is separated from Group 2 because of its very early-flowering character as well as its small photoperiod sensitivity coefficient (0.08). Mean days to flowering for Group 2 was similar at about 100 days in all cultivars. On the other hand, cultivars in weakly sensitive Group 3 (sensitivity coefficient between 0.3 and 0.7) varied greatly in mean time taken to flowering. NSG19 and Leuang Bun-ma flowered on the average in less than 100 days whereas BKNBR82027-NSR-8-1 took 127 days to flower. Group 4 includes the two most popular cultivars (KDML105 and RD6) for the rainfed lowland ecosystem in Thailand, and they flowered about 15 days earlier than cultivars in Group 5. Both Groups 4 and 5 are considered to be strongly sensitive, and included most traditional Thai cultivars used in this study.

Thus, early-flowering cultivars used in the multilocation trials were mostly classified as photoperiod insensitive or mildly sensitive and were mostly improved cultivars and advanced lines. The traditional Thai cultivars were mostly late-flowering and photoperiod sensitive. The popular cultivars RD6 and KDML105 were strongly photoperiod sensitive with a sensitivity coefficient of 0.77 for each cultivar.

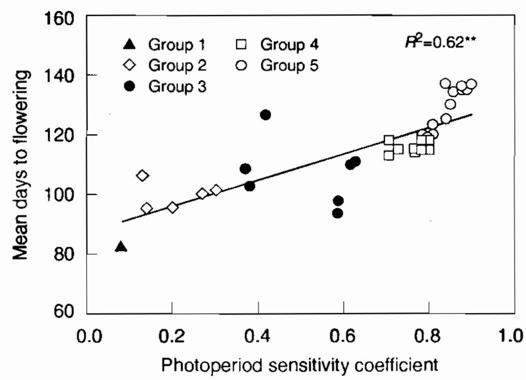

Figure 2. Relationship between days to flowering and photoperiod sensitivity coefficient obtained from 35 rice cultivars grown under rainfed lowland conditions at 12 locations in Thailand and Lao PDR (** = $P < 0.01$).

Table 2. Cultivars in different photoperiod sensitivity groups.

Group	Photoperiod sensitivity[1]	Coefficient	Cultivars
1	Insensitive (1)	0.0–0.1	Lemont
2	Insensitive (5)	0.1–0.3	RD23, RD10, IR43450-SKN-506-2-2-1-1, IR49766-KKN-54-B-B-6-1, IR43049-CPA-510-3-3-1-1
3	Weakly sensitive (7)	0.3–0.7	NSG19, IR20, Leuang Bun-ma, Khao Strok, IR57514-PMI-5-B-1-2, IR43062-PMI-B-15-1-2-2, BKNBR82027-NSR-8-1
4	Strongly sensitive (10)	0.7–0.8	KDML105, RD6, Lum Narai, Puang Sawan, E-Nawn, Leuang Samer, Jumpah Tawng, IR52532-SKN-23-B-1-2, IR57546-PMI-1-B-2-2, IR43506-UBN-520-2-1-1
5	Strongly sensitive (12)	0.8–0.9	KPM148, LPT123, Chiangsaen, Khao Luang, Tah Tae, E-Pad, Leum Dern, Leuang Dawk Koon, Khao Yai, Daeng Noi, Chabah Sarahn, Taw Chaw Daw

[1] Numbers in brackets indicate number of cultivars

Therefore flowering will take place slightly earlier if sown earlier, as observed by Pushpavesa and Jackson (1979) for KDML105 at Ubon Ratchathani. Our results indicate that sowing 30 days earlier in mid-June (from mid-July) would hasten flowering date by about seven days and would somewhat reduce the risk of encountering late-season stress, which is common in the northeast of Thailand (Fukai et al. 1995). However, if planted in mid-June they would take 130 days to flower, which is probably too long for high yield (Rajatasereekul et al., this volume). It is therefore likely that photoperiod insensitive or mildly sensitive cultivars are suited to early sowing.

When days to flowering of all cultivars in each of groups 2–5 were averaged for each experiment, all groups show a general trend in their response to sowing date, but there were rather large variations along regression lines, particularly in the photoperiod insensitive and mildly sensitive groups. The results from 3-year experiments at Ubon Ratchathani indicate that the cultivars in the insensitive group flowered 10–20 days later and those in the mildly sensitive group about 10 days later than expected from the regressions, though the effect was negligible in the strongly sensitive groups. Flowering was also rather late in Vientiane, compared with the dates expected from the regression equations. Some of these deviations from the regression are explained by the age of seedlings at transplanting; the use of old seedlings for transplanting, as happened at Ubon Ratchathani (42, 40 and 36 days old for the three years, respectively), delayed flowering in the insensitive and mildly sensitive groups. Multiple linear regression analysis for the time to flowering showed that the age effect was more important than sowing date effect in the insensitive group, and it was also significant in the mildly sensitive group but not in the strongly sensitive groups. Similarly, Gines et al. (1985) noted that photoperiod sensitive cultivars were relatively insensitive to age of seedling at transplanting. In this study the regression coefficients of the age effect were 0.45 and 0.27 for the insensitive and mildly sensitive groups respectively, indicating that 20 days delay in transplanting from 25 to 45 days after sowing would delay flowering by 5–9 days in these cultivars. Figure 3 shows the date of flowering estimated from the linear regressions for different sowing times for RD23 (insensitive), NSG19, BKNBR82027-NSR-8-1 (mildly sensitive) and KDML105 and KPM148 (strongly sensitive). For RD23, the two regressions are for crops transplanted with 25- and 45-day-old seedlings. The effect of photoperiod sensitivity is large when crops are sown in June, but is rather small when sown in mid-July. Among the five cultivars shown in Figure 3, flowering in early October can be achieved only when insensitive or mildly sensitive cultivars are sown in June. When sowing is delayed to late July or later, NSG19 would flower earlier than RD23.

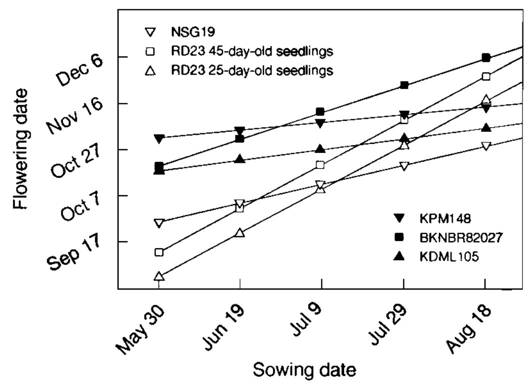

Figure 3. Estimated flowering dates of five contrasting cultivars for different sowing dates. For the photoperiod insensitive cultivar RD23, the effect of age of seedlings at transplanting (25 vs 45 days old) is also shown.

Thus, while photoperiod insensitive or mildly sensitive cultivars can be sown early in the season for early flowering and hence escape late-season drought, flowering time appeared to be affected by the age of seedlings used for transplanting. Several studies in India have shown that delay of 20 days in transplanting causes delay of flowering of about eight days (Joseph 1991), as found in the present study, or causes slightly longer delay of up to 13 days (Murty and Sahu 1979; Raju et al. 1989; Paraye and Kandalkar 1994). As demonstrated in many locations in 1993, there is not always standing water at the appropriate time for transplanting in rainfed lowland conditions and it is common for transplanting to be delayed with subsequent use of old seedlings. This would delay flowering date and to some extent predispose cultivars to late-season drought, although photoperiod insensitive and mildly sensitive cultivars would still flower earlier than strongly photoperiod sensitive, traditional cultivars if sown in June to early July in Thailand and Lao PDR. Change from transplanting to direct seeding will eliminate this possible delay in flowering due to the use of old seedlings for transplanting.

The delay in flowering date observed in some locations of the multilocation trials may not be due only to the use of old seedlings. The use of old seedlings was caused by the lack of standing water at the appropriate time for transplanting, and water stress often developed in these crops after transplanting in the main paddies. This was the case in all three years at Ubon Ratchathani, and it is possible that delayed flowering at this location was caused by water stress. Delayed flowering due to water stress in vegetative and panicle development stages is well documented in rice (Lilley and Fukai 1994). The soils at Ubon Ratchathani also had extremely low soil fertility, and application of farmyard manure hastened flowering in accompanying experiments conducted in 1992 and 1993 (Wonprasaid et al. 1996). In their experiments, cultivars with different photoperiod sensitivities, including RD23 (insensitive), NSG19, Leuang Bun-ma and IR57514-PMI-5-B-1-2 (mildly sensitive) and KDML105, RD6, Chiangsaen, E-Pad and Taw Chaw Daw (strongly sensitive), flowered on average 3–4 days earlier with farmyard manure application. In the same experiment, irrigation hastened flowering of all cultivars on average by 6–7 days.

RIL trial

Frequency distribution of flowering time of F_7 lines in each cross in the July sowing is shown in Figure 4. When both parents flowered at about the same time between 100 and 109 days after sowing (IR66321, IR66322, IR66369), the distribution of F_7 lines was normal with small standard deviations of around seven days, although this was not the case with IR66368. When flowering dates of the parents differed greatly in IR66327 and IR66364, flowering

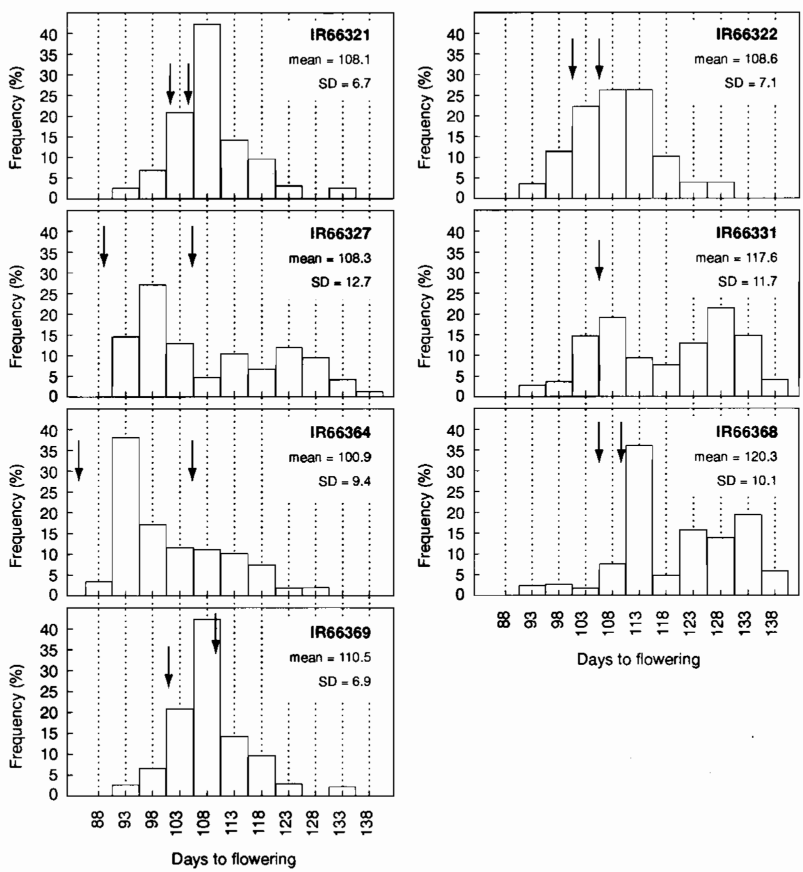

Figure 4. Frequency distribution for days to flowering of F_7 recombinant inbred lines of seven crosses. Arrows indicate days to flowering of the parents of each cross, except IR66331, where only one parent was available.

date of F_7 lines was skewed with a higher frequency of early-flowering lines.

Photoperiod sensitivity coefficients in F_7 lines were normally distributed in IR66368 and IR66369, in which parent lines had similar coefficients in the 0.75–0.95 range (Fig. 5). In other populations the photoperiod sensitivity coefficients of parents were more evenly distributed between 0.0 and 1.0, particularly in IR66321, IR66327 and IR66364, with two peaks, one at 0.6–1.0 and the other at 0–0.4. In both IR66327 and IR66364 the photoperiod sensitivity coefficients of parents differed greatly, with one in the low range (0.2) and one in the high (0.8). However, for IR66321 the coefficients of both parents were similar, in the low range (0.3–0.4). The photoperiod sensitivity coefficients of parent lines of all populations except IR66321 and IR66327 coincided with the peaks in the F_7 generation.

There were no correlations between days to flowering in the July sowing and photoperiod sensitivity coefficient in any of the populations studied, even for IR66327 where the frequency distribution of both

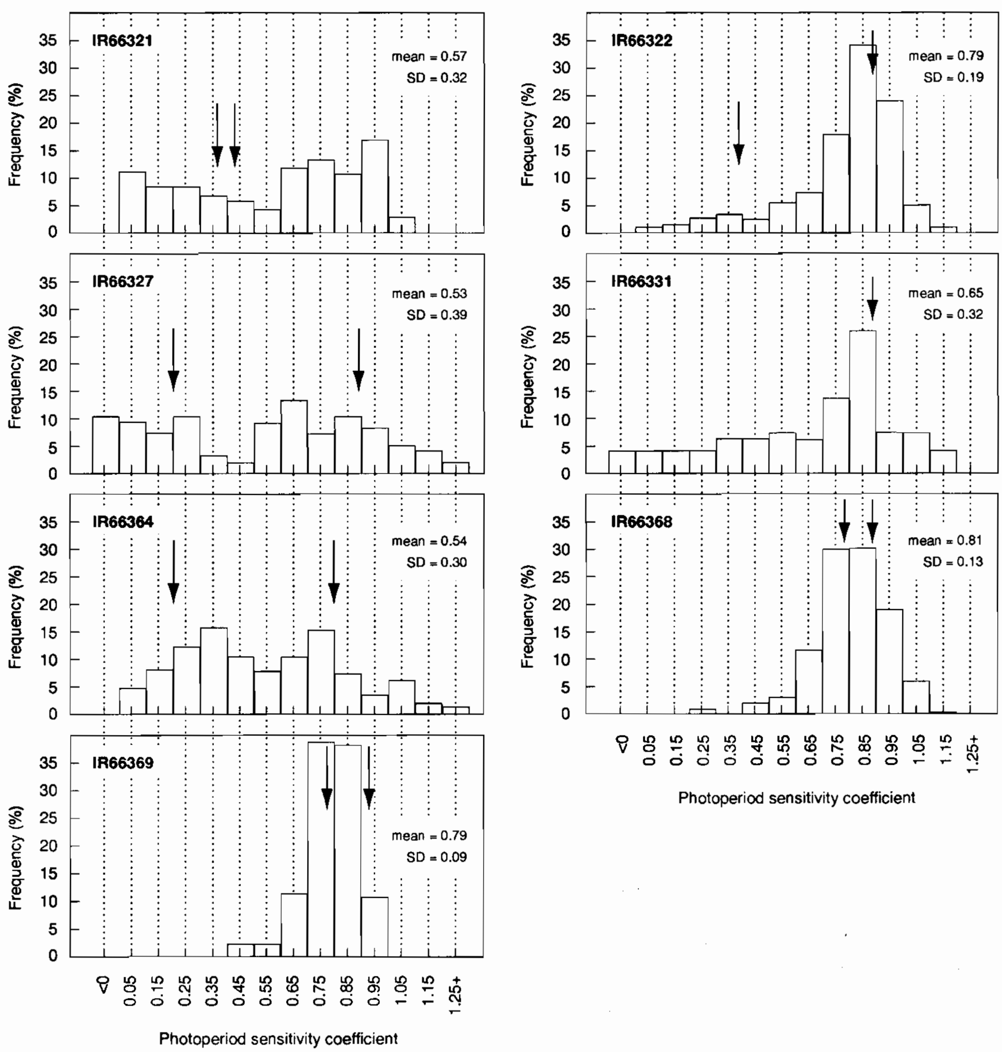

Figure 5. Frequency distribution for photoperiod sensitivity coefficient of F_7 recombinant inbred lines of seven crosses. Arrows indicate photoperiod sensitivity coefficient of the parents of each cross, except IR66331, where only one parent was available.

days to flowering and photoperiod sensitivity coefficient was widely spread.

Some traditional cultivars flower early, e.g. Leuang Bun-ma, and are not strongly sensitive to photoperiod. There are also some Lao traditional cultivars that flower in September (Inthapanya et al. 1995). These or similar cultivars from other countries can be used in a breeding program for development of early-flowering, high-yielding cultivars. Early-flowering, photoperiod sensitive cultivars can be developed using photoperiod sensitivity genes from late-flowering, traditional cultivars (Pushpavesa and Jackson 1979). The results of the RIL trial show that photoperiod sensitivity is not directly linked with lateness of flowering, and hence it should be possible to have early flowering, i.e. late September–early October, cultivars that differ in photoperiod sensitivity. Nwe and Mackill (1986) recovered photoperiod sensitive progeny with different flowering dates from crosses with a particular sensitive parent. Sowing early in the rainy season of early-flowering cultivars is likely to result in higher yield by escaping late-season drought that is common in the rainfed lowland areas in Thailand (Fukai et al. 1995), and cultivars are required that are well suited for early sowing.

Acknowledgments

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Phenology Requirement for Rainfed Lowland Rice in Thailand and Lao PDR

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Abstract

Rainfed lowland rice experiments were conducted for three years with 35 cultivars grown in 12 locations in Thailand and Lao PDR to identify types of cultivars required in these countries. The study covered three broad regions — high rainfall areas along the Mekong River, the central Korat Basin of Northeastern Thailand and Northern Thailand. In most locations yield was highest with early–medium flowering cultivars and it decreased in later-flowering, more traditional cultivars. Cultivars with high yield potential under favourable conditions generally performed better than other cultivars under unfavourable conditions where drought and low soil fertility reduced yield greatly. There were, however, some differences in cultivar requirement in different regions. In the high rainfall areas along the Mekong, sowing was generally early (June) and photoperiod insensitive or mildly sensitive cultivars with flowering in late September to early October were the best. In the central Korat Basin, sowing was often later, in late June to mid-July, and early to medium-flowering cultivars also performed best, although in some environments later-maturing cultivars did well. In Northern Thailand, sowing was often late (mid-July) and medium–late flowering, improved cultivars did well.

IMPROVED and traditional rice cultivars commonly grown in rainfed lowland ecosystems in Thailand are photoperiod sensitive. These cultivars, adapted to local conditions, commonly flower towards the end of the wet season and mature at the beginning of the dry season. Among 35 cultivars examined recently in 12 locations in Thailand and the Lao People's Democratic Republic (Lao PDR), the two most widely grown Thai cultivars, KDML105 and RD6, flowered in late October, whereas most traditional cultivars flowered commonly in late October to November (Immark et al., this volume). The phenology group of KDML105 and RD6 is recommended for Northern Thailand and while a wider range of phenology groups is recommended for Northeastern Thailand (Pushpavesa and Jackson, 1979), these two cultivars at present occupy 80% of 5 million ha in the northeast. In areas where soil fertility is high and water control is possible, photoperiod insensitive cultivars with 100–120 days to mature are generally grown. Paddies in higher positions or risky areas are commonly planted with quick-maturing cultivars, such as NSG19 and HY71, which flower in early October. In areas where water availability is more favourable in October to November, commonly grown cultivars are photoperiod sensitive cultivars which flower in late October, such as KDML105, RD6, RD8 and NSPT, or in November, such as KPM148, KTH17 and LPT123.

In the Lao PDR, traditional cultivars are also photoperiod sensitive, but cultivars recently released are photoperiod insensitive (Inthapanya et al. 1995). The photoperiod insensitive cultivars flower in late September to early October when sown in mid-June, and in the study of 39 cultivars in rainfed lowland conditions in Lao PDR, Thadokkham 1, one of the new Lao cultivars, out-yielded any Thai cultivars (Inthapanya et al., this volume).

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Cultivar phenology requirement for rainfed lowland rice in Thailand and Lao PDR was affected by the time of sowing, but Immark et al. (this volume) found that the flowering time of cultivars with different photoperiod sensitivities responded differently to the sowing time during the wet season in these countries. These authors found that genotypic variation in flowering time was large when sown in mid-June, and was smaller as sowing was delayed to mid-July. Sowing time in the rainfed lowland ecosystem is determined by the onset of wet-season rainfall. Sowing early in the season, however, may be risky because there is a high probability of no standing water at the appropriate time of transplanting. Thus the cultivar phenology requirement needs to be considered in the context of available water in both the early and late parts of the wet season.

The objective of this work was to determine appropriate phenology types of the cultivars required for different areas of rainfed lowland ecosystems in Thailand and Lao PDR. Grain yields of 35 cultivars in the study mentioned earlier (Somdej Immark et al., this volume) were analysed in relation to their flowering time.

Materials and Methods

Details of a multilocation experiment involving 35 cultivars in 12 research stations in Thailand and Lao PDR (Table 1) for three years are described by Immark et al. (this volume). All the experiments were conducted on research stations under rainfed lowland conditions, except for the use of irrigation for transplanting in a number of stations in 1993. In SPT, paddies were irrigated for transplanting in all years and also at booting stage with development of drought in 1993 and 1994. The sowing in each station took place at a time that is common for the region each year, except in 1992, when delay in commencement of the project resulted in late sowing in three stations (SKN, SRN and KKN).

Plot size was 1.5 × 5 m and the centre 1 × 4 m area was harvested for determination of grain yield (14% moisture).

Rainfall

Mean monthly rainfalls for May–December of the last 20 years for the 12 locations are shown in Figure 1. Rainfall was generally high at VTN, SKN, CPK and UBN, which are located near the Mekong River. In these places the highest monthly rainfall was obtained in August and monthly rainfall exceeded 200 mm for five months from May to September. Rainfall decreased sharply in October, particularly in the two northern stations (VTN, SKN). The four stations in the central Korat Basin in Northeastern Thailand (CPA, KKN, PMI and SRN) had much lower rainfalls than those along the Mekong River. In these stations rainfall tended to decrease slightly after May, and then increased to a peak in September. Among these four locations rainfall was highest in SRN, followed by KKN, and lowest in CPA and PMI.

Table 1. Rice research stations in Thailand and Lao PDR.

Country	Rice research station	Abbreviation
Thailand	Ubon Ratchathani	UBN
	Sakon Nakhon	SKN
	Surin	SRN
	Phimai	PMI
	Khon Kaen	KKN
	Chum Phae	CPA
	Kok Samrong	KSR
	Phitsanulok	PSL
	Phrae	PRE
	Sanpatong	SPT
Lao PDR	Vientiane	VTN
	Champassak	CPK

Note: See map on page x (Introduction).

Among the four stations in Northern Thailand (SPT, PRE, KSR and PSL), rainfall was highest in PSL. Rainfall at the other stations was similar to that of CPA, KKN and PMI in the northeast. There was little rainfall in November except in SPT, where monthly rainfall was about 50 mm.

Results

The sowing date at each location reflected, to a large extent, the differences in rainfall patterns in these regions (Table 2). Thus, in the areas of heavy rainfall along the Mekong, sowing was early in mid–late June, except in UBN, where it was about one month later. Among the four stations in the central Korat Basin, sowing was about 15 days earlier in SRN and KKN than in CPA and PMI, and

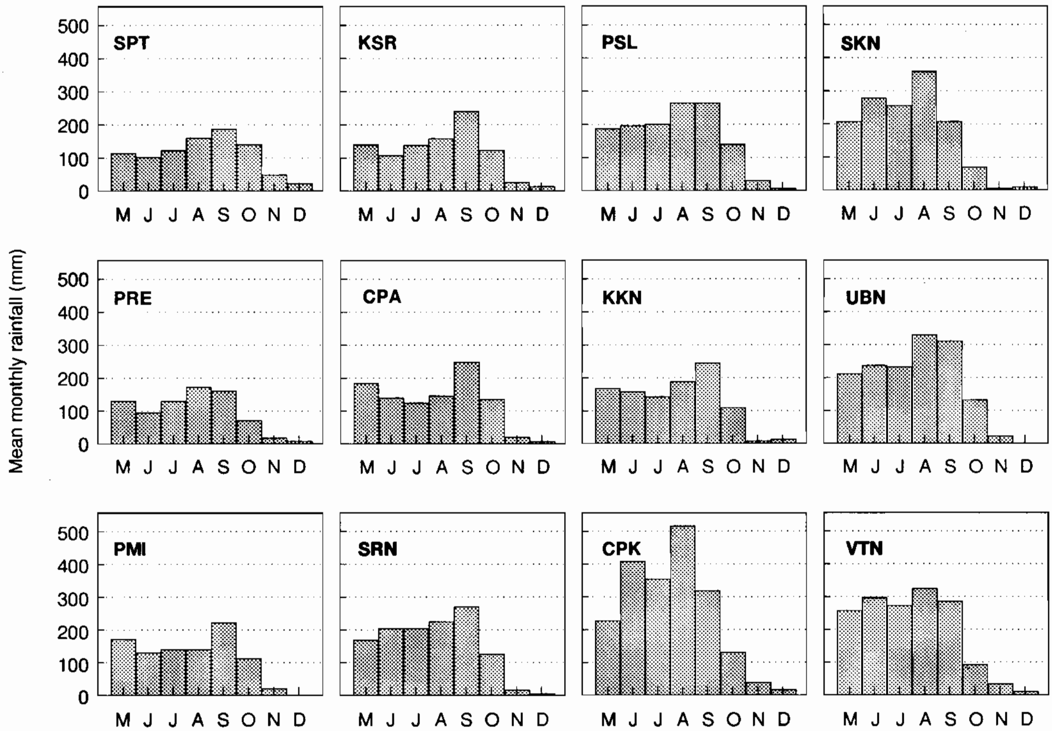

Figure 1. Monthly rainfall in 12 research stations in Thailand and Lao PDR (see Table 1), mean of 20 years.

this difference was associated with higher rainfalls early in the season in the former. Sowing was mid-July in Northern Thailand and SPT had the last mean sowing date.

Phenology had a large effect on grain yield, although the actual relationship between the two depended strongly on growth conditions. Six examples are shown in Figure 2. One common type of response was that of reduced grain yield in late-maturing cultivars, as shown for PRE 1994 and VTN 1993. Late-season drought was a common reason for this. In other environments, early-flowering cultivars produced lower yield (e.g. SPT 1994, PMI 1993), probably as a result of stress during early stages of growth, which affected the yield of earlier-flowering cultivars more severely. In PMI 1993, prolonged mild water stress reduced grain yield to a low level for all cultivars, but particularly early-flowering cultivars. In some other locations, yield was not affected by flowering date (SRN 1992) or the effect was rather small (SRN 1993). Comparison of SRN 1992 and 1993 results reveals that flowering dates among cultivars were much more spread in 1993 than in 1992, due to much

Table 2. Time of sowing of rainfed lowland experiments at 12 locations in three years.

	Year 1	Year 2	Year 3	Average
VTN	17 June	29 June	22 June	23 June
CPK	18 June	13 June	14 June	15 June
SKN	13 July[1]	8 June	16 June	12 June
UBN	23 July	16 July	11 July	16 July
SRN	31 July[1]	21 June	1 July	26 June
KKN	20 July[1]	25 June	1 July	28 June
CPA	13 July	9 July	8 July	10 July
PMI	15 July	13 July	12 July	13 July
PSL	20 July	16 July	12 July	16 July
KSR	21 July	26 Aug[2]	10 July	16 July
PRE	16 July	8 July	8 July	11 July
SPT	17 July	20 July	19 July	19 July

[1] Year 1 sowings excluded from average calculation due to late start of the project at these sites

[2] KSR year 2 is a replant, and not included for average calculation

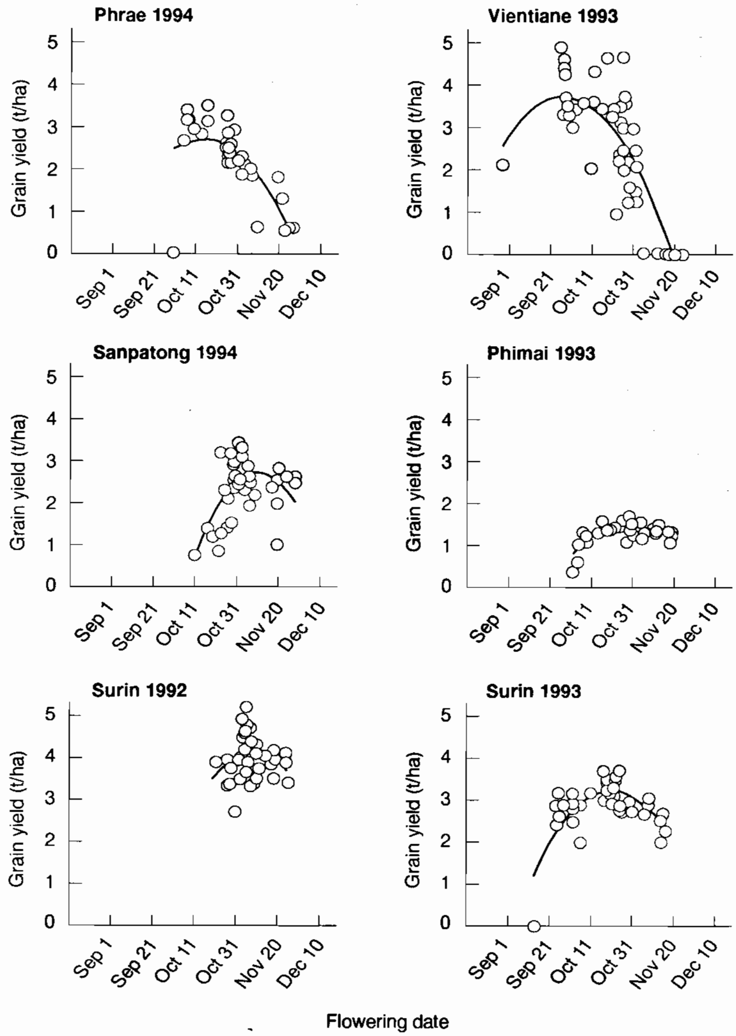

Figure 2. Grain yield of 35 rice cultivars in relation to flowering time in six selected experiments.

earlier sowing in the former (21 June vs 31 July). Despite no apparent stress developing late in the season, late-flowering cultivars produced lower yields than did early–medium flowering cultivars in 1993.

When all 36 environments were combined to calculate mean yield and mean flowering date for each cultivar, there was a strong relationship between the two, with the R^2 for the second order polynomial being 0.88. All high-yielding cultivars flowered in mid–late October, whereas a large number of traditional cultivars that flowered in November produced lower yields (Fig. 3). The highest mean yield was obtained by IR57514-PMI-5-B-1-2, followed by Khao Strok, RD6, KDML105 and IR43602-PMI-B-15-1-2-2. For each cultivar, the five highest yields were selected out of the 36 environments to estimate the potential yield that would be largely unaffected by drought or low soil fertility. The potential yield was also highest in cultivars that flowered in mid–late October and was above 4 t/ha in several cultivars. Cultivars with high potential yield also produced high average yield across the 36 environments. The potential yield was lower in later-flowering cultivars, although late flowering caused a smaller decrease in the potential yield than in the average yield obtained in 36 environments, indicating the likely adverse effect of late-season drought on these cultivars. The highest

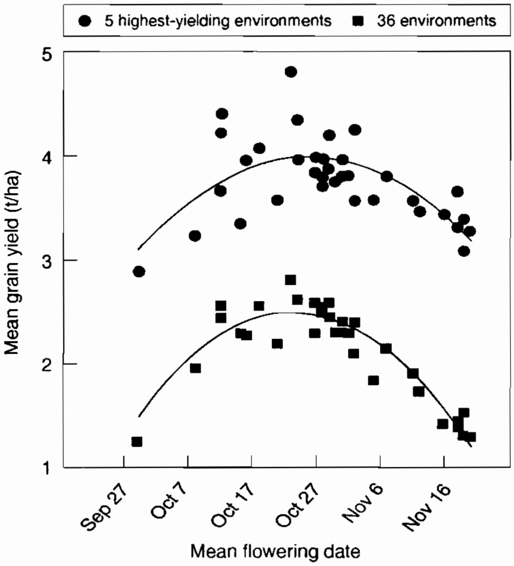

Figure 3. Relationship between mean grain yield and mean flowering date of 35 rice cultivars grown in 36 different environments; and five environments where yield was highest for each cultivar.

potential yield was again achieved by IR57514-PMI-5-B-1-2, followed by RD23 and Khao Strok.

Since grain yield varied consistently with flowering date in most environments, either curvilinear or linear regressions were fitted to describe the relationship between the two, and to identify the flowering date at which grain yield was highest in each of the 36 environments. There were four environments (including SRN 1992) where the relationship was not significant ($P < 0.05$), but in others an optimum flowering date could be estimated from the regression. Optimum flowering date was late September to mid-October when sown in June, and was generally later as sowing date was delayed (Fig. 4), as expected from the delay in flowering time of most cultivars with delayed sowing. Coefficient of determination (R^2) was 0.22 when the very late sowing was excluded and was 0.18 with all environments. There is, however, large variation along the regression, particularly when sown in mid-July. Optimum flowering dates in some environments were earlier than expected from the regression when severe late-season drought developed in the crops sown commonly in mid-July or later (CPA 1992–94, KSR 1992, 1993, SKN 1992), but also when sown in June (VTN 1993, 1995). When these stressed crops were excluded, 32% of the variation in optimum flowering date was explained by sowing date.

When individual cultivars were examined across 36 environments, the relationship between grain yield and flowering date was not significant for most cultivars, because of large yield variation among the environments (Fig. 5). Most cultivars were also strongly photoperiod sensitive, and hence variation in flowering date was rather small. Photoperiod insensitive or mildly sensitive cultivars tended to flower early and escaped late-season drought in most cases. There was, however, a significant association between yield and flowering date in mildly sensitive cultivars NSG19 and BKNBR82027-NSR-8-1, in which early sowing tended to be advantageous.

Discussion

The study has shown general phenology requirements for rainfed lowland rice in Thailand and Lao PDR. The region may be grouped into three areas: high rainfall areas along the Mekong River; the central Korat Basin that is commonly exposed to late-season drought; and Northern Thailand, where drought around the time of transplanting is a major problem.

In the high-rainfall areas, which are represented by research stations in VTN, CPK, SKN and UBN, and to a lesser extent by SRN and KKN, early sowing in June and transplanting in July are possible in most seasons. The use of photoperiod insensitive and mildly sensitive cultivars that flower in late September–early October should be encouraged. In areas with high soil fertility,

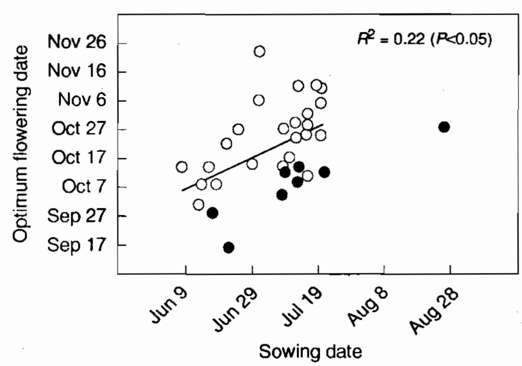

Figure 4. Optimum flowering date in relation to sowing date, estimated for each of 32 environments. Solid symbol indicates that crop experienced late-season drought.

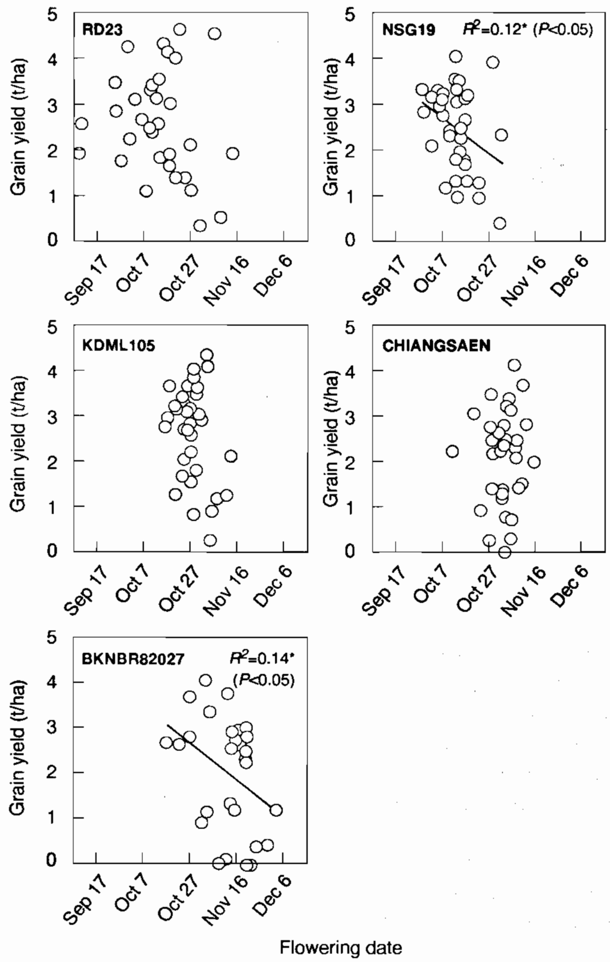

Figure 5. Grain yield of five selected rice cultivars in 36 environments in relation to flowering time.

semidwarf types may be most appropriate. Photoperiod sensitive cultivars that flower in late October do not appear suitable because they are more likely to be affected by late-season drought, particularly in areas where rain stops early, e.g. SKN, VTN. It may also be that these cultivars take too long to flower when sown in June, and yield potential may be reduced. It is noted that sowing was generally later at Ubon than at other stations in the region, and it is likely that earlier sowing in June would increase yield (Fukai et al. 1995). It should be pointed out, however, that sandy soils in the Ubon area do not accumulate water readily in the paddy and this increases the chance of having no standing water at the appropriate time of transplanting, particularly if sown too early in the season.

In the central Korat Basin, including CPA, PMI, KKN and SRN, and also in the eastern part of the Central Plain, represented by KSR, both early-season water availability and late-season drought are constraints for rice production as shown in the results of CPA, PMI and KSR. With sandy-textured soil, the Ubon area may be included in this group of unfavourable environments. In the current practice of early to mid-July sowing, the use of cultivars that flower in early to mid-October appear most suitable (e.g. NSG19). These cultivars, however, appear to be more susceptible to delay in transplanting and early-season stress. Later-flowering cultivars may perform better in some areas where late-season drought may not be severe (as shown in the results of SRN, PMI and KKN). The advantage of the use of strongly photoperiod sensitive cultivars is that they can still flower at the same time when sowing is delayed due to the late commencement of the wet season. These results agree with the recommendation of Pushpavesa and Jackson (1979) that a wide range of phenology type is required for the northeast. Higher yield may be obtained by earlier sowing in June, if the risk of transplanting failure is reduced. One possibility is the use of direct seeding, with which earlier sowing than the current practice would be possible, and higher and more stable yield could result if flowering took place in early to mid-October.

In Northern Thailand, cultivars that flower in late October to early November appear suitable, e.g. RD6, KDML105. Development of cultivars with higher potential yield appears particularly appropriate for this region. This could be achieved by choosing a semidwarf parent with high harvest index in crossing processes (Jearakongman et al. 1995). A major problem appears to be lack of standing water at the appropriate transplanting time and direct seeding may also be appropriate in this region.

In addition to rainfall, soil characters, particularly deep percolation rate and lateral water flow, determine water balance and hence the time and severity of drought in individual paddies of rainfed lowland ecosystems. Thus, soil types and topography also need to be considered for determination of optimum flowering time. Upper paddies are likely to lose standing water earlier than those in lower positions, and hence would generally require earlier-flowering cultivars. Similarly, paddies with sandy soils with high deep-percolation rates would require early-flowering cultivars (Fukai 1996). The time of disappearance of standing water from paddies can be used to estimate phenology requirement for each paddy, as yield decreases sharply if flowering takes place after the disappearance of standing water (Jearakongman et al. 1995).

It should be mentioned that the results were obtained from 35 cultivars with differing yield potentials. Thus, different phenology requirements may be obatined, to some extent, if different cultivars, with different yield potentials from those used in the present study, are used. Also, the experiments were conducted on research stations, and the growing environments were somewhat different from farmers' paddies. In one station (SPT), irrigation was used every year and this makes it difficult to apply the result to the farmers' fields, which are strictly rainfed. Nevertheless, it appears clear that traditional cultivars that have low yield potential and flower in November will not give suitable high yields in rainfed lowland ecosystems in Thailand and the Lao PDR. As Fukai and Cooper (1995) suggested in their review of plant characteristics required for rainfed lowland rice in drought-prone environments, it is most important to define drought environments so that appropriate phenology requirements are identified. Within the appropriate phenology group, drought-tolerant characters may be identified and used as selection criteria in plant breeding programs. This work has identified phenology requirements for different regions, and selection may be made against late-season drought within the phenology group. The present study also indicates the importance of increasing potential yield in early–medium flowering cultivars, as drought does not develop all the time in Thailand and Lao PDR, particularly if appropriate sowing time and phenology groups are selected.

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Implications of Genotype-by-Environment Interactions for Yield Adaptation of Rainfed Lowland Rice: Influence of Flowering Date on Yield Variation

M. Cooper* and Boriboon Somrith†

Abstract

The objective of this study was to investigate the major causes of yield variation among rice genotypes under rainfed lowland conditions in Thailand and Lao PDR. Strong genotype-by-environment (G×E) interactions were identified for yield. Genotype-by-site-by-year (G×S×Y) interactions were the largest source of G×E interactions, followed by genotype-by-site (G×S), then genotype-by-year (G×Y) interactions. These interactions were largely explained by genotypic variation for flowering time and environmental variation in the timing and intensity of drought. There was variation for yield among genotypes with similar days to flowering, and high-yielding genotypes were identified from both the Thai and Lao breeding programs. Pattern analysis identified groups of genotypes that differed for both mean yield and phenology, and groups of environments that were different in terms of the water limitations imposed on the genotypes. One group of three genotypes (one from Thailand and two from Lao PDR) were predicted to yield well across both water-limited and well-watered environments, giving scope to improve the yield of rainfed lowland rice in Thailand and Lao PDR. The groups of environments did not have a strong regional basis within Thailand. The Lao environments grouped together and also with a large group of Thai environments. It is recommended that to establish a breeding strategy that accommodates the effects of the large G×E interactions for yield, two fundamental elements are required: a multienvironment trial system that tests genotypes in the major rainfed lowland production regions and across years to deal with the large G×S×Y interactions; and selection for genetic variation contributing to high yield within groups of genotypes that have similar phenology, in particular similar days to flowering.

RAINFED lowland rice in Thailand and the Lao People's Democratic Republic (Lao PDR) is grown in a crop production system that is highly prone to periods of moderate to severe drought (Somrith and Awakul 1979; Pushpavesa and Jackson 1979; Pushpavesa et al. 1986). The timing and intensity of these drought periods determine their effect on crop yield (Fukai and Cooper 1995). There is widespread interest in evaluating the potential for increasing the yield of rainfed lowland rice by breeding for improved stress tolerance, with drought resistance a major component (Singh et al. 1996). However, the potential for genetic improvement of drought resistance is unknown. The Australian Centre for International Agricultural Research (ACIAR) project PN9045 was established to obtain strategic information on the potential for improving the drought resistance of rainfed lowland rice in Thailand and Lao PDR. As part of this project, a series of multienvironment trials (METs) was conducted to obtain information on the extent of genotype-by-environment (G×E) interactions for yield and the key factors that contributed to these interactions. While there was an expectation that variation for flowering time would be important, there was a need to quantify its influence and assess the extent of yield variation after its effects were taken into consideration.

METs are routinely used in plant breeding programs to evaluate the relative performance of breeding lines (genotypes) over the range of environ-

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ments expected in the target population of environments. Definition of superior genotypes is often complicated by G×E interactions. In response to the ubiquitous nature of G×E interactions, an array of statistical methods has been developed for the analysis of the genetic variation observed in METs. The choice of an appropriate statistical method has been debated on a number of grounds, but the two guiding principles recommended here are:

- that the genetic models used are relevant to the genotype–environment system being studied; and
- that the statistical analyses applied are related to the fundamental questions being asked of the experiments.

To design a MET strategy that accommodates G×E interactions, it is necessary to determine the extent of the components of the G×E interactions that are repeatable and those components that are random and non-repeatable. It is then possible to develop an understanding of the genetic and environmental factors contributing to the repeatable interactions and exploit both broad and specific adaptation in a breeding program (e.g. Cooper and Byth 1996; Brennan, this volume).

The objectives of this paper are:

- to quantify the magnitude and causes of G×E interactions for grain yield;
- to examine the influence of variation for flowering time on yield variation for rainfed lowland rice in Thailand and Lao PDR; and
- to identify the extent of yield variation after the effects of flowering time are taken into consideration.

This study updates earlier analyses by Henderson et al. (1996), who examined part of the larger data set considered here. Other papers in this volume that are relevant to the analysis of this MET data set are those by Somdej Immark et al., Phoumey Inthapanya et al. and Satit Rajatasereekul et al.

Materials and Methods

Multienvironment trial

A total of 62 genotypes were used in the multienvironment trial. The genotypes were predominantly from Thailand, with one from the United States (Lemont) and four from Lao PDR. Some of the genotypes are adapted to irrigated lowland conditions but most are commonly grown in rainfed lowland conditions. The trial was conducted over three years (1992–94), with 13 sampling sites, 11 from Thailand and 2 from Lao PDR (Table 1). At one location (Phitsanulok), lowland and upland experiments were conducted in all three years. A total of 37 environments were sampled. The sites were from four major regions in the rainfed lowland rice system in Thailand and Lao PDR:

- upper north of Thailand;
- lower north of Thailand;
- northeast Thailand; and
- Lao PDR.

The majority of sites were in the Northeastern Region of Thailand. The data set was highly unbalanced, with some genotypes only grown in one year and others at a restricted number of sites over the three years. Twenty of the Thai genotypes were grown at only four sites in Northeastern Thailand in 1992 and the four Lao genotypes were only grown at the two Lao sites in 1993 and 1994. The two Lao sites were not sampled in 1992. In general a core set of 35 genotypes was grown in each of the environments (location–year combination) sampled.

Table 1. Name, code and region of the 13 sites sampled from Thailand and Lao PDR for evaluation of genotypes.

Country/region	Site	Code
Thailand		
Upper north	Sanpatong	SPT
	Phrae	PRE
Lower north	Phitsanulok lowland	PSLl
	Phitsanulok upland	PSLu
	Kok Samrong	KSR
Northeast	Sakon Nakhon	SKN
	Khon Kaen	KKN
	Chum Phae	CPA
	Phimai	PMI
	Surin	SRN
	Ubon Ratchathani	UBN
Lao PDR	Vientiane	VTN
	Champassak	CPK

Note: See map on page x (Introduction).

The genotypes were evaluated in a randomised complete block experiment with three replicates in each experiment. Plots were 1.5 × 5 m in size, with

0.25 m between rows and hills. Generally three plants were transplanted per hill, but at one site in 1992 one plant was transplanted per hill and at the same site in 1993 direct seeding was used. In 1992 many of the experiments were established later than normal. Because of widespread drought conditions at the time of transplanting in 1993 (July to early August), many of the experiments were irrigated to enable transplanting. At Sanpatong the paddies were irrigated for transplanting in all three years and also at the booting stage in 1993 and 1994 when drought had developed. For each plot, 4 m of the central four rows was harvested to determine grain yield (adjusted to 14% moisture). The number of days to flowering was determined as the number of days from seeding of genotypes to when 75% of the plants in a plot had reached anthesis.

Analysis of variance

The analysis of variance was computed for grain yield and days to flower using the model applied by Henderson et al. (1996). This recognised the cross-classification structure of years and sites and enabled partitioning of the G×E interaction component into genotype-by-site (G×S), genotype-by-year (G×Y) and genotype-by-site-by-year (G×S×Y) interaction components of variance. It was assumed that the genotypes represented a random sample of rice germplasm that could be considered for rainfed lowland conditions in Thailand and Lao PDR and that the years and sites were a random sample of those used by the Thai and Lao breeding programs. The method of residual maximum likelihood (REML) was used to accommodate the unbalanced nature of the data set (Patterson and Thompson 1971, 1975). Components of variance and their approximate standard errors were estimated and the best linear unbiased predictors (BLUPs) were computed for the genotypes, sites and years and their interaction terms. The BLUPs are predictions of the performance of the genotypes in each of the environments sampled in the MET using a combination of the data and the components of variance obtained from the analysis of variance. Where a genotype was not grown in an environment or a site was not sampled in a year, the BLUPs can be obtained for these missing values and used as predictors of performance.

Pattern analysis

Pattern analysis of grain yield was conducted following the procedures discussed by Cooper and DeLacy (1994) and was implemented using the GEBEI software package available from The University of Queensland (Watson et al. 1996). This involved a combination of grouping and ordination analysis of the genotypes and environments, based on environment standardised data (Fox and Rosielle 1982). To accommodate the unbalanced nature of this data set for the pattern analysis, the BLUPs for the genotypes and environments were used in place of the original data. Thus, all missing values were replaced by their appropriate BLUP. Therefore, a matrix of BLUPs was constructed for the 62 genotypes at the 13 locations in the three years. The pattern analysis described here should be viewed as a summary of the BLUPs obtained from the REML analysis, which are in turn predictions of performance based on the results from the analysis of variance.

To display the results of the cluster analysis, dendrograms for the hierarchical relationships among genotypes and environments were constructed (Williams 1976); for the ordination, biplots (Kempton 1984) were constructed for the first two principal components. The genotypes were represented on the biplots as points derived from their scores on the first two components and the environments as vectors from the origin to their points. The angles among the environment vectors can be interpreted in terms of the correlations among the environments based on the genotype yields in the environments. A small angle (<<90°) indicates a strong positive correlation, an angle close to 90° indicates the results are not correlated and an angle close to 180° indicates a strong negative correlation. The association between days to flowering and grain yield was investigated for each of the groups of environments identified by cluster analysis. In addition, the genotype mean yield and days to flowering across all environments were correlated with the scores of the genotypes on the principal component axes to quantify their correspondence.

Results

Analysis of variance

The estimated components of variance for genotype means, G×S, G×Y, G×S×Y interactions and error for grain yield and days to flowering were all large relative to their respective standard errors (Table 2). For grain yield, the genotype component was similar in magnitude to the G×S×Y interaction component and both were larger than the G×S and G×Y interaction components. The G×Y interaction component was the smallest interaction component. The relative magnitude and the error component of variance were similar to the estimates obtained by Henderson et al. (1996) when they examined the first two years (1992 and 1993) of this data set. For days to flower the genotype component of variance was large relative to all other components of variance (Table 2). The G×S×Y interaction component was the largest interaction component of variance. The G×S interaction component was larger than the G×Y interaction component, with the former of similar magnitude to the error component.

Table 2. Residual maximal likelihood (REML) components of variance and approximate standard errors for grain yield (t/ha) and days to flower for genotypes (G), genotype-by-site (G×S), genotype-by-year (G×Y), genotype-by-site-by-year (G×S×Y) interactions and experimental error.

Source	Attribute	
	Grain yield (t/ha)	Days to flower
Genotype	0.198±0.044	138.3±26.4
G×S	0.082±0.014	7.4±1.6
G×Y	0.018±0.007	3.9±1.2
G×S×Y	0.199±0.014	31.4±1.9
Error	0.178±0.004	6.4±0.2

Note: Based on 62 genotypes tested at 13 sites for three years (1992–94) in Thailand and Lao PDR.

There was a quadratic relationship between genotype mean grain yield and days to flower, with late-flowering genotypes generally yielding less than those that flowered between 95 and 115 days after seeding (Fig. 1). Comparing genotypes with similar days to flowering, there was variation for grain yield after taking into account the genotype mean differences for days to flower. The grain yield deviations from the yield predicted by the quadratic relationship tended to be positive for the genotypes with higher mean yield (Fig. 2a) and were larger for those genotypes with early to intermediate flowering (Fig. 2b). This suggests that more genotypic variation for grain yield was detected among the genotypes with short to intermediate duration from seeding to flowering.

Pattern analysis

The one-way cluster analysis of the genotypes was truncated at the eight-group level (Fig. 3; Table 3) and this retained 91% of the genotypic and 46% of the G×E interaction variation for the standardised grain yield BLUPs. While the eight genotype groups were identified on grain yield data, they also differed for the attribute days to flower, indicating that genotypic variation for days to flower influenced the patterns of grain yield variation identified by cluster analysis (Table 3; Fig. 1). The one-way cluster analysis of the environments was truncated at the four-group level, and this retained 39% of the G×E interaction variation for standardised grain yield BLUPs (Fig. 4). The mean yield of the environment groups differed even though the environment main effect was removed by the standardisation transformation. This indicates that the patterns of G×E interaction contributing to the grouping of environments were associated with mean yield level of the environments. For the two-way grouping (eight genotype groups and four environment groups truncation level), 29% of the original variation for G×E interaction variation was retained among the groups. The yield performance profiles of the eight genotype groups over the four environment groups (Fig. 5) indicated that there were genotype groups that performed well with some consistency across the environment groups (genotype groups 1 and 4). Other genotype groups showed marked changes in relative yield (genotype groups 3, 5 and 8).

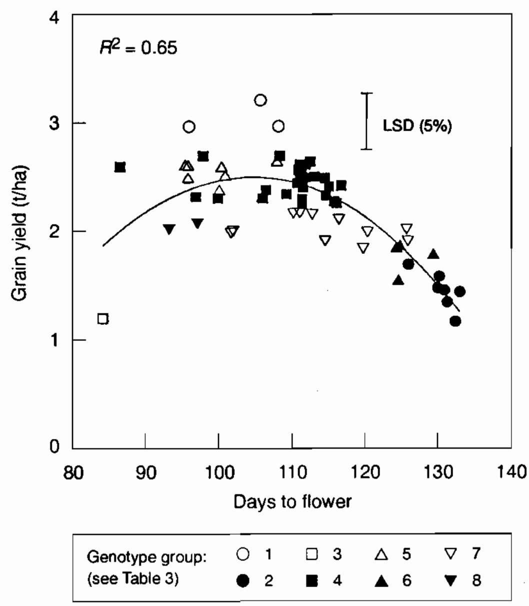


Figure 1. Relationship between the best linear unbiased predictors (BLUPs) for mean days to flowering and mean grain yield for 62 rice genotypes tested at 13 sites from rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94). (LSD (5%) = least significant difference; 5% probability level.)

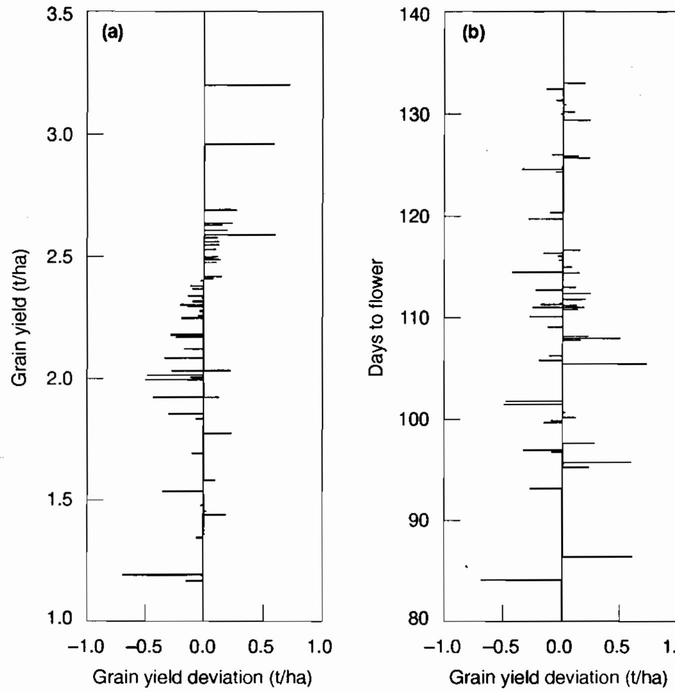


Figure 2. Grain yield deviations from the quadratic relationship between mean days to flower and mean grain yield for 62 rice genotypes tested at 13 sites in three years (1992–94) ranked for (a) mean grain yield based on best linear unbiased predictors (BLUPs), (b) mean days to flower BLUPs.

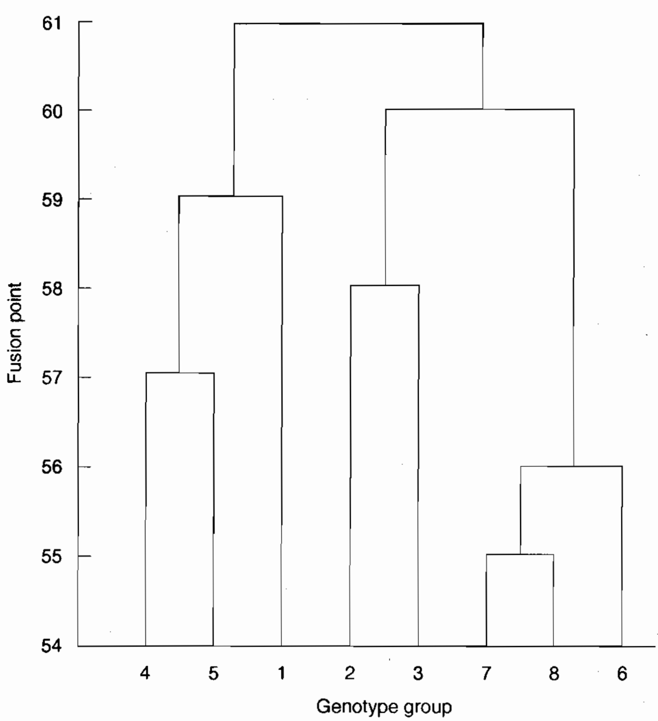


Figure 3. Dendrogram, truncated at the eight-group level, for hierarchical clustering of 62 rice genotypes, based on the matrix of standardised grain yield best linear unbiased predictors (BLUPs) for 13 sites from rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94). The membership of the groups is given in Table 3.

Table 3. Membership of eight genotype groups identified by cluster analysis based on standardised grain yield best linear unbiased predictors (BLUPs) for 62 genotypes at 13 locations in three years (1992–94).

Group	No.	Genotypes[1]	Yield (t/ha)	Days to flower
1	3	**IR57514-PMI-5-B-1-2**, *Thadokkham 1*, *Phon Ngam 1*	3.03	102.9
2	7	**LPT123, Leuang Dawk Koon, Leum Dern, Khao Yai, Chabah Sarahn, Taw Chaw Daw, Daeng Noi**	1.45	130.4
3	1	**Lemont**	1.19	84.2
4	26	**KDML105, RD6, Jumpah Tawng, Khao Strok, E-Pad, E-Nawn, Lum Narai, Leuang Samer, Puang Sawan, Khao Luang**, Sahn Ruang, Daw Hawm, Gahb Lai, Jao Daw, Jao Chumpae 60, Hawm Pae Polo, RD8, *Khao Leuang*, *Khao Takiad*, **IR52532-SKN-23-B-1-2, IR43506-UBN-520-2-1-1, IR57546-PMI-1-B-2-2**, IR45490-SRN-25-2-2-3, IR51128-SKN-42-B-1-4-1, IR49835-SKN-16-B-1-5-1, IR57548-PMI-7-B-1-1	2.44	109.1
5	8	**NSG19, RD10, RD23, IR20, IR49766-KKN-54-B-B-6, IR43602-PMI-B-15-1-2, IR43450-SKN-506-2-2-1, IR43039-CPA-510-3-3-1**	2.49	100.0
6	4	Niang Kanow, Udom, Nahng Sa-ad, Khao Noi	1.75	125.7
7	11	**Chiangsaen, KPM148, Tah Tae**, Kra Tom, Dawk Mai, Khao Lao, Sao Leum Yang, Khi Kwai, Hawm Sa-dung, Jao Noi, **BKKBR82027-NSR-8-1**	2.03	114.4
8	2	IR29, **Leuang Bun-ma**	2.05	95.0

[1] The core set of 35 genotypes grown in all environments is highlighted in bold and the four Lao genotypes are highlighted in italics

The grouping of the environments reflected the information obtained from the REML analysis of the grain yield data (Table 2). Considering the allocation of environments at the four-group level, there was evidence of G×S, G×Y and G×S×Y interactions in the way the environments were grouped. Since the G×S×Y interaction was the largest interaction component, there was not a dominant tendency for environments to be grouped on a year or site basis (Fig. 4). However, since there were significant G×S and G×Y interaction components, there were tendencies for some sites from the same year to group (group D was dominated by sites from 1992) and a tendency for some sites to group across years. There

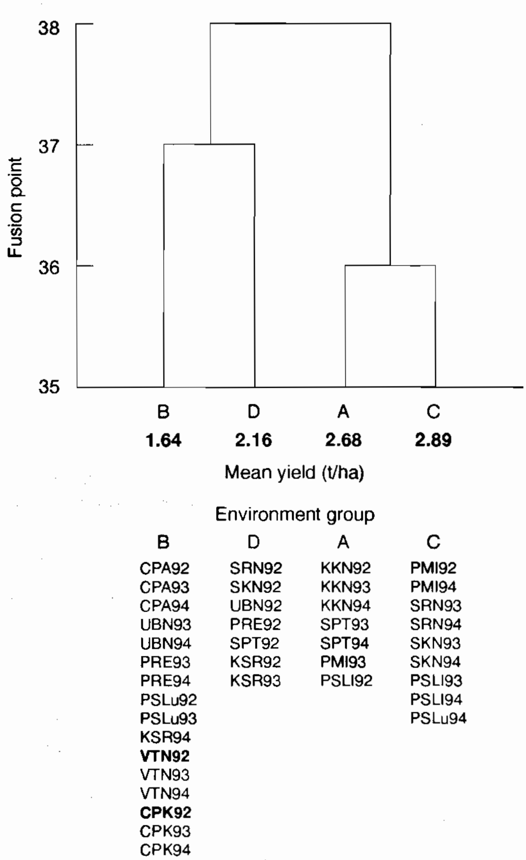


Figure 4. Dendrogram, truncated at the four-group level, for the hierarchical clustering of 39 environments, based on the matrix of standardised grain yield best linear unbiased predictors (BLUPs) for 62 genotypes tested at 13 sites from rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94). The two Lao sites in 1992 (VTN92 and CPK92) are highlighted in bold since these are the two experiments that were not conducted and their allocation to group B is based on the BLUPs from the residual maximal likelihood (REML) analysis. (See Table 1 for abbreviations.)

were two sites where the three years from that site were allocated to the same group (CPA, Chum Phae, in group B; KKN, Khon Kaen, in group A) and other examples where two years from a site were allocated to the same group (e.g. UBN, Ubon Ratchathani, in group B; PRE, Phrae, in group B; KSR, Kok Samrong, in group D). No sites had all three years allocated into three different groups. While the two Lao sites, Champassak and Vientiane, were not sampled in 1992 (CPK92 and VTN92), a prediction of which group they may have belonged to, if they had been sampled, was based on the BLUPs. Group B contained all of the Lao environments, and also contained a number of Thai environments from the Northern and Northeastern Regions.

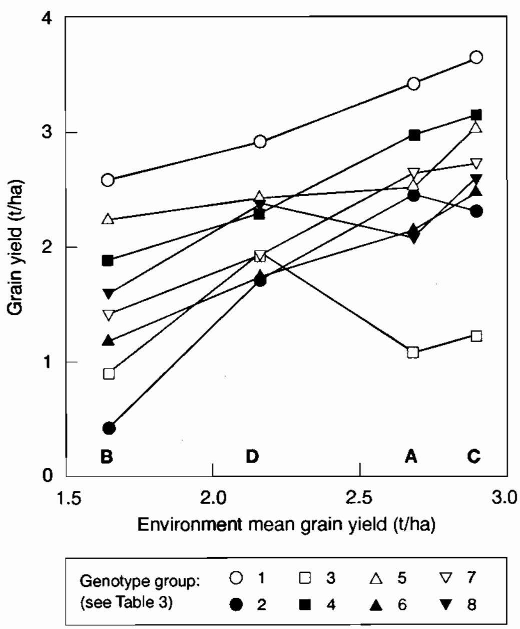


Figure 5. Group mean grain yield performance profiles for eight groups of genotypes and four groups of environments (A, B, C, D; see Fig. 4) identified by two-way cluster analysis of the matrix of grain yield based on best linear unbiased predictors (BLUPs) for 62 genotypes tested at 13 sites from the rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94).

The relationship between days to flower and grain yield changed among the four groups of environments identified by cluster analysis (Fig. 6). The two lower-yielding environmental groups, B and D, contained those environments where the later-flowering genotypes tended to be severely affected by water stress and thus had low yield relative to the early- to intermediate-flowering genotypes. Groups A and C contained higher-yielding environments where the severity of stress imposed on the late genotypes was reduced by either irrigation or rainfall and the later-flowering genotypes yielded relatively better. A quadratic relationship was fitted for each environment group and the R^2 ranged from 0.42 for group A (Fig. 6a) to 0.73 for group B (Fig. 6b). The degree of the yield contrast associated with flowering date differed among the groups. In environmental groups A (Fig. 6a) and C (Fig. 6c) there also tended to be a yield penalty associated with flowering too early. These two groups contained environments where stress during the early stages of growth was reported, e.g. SPT94 and PMI93 (Satit Rajatasereekul et al., this volume). For the other two groups, B (Fig. 6b) and D (Fig. 6d), there appeared to be little yield penalty associated with early flowering.

The principal component analysis for the standardised grain yield data explained 78% of the variation for yield in the standardised BLUP data set on the first two vectors (66% principal component 1 and 12% principal component 2) (Fig. 7). The genotype scores on principal component 1 were perfectly correlated with the mean yield of the genotypes across environments (r = 1.00, P < 0.01) and negatively correlated with days to flower (–0.55, P < 0.01). The genotype scores on principal component 2 were positively correlated with the mean days to flower for the genotypes (r = 0.62, P < 0.01) and not correlated with mean yield (r = –0.03). Therefore, the biplot for principal components 1 and 2 can be interpreted in terms of variation for mean yield and days to flower (Fig. 7). Genotypes to the right of principal component 1 are predicted to have higher mean yield and tended to be early- to medium-flowering, and genotypes towards the top of principal component 2 tended to flower later. The results of the two-way cluster analysis are represented on the biplot by using a different symbol for the eight genotype groups and plotting the vector for the mean score for the four environment groups, rather than the scores for individual environments.

There are consistencies between the grouping relationships among the environments identified by cluster analysis (Fig. 4) and the spatial relationships depicted in the biplot (Fig. 7). The most obvious is that the two environment groups B and D are distinguished from the other two environment groups (A and C) by both analyses. This also corresponds with the major distinction in the form of the relationship between days to flowering and grain yield for these environmental groups (Fig. 6). Groups B (Fig. 6b) and D (Fig. 6d) are the environmental groups where there is a tendency for later-flowering genotypes to have lower yield, whereas for environmental groups A (Fig. 6a) and C (Fig. 6c) there appears to be a stronger quadratic relationship, with an intermediate-flowering date contributing to higher grain yield. Projecting the genotype scores onto the environment group vectors, the relationships between days to flower and grain yield for each environment group (Fig. 6) can be observed on the biplot (Fig. 7). For example, the genotypes from group 1 (IR57514-PMI-5-B-1-2, Thadokkham 1, and Phon Ngam 1) are predicted to have high yield in each of the environment groups. In environment groups B and D the late-flowering genotypes are predicted to have lower yield than the genotypes with early and intermediate days to flower. For environmental groups A and C, neither early- nor late-flowering genotypes are predicted to have high yield. The highest yield was predicted for those genotypes with intermediate days to flowering. The consistency of the interpretation of the observed G×E interactions in terms of the effects of flowering time emerges because of the dominant influence of days to flower on yield of the genotypes in these environments.

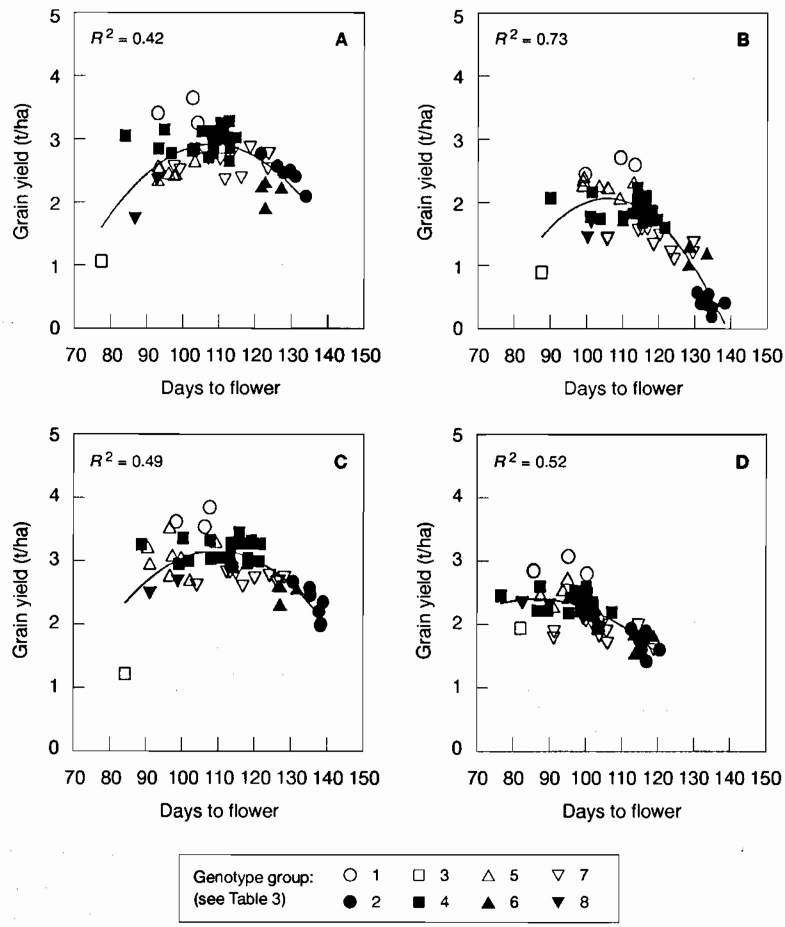
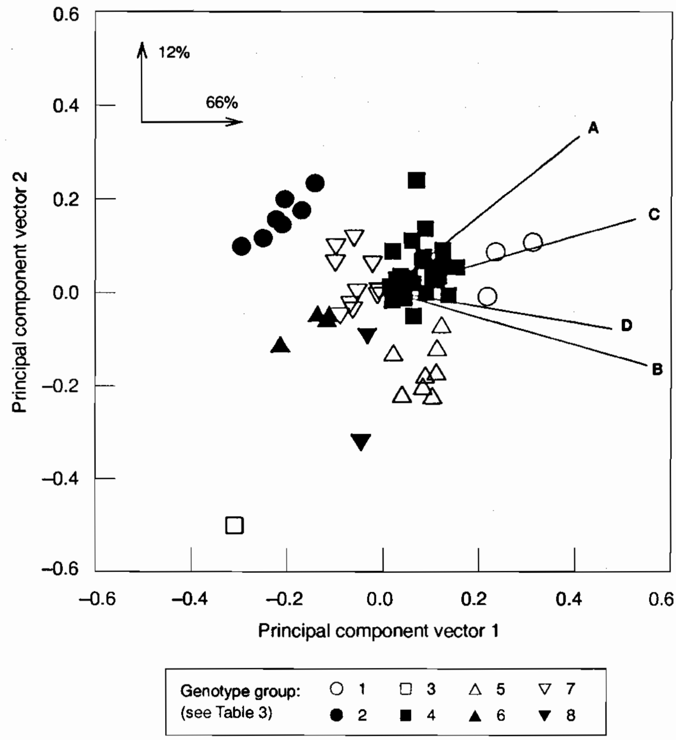


Figure 6. Relationship between the best linear unbiased predictors (BLUPs) for mean days to flowering and mean grain yield for 62 rice genotypes in four groups of environments (A, B, C, D; see Fig. 4), identified by cluster analysis of the matrix of grain yield BLUPs for the 62 genotypes tested at 13 sites from rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94).

Figure 7. Biplot of the first two principal component vectors for the ordination of 62 genotypes and 39 environments based on the matrix of grain yield best linear unbiased predictors (BLUPs) for the 62 genotypes tested at 13 sites from the rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94). The vectors for the 39 individual environments are replaced by the mean vector for the four groups of environments identified by cluster analysis and shown in Figure 4. Inserted arrows indicate the percentage of total variation accounted for by each principal component vector.



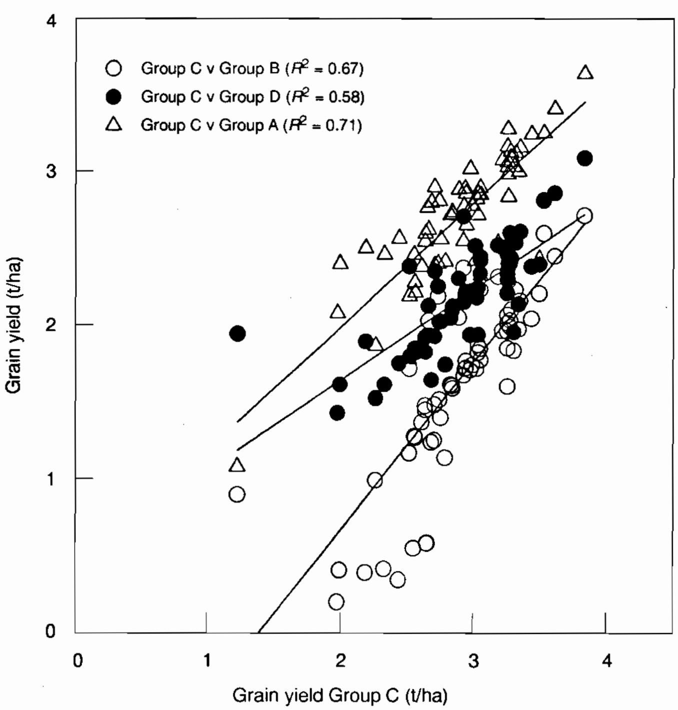


Figure 8. Relationship between the best linear unbiased predictors (BLUPs) for grain yield in the high-yield environmental group C and grain yield in the three water-limited environmental groups A, B and D (see Fig. 4) for the four groups of environments identified by cluster analysis of the matrix of grain yield BLUPs for the 62 genotypes tested at 13 sites from rainfed lowland regions from the north and northeast of Thailand (11 sites) and Lao PDR (two sites), for three years (1992–94).

The relatively small angles among the four environment group vectors suggest that there are no major changes in the rankings of the genotypes across the four environment groups (Fig. 7). Generally the yield of the genotypes in the high-yielding environment group C was positively correlated with yield in the lower-yielding environmental groups (Fig. 8). Thus, yield under low-stress conditions, where water limitations were relieved by either irrigation or high rainfall, was generally a good predictor of yield under water-limited conditions where water stress was imposed on the genotypes.

Discussion

The yield results obtained from the METs clearly identify that genotypic variation for days to flower can generate substantial genotypic variation and G×E interactions for grain yield of rainfed lowland rice. Many of the observed interactions can be explained in terms of variation for days to flower among the genotypes and environmental variation in the timing and severity of water deficits. Consequently the grouping of the genotypes and environments obtained from the cluster analysis was dominated by the variation for grain yield associated with genotypic variation for days to flowering and the timing of water limitations within the environments. Despite the strong G×E interactions, generally the yield of genotypes under low-stress conditions, where water limitations were relieved by either high rainfall or irrigation, was a relatively good predictor of yield under water-limited conditions where moderate to severe water stress occurred.

While genotypic variation for days to flower had a major influence over yield variation, there was variation for yield among genotypes with similar days to flower, indicating that there is scope for yield improvement of rice within the rainfed lowland environments after the influence of days to flower is taken into consideration. Of particular interest is genotype group 1 identified in this study, which comprised three genotypes, IR57514-PMI-5-B-1-2 and the two Lao cultivars Thadokkham 1 and Phon Ngam1. This group of genotypes was predicted to yield well relative to the other genotypes over all of the environment groups.

The three major conclusions that can be drawn from this study are:

1. There are strong G×E interactions for yield of rainfed lowland rice in Thailand and Lao PDR and these are largely explained by genotypic variation for days to flowering and the timing and intensity of drought events during crop growth and development. Generally these interactions were not strong enough to give rise to consistent major changes in the rank of genotypes across environments. Consequently, genotypic variation for yield under low-stress conditions was a relatively good predictor of yield under water-limited conditions.
2. There is yield variation among rainfed lowland rice genotypes after the effects of flowering time are taken into consideration. This variation appears to offer scope for improvement of both broad and specific adaptation of the two popular cultivars RD6 and KDML105. Germplasm from the Lao breeding program shows potential for contributing to yield improvement in Thailand.
3. Genotypic variation for days to flower must be explicitly accounted for in any breeding strategy focusing on improving drought resistance of rice in the rainfed lowland systems of Thailand and Lao PDR.

The results of this MET study have obvious and strong implications for the development of any plant breeding strategy for improving the drought resistance of rainfed lowland rice in Thailand and Lao PDR. Emphasis needs to be given to three major components:

- screening for yield potential under low-stress irrigated conditions;
- screening within flowering groups for any genetic variation that will contribute to higher yield; and
- developing a coordinated multienvironment testing program that focuses on dealing with G×E interactions associated with the differences among regions/sites and the effects of variation in timing and intensity of drought in relation to crop growth and development.

A plant breeding strategy that incorporates these three components would be targeted at developing cultivars that have the potential to yield under low-stress conditions, that possess broad adaptation to water-limited environments and that have the correct flowering time for the major rainfed lowland rice production regions. Rajatasereekul et al. (this volume) proposed that three major regions should be considered: the high rainfall areas along the Mekong River; the central Korat Basin; and Northern Thailand. These regions were proposed on the basis of differences in the probability of significant drought events. This would appear to be a useful stratification of the target rainfed lowland system for a coordinated MET program linked to the Thai and Lao breeding programs.

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Genotype-by-Environment Interactions: RLRRC Experience

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Abstract

Rainfed lowland rice is grown in bunded fields on 37 million ha of South and Southeast Asia, with yields averaging only 2.3 t/ha. Hydrologic conditions may fluctuate from submergence to drought, with major consequences for root growth, nutrient availability and weed competition. Because of the fluctuating conditions encountered, selection of improved cultivars is difficult. This paper examines the nature of genotype-by-environment (G×E) interactions in the rainfed lowlands, using data from nine locations in India, Thailand and the Philippines from 1995. G×E interaction accounted for 38% of the total sum of squares, with environment and genotype responsible for 48% and 14%, respectively. More than 75% of the G×E interaction sum of squares was captured in the pattern analysis. Philippine sites were tightly grouped, as were related entries. Discrimination of environments appeared to be related to general seasonal condition, and to the water regime later in the season. Groupings of entries could be explained by their performance in relation to these conditions. When conditions were more favourable, CT9897, IR20, IR36 and IR64 performed well, while Sabita, KDML105 and IR57546 performed well in less favourable conditions. There was some evidence that NSG19 was better able to withstand a rapid onset of late-season drought, while IR66516 and IR66469 were more tolerant of flooding. Factors contributing to the patterns identified are discussed, and the results compared with those from G×E interaction studies in Thailand and the Lao People's Democratic Republic. The patterns of adaptation require further testing when the 1996 and 1997 data become available. Research is proceeding to understand the basis of these adaptation patterns, in order to assist selection of improved cultivars of rainfed lowland rice.

RAINFED lowland rice is grown on 37 million ha in South and Southeast Asia, by some of the poorest subsistence farmers in the world (IRRI 1993). With yields averaging only 2.3 t/ha, rainfed lowland rice encounters an environment more complex than for most other rainfed crops. Because rainfed lowland rice is grown in bunded fields without water control, hydrologic conditions may fluctuate from submergence to drought, with major consequences for root growth, nutrient availability and weed competition (Garrity et al. 1986). Various systems of crop establishment are employed, from direct dry seeding to transplanting. Seedling vigour, weed competitiveness and capacity to withstand stress are influenced by the choice of crop establishment system. Most surveys of constraints to rainfed lowland rice production indicate that drought, weeds, submergence, and soil physical and chemical characteristics are the major problems (Widawsky and O'Toole 1990).

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In rainfed lowland rice, crop performance is highly variable. Yields are strongly influenced by seasonal characteristics, and by spatial heterogeneity over soil types, topographic sequences and agrohydrologic conditions. These variables, in turn, interact with the cultivar chosen and the cultural practice employed. As a result, the interactions between genotype and environment are highly significant, complicating the task of identifying an improved cultivar. In order to be higher yielding on average, the desired cultivar is one that is more stable over environments, with a reduced probability of crop failure. This is especially important in subsistence agriculture, where survival of the farmer and the family is largely dependent on the season's harvest.

Because of genotype-by-environment (G×E) interactions, selection of improved genotypes is difficult. Our studies on G×E interactions in rainfed lowland rice commenced in 1994, to define the target population of environments, identify traits that confer improved adaptation to the key constraints, develop effective selection procedures for those traits, and understand and predict the performance of the resulting genotypes over environments (Wade 1995; Wade et al. 1995b; Wade et al. 1996). This paper examines the nature of G×E interactions in the rainfed lowlands, using data from nine locations in India, Thailand and the Philippines from 1995. Factors contributing to the patterns of performance identified are discussed, and the results compared with those from related G×E interaction studies in Thailand and the Lao People's Democratic Republic (Lao PDR) (Cooper and Boriboon Somrith, this volume).

Materials and Methods

The experiments were described by Wade et al. (1995b). Only necessary details are provided here. At each location, an experiment was conducted using a 7 × 7 triple lattice design. Entries included 30 advanced breeding lines, 5 probe lines, 5 reference lines and 4 local checks. The probe lines were chosen with known environmental adaptation, and were repeated twice in each replicate to ensure precise observations, because their known properties will be used to interpret observed interactions. The reference lines were chosen to represent distinct groups of germplasm, and the local checks were to provide a basis for local comparison. Due to a shortage of seed not all breeding lines were the same over all sites, and this paper considers the common subset of 31 genotypes (Table 1). Experiments were conducted at locations associated with the Rainfed Lowland Rice Research Consortium (RLRRC). Data were available from nine of the 11 sites planted in 1995 (Table 2).

Statistical analysis

Mean yields for the common set of 31 genotypes over the nine environments were extracted from the single-site analyses for each site. Means were the adjusted means from the lattice analysis when the blocks variance component was positive, and ordinary means from the randomised blocks analysis when it was not. Factorial analysis of variance (ANOVA) was used to quantify sources of variation in the data set and correlations were computed to measure relationships among environments.

G×E interaction was analysed using pattern analysis (DeLacy et al. 1996). This involved the joint application of cluster analysis and ordination to a transformed G×E matrix. The G×E matrix was the array of mean yields for each genotype in each environment. This was transformed by double centring by row and column means because the objective of the analysis was the quantification and interpretation of interaction between genotypes and environments rather than an investigation of adaptation or of selection (McLaren 1996). Double centring results in a matrix of residuals from the two-way additive, main effects model and since the ordination component of pattern analysis used principal components analysis, it corresponds to the additive main effects and multiplicative interaction (AMMI) analysis (Gauch 1992).

Clustering was computed, both for genotypes and for environments, using an agglomerative hierarchical algorithm based on minimising incremental sums of squares (Ward's method). For genotypes the attributes were the transformed responses (residuals) in each environment, and for environments, the transformed responses of each genotype. Since main effects of genotypes and environments had been removed by the transformation, clusters reflect patterns of interaction for genotypes and patterns of discrimination for environments. The number of genotype and environment groups retained in the cluster analysis was based on a requirement to retain a reasonable minimum amount of the G×E interaction sum of squares among group means and to select the pair of group numbers that had the smallest pooled within-group mean squares of all groupings which just achieve this minimum.

Results

Genotype and environment mean yields are given in Tables 1 and 2, with the ANOVA shown in Table 3.

Table 1. Common genotypes, their mean yields (t/ha) and rank based on mean yields over nine sites in the rainfed lowland rice ecosystem.

Code	Entry name		Mean yield	Rank
09	IR64	(Reference)	2.38	3
10	IR36	(Reference)	2.57	1
21	IR57546-PMI-1-B-2-2		0.73	30
22	IR54977-UBN-6-1-3-3-3		1.79	10
23	IR66506-5-1-B		1.50	18
24	IR66516-24-3-B		1.01	28
25	IR66516-37-7-B		1.30	25
26	IR66879-2-2-B		1.86	7
27	IR66879-20-2-B		1.85	8
28	IR66882-4-4-B		1.90	6
29	IR66883-11-1-B		1.46	19
30	IR66469-17-5-B		1.00	29
31	IR63429-23-1-3-3		1.80	9
32	CT9897-55-2-M-3-M		2.49	2
33	IR66883-18-2-B		1.07	27
34	IR66883-18-3-B		1.34	24
35	IR66893-5-2-B		2.06	4
36	IR66879-8-1-B		1.50	16
37	IR66879-19-1-B		1.58	14
38	IR66883-44-3-B		1.18	26
39	IR66516-11-3-B		0.68	31
A1	IR20	(Probe)	1.71	12
B1	IR20	(Probe)	1.93	5
A2	NSG19	(Probe)	1.59	13
B2	NSG19	(Probe)	1.53	15
A3	Sabita	(Probe)	1.45	22
B3	Sabita	(Probe)	1.41	23
A4	KDML105	(Probe)	1.45	20
B4	KDML105	(Probe)	1.45	21
A5	Mahsuri	(Probe)	1.50	17
B5	Mahsuri	(Probe)	1.75	11
Overall mean			1.57	
SE of genotype means			0.263[a]	

[a] Based on G×E mean squares (MS)

Table 2. Test sites for 1995 G×E interaction studies in the rainfed lowland rice ecosystem.

Code	Place name	Soil type	Planting Method	Planting Date	Mean yield (t/ha)	Rank
India						
IA	Raipur-1	Inceptisol	DSR	5 July	1.75	6
IB	Raipur-2	Vertisol	DSR	13 July	2.43	1
IC	Raipur-3	Vertisol	TPR	14 August	0.35	8
Philippines						
PA	Guimba	Light soil	DSR	8 June	1.83	5
PB	Masalasa	Heavy soil	DSR	16 June	2.02	4
PC	Munoz	Very heavy soil	DSR	24 June	2.38	2
Thailand						
TA	Ubon	Light soil	DSR	24 July	2.29	3
TB	Phimai	Medium soil	DSR	25 July	0.95	7
TC	Chum Phae	Heavy soil	DSR	26 July	0.17	9
Overall mean					1.57	
SE of environment means					0.142[a]	

[a] Based on G×E MS
DSR = direct seeding; TPR = transplanting

Although there were large differences among environments, the main effect of genotypes was relatively small, accounting for only 14% of the total sum of squares (TSS) in the G×E matrix. In contrast, the G×E interaction accounted for 38% of the TSS, and was not well represented by linear regressions of genotype site means on overall site means because the sum of squares (SS) for the stability regressions only accounted for 17% of the G×E SS (Table 3). The correlations (Table 4) clearly indicate that the three Philippine sites (PA, PB and PC) and the first Indian site, Raipur-1 (IA), give similar responses which were negatively correlated with Phimai (TB). Raipur-2 (IB), Raipur-3 (IC) and the Thai site Chum Phae (TC) also show similar response patterns in mean yields.

Ordination of transformed data

The ordination of the transformed G×E matrix indicates that the first two principal component axes account for 78% of the G×E interaction sum of squares (AMMI components 1 and 2 in Table 3). The third component was considerably less influential, and the AMMI residual was of the same order of magnitude as the pooled residual from single-site analyses. This indicates that a large proportion of the G×E interaction in the data set was described by a two-component interaction principal component model (IPCA). The scores for both genotypes and environments were computed for each component (IPCA1 and IPCA2 scores). These were scaled to have variances equal to the square of the corresponding singular value of the transformed G×E matrix and plotted in the biplot of Figure 1.

In Figure 1, environment points are at the end of the spokes with the relevant codes from Table 2. Genotype points are labelled with the two-digit codes indicated in Table 1. Ovals and plot symbols indicate groupings from the cluster analysis (discussed below). Genotype points that plot close together indicate genotypes with similar patterns of interaction over the sites. It is clear that the repeated probes IR20 (A1 and B1), NSG19 (A2 and B2), Sabita (A3 and B3), KDML105 (A4 and B4) and Mahsuri (A5 and B5) have all been modelled consistently which indicates that the trials were conducted with an acceptable level of precision and the IPCA model is truly representing interaction, and not spurious effects. It is also interesting to note that breeding lines derived from the same cross are exhibiting similar interaction patterns—24, 25 and 39 from cross IR66516; 26, 27, 36 and 37 from IR66879; and 29, 33, 34 and 38 from IR66883—but that these generally diverge more than the patterns of the repeated probes, as would be expected.

The first ordination axis separated the sites in a fairly continuous manner with the three Philippine sites (PA, PB and PC) at one extreme; Raipur-1 (IA) intermediate but towards the Philippine sites; and

Table 3. Across-site analysis of variance and analysis of stability regressions and additive main effects and multiplicative interaction (AMMI) models showing degrees of freedom (DF), sum of squares (SS), percentage of total sum of squares (% TSS), mean squares (MS), F ratio statistic (F), and the probability of a larger F value by chance (FPROB).

Source	DF	SS	% TSS	MS	F	FPROB
Environments (E)	8	187.0	48	23.37	37.4	0.000 [a]
Genotypes (G)	30	54.5	14	1.82	2.9	0.000 [a]
G×E	240	150.0	38	0.62		
Source	**DF**	**SS**	**%G×E SS**	**MS**	**F**	**FPROB**
Stability regression	30	25.8	17	0.86	1.5	0.069 [b]
Regression deviations	210	124.2	83	0.59		
AMMI component 1	37	76.0	51	2.06	5.6	.000 [c]
AMMI component 2	35	40.5	27	1.16	5.8	.000 [c]
AMMI component 3	33	11.4	8	0.35	2.1	.001 [c]
AMMI residual	135	22.0	14	0.16		
Total	278	391.5				
Pooled residual	748			0.10 [d]		

[a] F-tests based on G×E MS as error estimate
[b] F-test based on regression deviations as error estimate
[c] Approximate F-tests based on pooled AMMI components of lower order + AMMI residual as error estimate
[d] Pooled effective mean square error from single-site analyses divided by three for mean basis

Table 4. Inter-site correlations for mean yields of 31 common genotypes tested at nine sites[a] in the rainfed lowland rice ecosystem (SEs on the diagonal, correlations on subdiagonal).

	IA	IB	IC	PA	PB	PC	TA	TB	TC
India									
IA	0.799								
IB	0.263	1.20							
IC	0.264	0.464**	0.571						
Philippines									
PA	0.684***	0.017	0.003	0.863					
PB	0.580***	0.248	0.323	0.800***	1.06				
PC	0.666***	0.154	0.115	0.873***	0.877***	1.15			
Thailand									
TA	0.240	0.415*	0.181	0.067	0.050	0.053	0.598		
TB	−0.388*	−0.284	−0.300	−0.522**	−0.614***	−0.609***	0.175	0.878	
TC	0.509**	0.383*	0.751***	0.308	0.555***	0.474**	0.083	−0.448*	0.268

[a] Notation for sites defined in Table 2
* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Ubon (TA), Chum Phae (TC) and Raipur-3 (IC) at the other extreme, with Phimai (TB) and Raipur-2 (IB). However, the latter two were clearly separated from the former three and from each other by the second axis. This indicates that the correlations between the Philippine sites and Raipur-1 (IA) noted earlier are due more to interaction effects than to main effects of genotypes. The different interaction effects of Raipur-2 (IB) from Raipur-3 (IC) and Chum Phae (TC) shown in Figure 1 appear to have been masked to some extent by main effects in the correlation analysis.

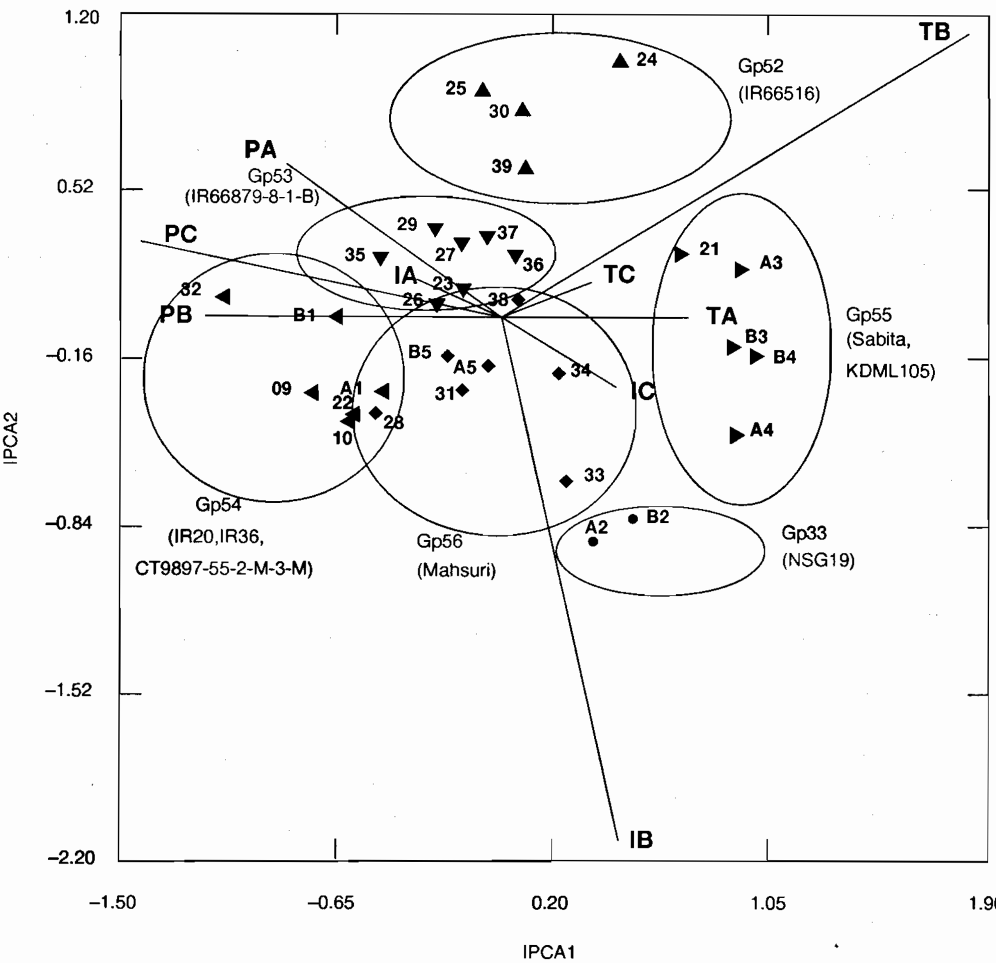

Figure 1. Biplot of interaction principal component scores for yield of 31 genotypes tested at nine rainfed lowland sites. Scores on the first axis (IPCA1) account for 51% of G×E SS, and scores of the second (IPCA2) account for 27%. Environment points are at the end of spokes. Symbols for genotype points and ovals indicate groups defined by cluster analysis of transformed genotype yields.

The interaction of any genotype with any environment is proportional to the distance from the origin to the foot of the perpendicular projection of the genotype point onto the environment spoke or onto its extension. This interaction is negative if the environment spoke must be extended back through the origin to meet the perpendicular (Kempton 1984). Line CT9897-55-2-M-3-M (32) has the highest positive interaction with the Philippine sites, followed by IR20 (A1 and B1), and the highest negative interaction with Raipur-3 (IC), Ubon (TA) and Chum Phae (TC). The converse is true of Sabita (A3 and B3) and KDML105 (A4 and B4). NSG19 (A2 and B2) had a large positive interaction at Raipur-2 (IB) and IR66514-24-3-B (24) and Sabita (A3 and B3) had large positive interactions at Phimai (TB).

As noted in the ANOVA, GxE interaction was the dominant feature of this data set, and the best adapted genotypes (those with highest predicted yield) in any region of the IPCA environment space are those furthest from the origin and closest to the region of interest. Hence CT9897-55-2-M-3-M (32) was best adapted in the Philippine sites, IR66516-24-3-B (24) and Sabita (A3 and B3) were best adapted in the top right region exemplified by Phimai (TB), KDML105 (A4 and B4) was best at Ubon (TA), Chum Phae (TC) and Raipur-3 (IC), NSG19 (A2 and B2) did well in the bottom right region, Raipur-2 (IB) and IR36 (10) was best in the centre and bottom left regions.

Cluster analysis

Cluster groupings, which summarise the patterns of G×E interaction in the transformed data matrix, are shown in the dendrograms of Figure 2 for sites and Figure 3 for genotypes. A reasonable limit on the amount of G×E SS retained between groups appeared to be 70% for this data set, and accordingly six genotype and six site groups were identified. The dendrograms indicate the levels at which the selected groups fuse if the cluster analysis is continued. This is proportional to the increase within group SS at each fusion since Ward's clustering criterion was used. The higher the fusion level the more dissimilar the groups.

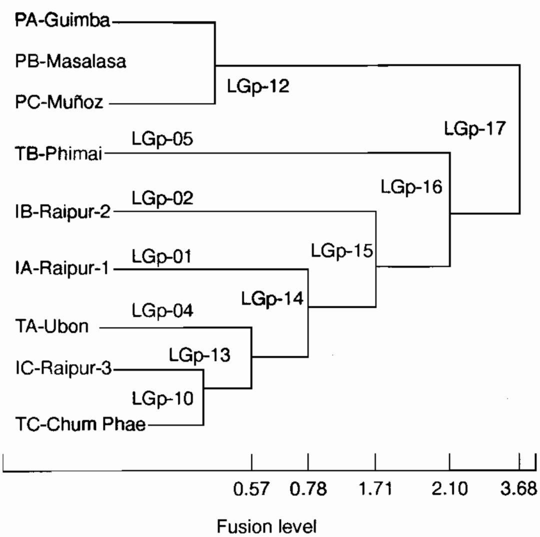

Figure 2. Environment groups at the six-group truncation level of Ward's agglomerative clustering algorithm applied to transformed yield data over 31 genotypes. The dendrogram shows fusion levels at which the groups join. (The fusion level is proportional to the increase in pooled within-group SS at each fusion.)

Among environments, Raipur-3 (IC) and Chum Phae (TC) were the first to fuse (most similar), and then the three Philippine sites (PA, PB and PC) fused, making the six groups with the remaining singletons. Ubon (TA) was the next site to fuse with group 10, (Raipur-3 and Chum Phae), followed by Raipur-1 (IA), and then Raipur-2 (IB) and Phimai (TB) at much higher fusion levels. This reflects a very similar structure to the ordination where the Philippine sites are at the extreme of the first IPCA axis and Raipur-2 (IB) and Phimai (TB) are separated from the bulk of the remaining sites by axis two.

For genotypes, the six groups presented in the dendrogram (Fig. 3) are also highlighted with special symbols and with ovals in the interaction biplot shown in Figure 1. The fusion level in Figure 3 has the same interpretation as for environments. The integrity of the grouping structure is again demonstrated by the fact that duplicate probes were never split across groups at the selected truncation level, and selections from a single cross frequently grouped together: 24, 25 and 39 from cross IR66516; 26, 27, 36 and 37 from cross IR66879; and 33, 34 and 38 from cross IR66883. The one exception was genotype 29 (IR66883-11-1-B), which was in group 53 while the other selections were in group 56. These groups were however the next to fuse after the six-group level and therefore the most similar at that level. The most distinct group of genotypes, in terms of interaction patterns, was group 55, containing Sabita (A3 and B3) and KDML105 (A4 and B4). These were joined by NSG19 (A2 and B2) to form a group different from the rest of the genotypes at the highest fusion level.

Discussion

These results indicated that, as expected, G×E interactions were large in the rainfed lowlands, being responsible for 38% of the total sum of squares. Clustering of sites and genotypes captured in excess of 75% of the G×E interaction sum of squares, suggesting a meaningful basis for the interactions, rather than simply random variation. Within groups, variation was small, and duplicate entries and lines from the same crosses grouped together. The clusters identified for genotypes and for sites may be explained by site conditions. As detailed soil analysis and weather data were not available for all sites when this report was prepared, observations of site conditions were used to consider the basis of the identified responses.

Water was generally adequate at the Philippine sites, while Ubon (TA), Chum Phae (TC) and the late-transplanted site at Raipur (IC) encountered late-season drought. The early direct-seeded location in Raipur (IA) was intermediate between these groups.

The remaining two sites encountered a severe constraint later in the season. The Phimai site (TB) was fully submerged after heading, while the onset of late-season drought was very rapid at the second Raipur site (IB). Following early direct seeding on the Vertisol at Raipur (IB), vegetative growth was excellent, but when the water was exhausted later in the season, onset of drought stress was severe.

For sites, discrimination was related to general seasonal condition (IPCA1), and the water regime later in the season (IPCA2), especially the severity of onset of too much or too little water. Groupings of genotypes could be explained by their performance in relation to these conditions. CT9897 and IR36 performed better in more favourable environments, while KDML105 and Sabita performed better in less favourable environments. NSG19 was better adapted to rapid onset of drought, and IR66516 to flooding. These responses permit some questions to be asked about such patterns of adaptation. Does IR66516 show some adaptation to flooded conditions because of an avoidance strategy through some elongation

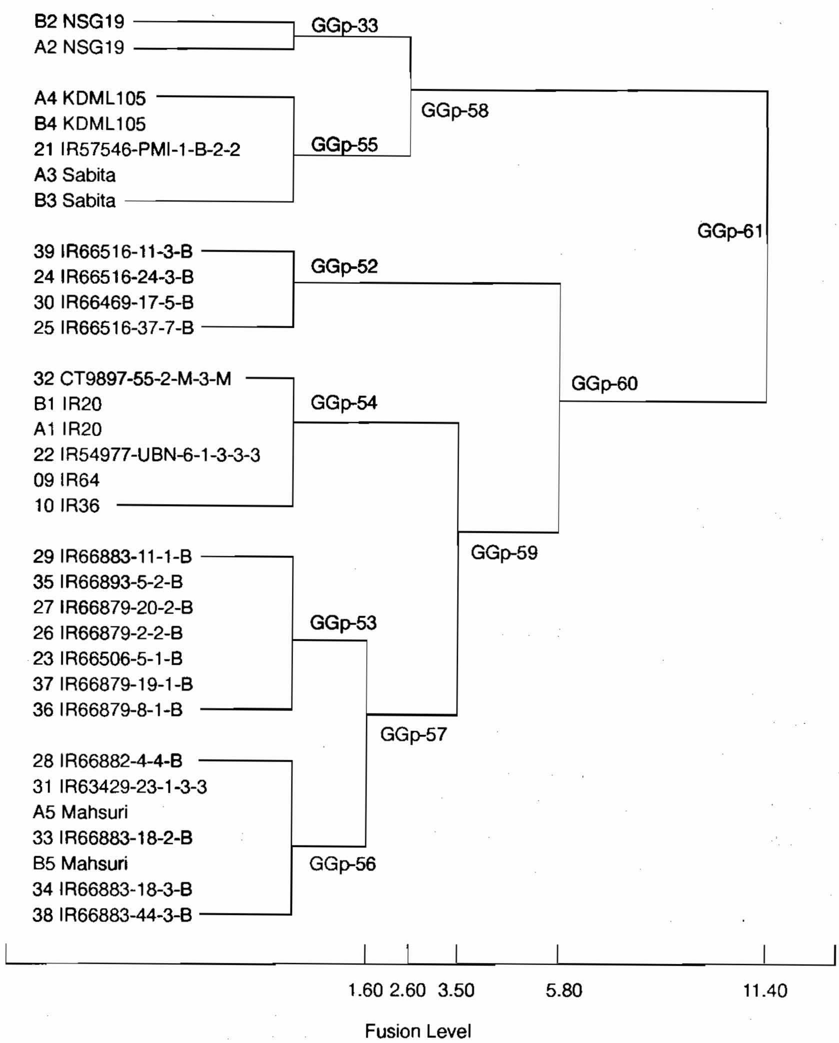

Figure 3. Genotype groups at the six-group truncation level of Ward's agglomerative clustering algorithm applied to transformed yield data over nine sites. The dendrogram shows fusion levels at which the groups join. (The fusion level is proportional to the increase in pooled within-group SS at each fusion.)

ability, or through submergence tolerance per se? Since Sabita also showed some flood adaptation but grouped separately, do these lines possess the same mechanism? Under drought, none of the breeding lines showed any advantage over KDML105 and Sabita. In particular, none grouped with NSG19 as having some adaptation to rapid onset of drought, which is quite common in the rainfed lowlands. Does this imply that progress is being made in selection for submergence tolerance, but not for drought tolerance?

For these 1995 data, there did not seem to be a strong relationship with growth duration. This may reflect the general favourability of the season prior to flowering, and the gradual transition to water deficit later in the season at most sites where drought did occur. Only Raipur-2 (IB) suffered severe drought with a rapid onset. Data from additional seasons are needed to further delineate these patterns of response. Studies in Northeastern Thailand and Lao PDR have indicated differential responses of lines were associated with differences in crop duration (Jearakongman et al. 1995; Wonprasaid et al. 1996; Satit Rajatasereekul et al., this volume; Phoumey Inthapanya et al., this volume). For comparable rainfed lowland sites at Tarlac, Rodriguez et al. (1996) considered flowering should be completed within 90 days; lines which took longer to flower performed poorly in late-season drought. A capacity to retain green leaves was also considered advantageous (Fukai and Cooper 1995; Henderson et al. 1993; Boonrat Jongdee et al., this volume). Why crop duration did not seem so important across our nine locations is not yet clear. Perhaps with such a range of seasonal durations across the nine sites, characteristics of the water regime were more important. With the addition of extra environments, or analysis for a particular region such as Northeastern Thailand or Lao PDR, clearer patterns of phenology may emerge.

Most of the interest in selection for drought resistance has focused on root traits, since these were considered important in the literature (O'Toole 1982; Fukai and Cooper 1995). Consequently, both upland and rainfed lowland programs have invested heavily in development of breeding populations and molecular markers for a number of root traits. Much effort is now being devoted to phenotyping of doubled-haploid and recombinant inbred lines (Surapong Sarkarung et al., this volume). There is some concern, however, that evidence derived from upland conditions may not directly apply in rainfed lowland conditions (Wade et al. 1997). Further, phenotyping of root traits for drought resistance in soils at Ubon may confound tolerance for drought with tolerance to low pH and other soil factors known to be influential at Ubon. There may also be questions regarding the conditions under which the drought is imposed, and its timing relative to growth stage in the field. Specifically, the questions are as follows. In order to have an effective root system in late-season drought, is it sufficient for a line to possess a capacity for deeper roots, more roots at depth and per tiller, thicker roots, and a higher root/shoot ratio? In order to express such desirable root traits, does the line need to be able to develop deeper roots in anaerobic soils earlier in the season, possess a capacity to penetrate hardpans or tolerate acid soils, have a reduced capacity for root signal production, and be able to develop new roots quickly with the onset of water stress? Is such a root system able to extract the water and take up the nutrients from deeper layers as the drought proceeds later in the season? For the latter, there is some evidence that roots in deeper layers can extract some water (B. Samson et al., unpublished data; Grienggrai Pantuwan et al., this volume). Nevertheless a clear understanding of the control of root growth and function in rainfed lowland conditions is still required.

The low random component of the G×E interaction sum of squares was probably associated with robust experimental design and care in implementation of the experiments. In 1994, standard errors for grain yield were about 0.5 t/ha for G×E interaction experiments in Raipur, Rajshahi, Ubon Ratchathani and Tarlac, where site mean yields ranged from 1.0 to 4.0 t/ha (Amarante et al. 1996). Site heterogeneity was large, and two-dimensional autocorrelation analysis was not able to define consistent trends in yield at the sites. These authors concluded that experiments needed to have sufficient border to minimise edge effects, and that robust designs such as lattice or other incomplete block designs should be employed to improve error partitioning. Care should also be taken to minimise experimental error wherever possible. Choice of replicate direction relative to slope, attention to land-leveling within each bunded area, establishing a uniform and vigorous plant stand, and eliminating confounding factors such as damage by birds and rats would all reduce error variance. Regular interpretative measurements, such as depth of ponded water in each plot, date of disappearance of ponded water, and scores for leaf rolling and leaf death, would assist interpretation of responses of individual lines at a site. Efforts should continue to be made at all sites to reduce experimental error, and to collect data which assist the meaningful interpretation of the patterns of response.

Probe lines may enhance prospects for effective selection of better adapted cultivars (Cooper and Fox 1996). Wade et al. (1996) considered alternative approaches to site characterisation, before examining the need to identify probe lines which differ in response to a target abiotic stress, without confounding by plant size or crop duration. Two cultivars were evaluated as probe lines for drought. IR72 and RC14 were considered a suitable probe pair, with the former drought susceptible and the latter drought resistant. The principles of deploying this probe set in characterised environments of a crop improvement program were discussed by Wade et al. (1996). Progress in selection for drought resistance was likely only if breeding nurseries were representative of the target population of environments, selection nurseries were adequately characterised, and probe lines that had similar plant size and crop duration but that differed in response to drought were used as a basis for comparison. As the analyses proceed, probe lines may need to be changed in the G×E interaction studies and in rainfed lowland breeding nurseries.

The site classifications showed the Philippine sites were quite different from the rest. Northeastern Thailand and Lao PDR are often considered to represent the drought-prone extreme of the rainfed lowlands. Soils are coarse in texture and low in pH, carbon exchange capacity, organic matter and fertility. Besides a low capacity to store water, the soils are highly permeable. Consequently, the soils are not able to buffer periods of inadequate rainfall, which are most common early and late in the season. As a result, yields average only 1.6 t/ha, with late-season drought a major factor. In comparison, much work has yet to be done in adequately characterising the RLRRC sites, to permit a robust comparison of conditions at the respective sites. In general terms, late-season drought is a major factor at Rajshahi (Saleh et al. 1997), Raipur and in the *walik gerami* season in Indonesia. In contrast, early-season drought may be important in the *gogorancah* season in Indonesia and the *besuani* in Raipur, and as the cropping pattern changes to direct dry seeding in Northeastern Thailand and elsewhere, early-season drought may assume greater importance (Kunnika Naklang, this volume). This may result in a requirement for greater attention to genotype adaptation to direct seeding (Mackill and Redoña, this volume; Dingkuhn et al., this volume). Soil types vary across the rainfed lowlands, often fertility is low, and hardpans may be present in some locations such as Rajshahi. Nutrient-by-water interactions may thus be important in the rainfed lowlands (Wade et al. 1995a; Prissana Hanviriyapant and Fukai, this volume). Finally, submergence is a regular feature at Faizabad and Cuttack, and may occur from time to time at other sites. Consequently, it is important for G×E interaction studies to be conducted at representative sites across the rainfed lowlands, in order to adequately sample the range of conditions which may occur. Research is proceeding to understand the basis of these G×E interaction patterns, in order to assist selection of improved cultivars of rainfed lowland rice.

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Direct Seeding for Rainfed Lowland Rice in Thailand

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Abstract

Rainfed lowland rice occupies 92% of the total rice-growing area in Northeastern Thailand, the largest rice-growing region in Thailand. In recent years, the traditional transplanting method of growing rice has been increasingly replaced by direct seeding, particularly dry-seed broadcasting. In 1992 this new method accounted for 25% of the rice-growing area in the Northeastern Region.

The change is associated with the increased cost of rice growing, particularly increased labour costs (broadcasting requires only a fraction of the labour required for transplanting). Direct seeding also avoids the risk of transplanting failure due to a lack of standing water at the appropriate time of transplanting.

Components of the new technology described here include land preparation, time and rate of seeding, weed management, rate and timing of fertiliser application, insect and pest management, and rice stubble and residue management. With the use of appropriate crop management, direct seeding can increase grain yield and reduce the cost and risk associated with transplanting in rainfed lowland areas.

THAILAND is divided geographically into four main regions — Northern, Northeastern, Central Plain and Southern (see map on page x). The total area planted with rice is 9 million ha (Table 1).

Northern Thailand, with about 21% of the total rice area, contributes about 25% of the total rice production. Northeastern Thailand has 56% of the total area, and 47% of total production. In Central Plain, the rice-planting area and rice production are 18% and 23% of the total, respectively, while in Southern Thailand, the corresponding percentages are only 5% and 5%.

About 92% of the total rice-planting area in Northeastern Thailand is in rainfed conditions, compared with 70% in the Northern Region, 27% in the Central Plain and 69% in the Southern Region. The average grain yield of rainfed lowland rice in the northeast in the 1992–93 crop season was 1.66 t/ha, compared with 2.22 t/ha for irrigated lowland rice. Among the four regions, the rice yield in the northeast is the lowest. It is badly affected by very poor soil conditions and unreliable rainfall.

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Methods of Growing Rice in Thailand

Transplanting and *direct seeding* are two methods of growing rice. For transplanting, seedlings are first grown in a seedbed for a month while the main fields are being ploughed along the bunds surrounding each paddy. When each field has been prepared, the seedlings are pulled from the seedbed and then transplanted in the field by hand.

In direct seeding, seeds are sown directly in an upland field or lowland paddy. In upland fields, seeds are sown only by dibbling on dryland preparation. In the case of lowland paddies, there are several ways of direct seeding, such as dry-seed broadcasting, germinated-seed broadcasting and dry-seed dibbling methods. These are described below.

Dry-seed broadcasting method

As soon as the rainfall has moistened the soil enough to make ploughing possible, the land is ploughed (late April, May or early June). In the heavy clay soils of the Central Plain, the seed is broadcast within a few days of ploughing, before the next shower. Much of the seed falls into cracks between, around or under the overhang of large clods. When the next shower comes, the heavy clay clods slake down, so that the clod fragments cover most of the seed. In irrigated areas, the field will be irrigated after seeding to promote germination.

In light-textured soil, such as loamy sand, sandy loam and sandy clay loam, in the lowland rice areas of Northeastern Thailand, the method of land preparation differs between farmers. Many farmers plough the field only once, but some plough twice before broadcasting the seed. The second ploughing is done just before broadcasting the seed and then the field is harrowed so that the loosened soil covers the seeds to retain moisture and protect them from birds.

Germinated-rice broadcasting method *(Na Wan Nam Tom)*

In areas where irrigation or water control is possible or the fields have some standing water, the farmers can also direct-seed onto soil with wetland preparation. Germinated rice seeds (soaked 24 hours and incubated 24 hours) are broadcast onto the well-puddled soil. The field is thoroughly prepared and if it has been flooded the soil particles are allowed to settle down, and the field is drained before seeding. This growing method is called *Na Wan Nam Tom.*

Dibbling and drilling method

Rice can also be direct-seeded by dibbling and drilling. The dibbling method is usually practiced for upland rice. The drilling method is to drill seeds by hand into furrows, then cover the furrows.

Importance of dry-seeded rice in Northeastern Thailand

Table 2 shows the total planted area and percentage of different growing methods in the four regions of Thailand from 1989 to 1992. In 1992 transplanting was used for about 74% of the total planted area of Northeastern Thailand and broadcasting for 25%. The area of rice grown by dry-seed broadcasting rapidly increased from 1989 to 1992, and it will cover an even larger area in the future. *Na Wan Nam Tom* and the dibbling method were used for only 0.3% and 0.7% of the total rice-planted area, respectively.

Reasons for Changing from Transplanting to Broadcasting Method

To save time and labour cost

Nowadays, farmers cannot afford to make a heavy investment, even in labour for transplanting. Generally, transplanting one hectare (at 20 × 20 cm spacing) takes 25–30 person-days but the same area can be broadcast by one person within a day. Farmer families not only produce food for the country but also produce the labourers for many factories and service sectors in the towns. Farmers usually cannot earn a living from just their farm products but need sufficient cash income from outside the farm to support their families. Consequently, they prefer the easier work of broadcasting, which takes less time and uses less labour. After broadcasting, they can go to town to work and come back again during harvesting.

To avoid drought during the transplanting period

Farmers wait for heavy rains to puddle the land before they transplant seedlings, no matter how long rains are delayed. If the heavy rains do not come, the land remains fallow. It is estimated that 30–40% of the total area under rainfed lowland rice in Northeastern Thailand either is not planted at all or is planted but results in the crop failing completely after transplanting. To avoid the problem of transplanting in dry soils,

Table 1. Rice area planted under rainfed and irrigated conditions, and rice production in different regions of Thailand in 1992.

Region	Planted area (million ha)						Rice production	
	Rainfed		Irrigated		Total			
	Area	%	Area	%	Area	%	tonnes (million)	%
Thailand (whole)	6.79	75	2.21	25	9.01	100	17.30	100
Northeastern	4.66	92	0.41	8	5.07	56	8.03	47
Northern	1.39	70	0.51	30	1.90	21	4.38	25
Central Plain	0.42	27	1.15	73	1.57	18	4.01	23
Southern	0.32	69	0.14	31	0.46	5	0.89	5

Source: OAE (1994)

the farmers may change to the dry-seed broadcasting method at the beginning of the rainy season or during the dry period. If the crop fails because of adverse conditions, reseeding is easier and less costly than retransplanting, and thus, overall, the broadcasting method is less risky than the transplanting method.

Yield of Direct-Seeded Compared with Transplanted Rice

The yield of rainfed lowland rice is low in Northeastern Thailand (Table 2). In the 1992–93 crop year, the average yield was 1.37 t/ha and 1.8 t/ha for dry-seeded and transplanted rice, respectively (OAE 1994). Grain yield of dry-seeded rice varied from less than 1.0 t/ha to above 3.0 t/ha depending on the rain (or drought), soil and cultural practices.

In an experiment conducted on loamy sand soil in Roi-Et, Khao Dawk Mali 105 (KDML105) was tested with two planting methods and three rates of fertiliser. In 1995, the response of broadcast rice to the rate of fertiliser was less than for transplanted rice, resulting in a significantly lower mean yield for broadcast rice than for transplanted rice (Table 3).

Another experiment was conducted at Khon Kaen Rice Experiment Station and Ubon Rice Research Centre to compare different cultural practices (Table 4, Khonthasuvon et al. 1994). At Khon Kaen, the grain yield from transplanted rice plots was lower with chemical fertiliser than with incorporation of *Sesbania rostrata* or mungbean, which were grown in the plots before transplanting. The highest yield was obtained when rice and mungbean seeds were broadcast together on the same day and rice straws were used to mulch the plots. At Ubon, on the other hand, this treatment gave the same grain yield as did transplanted rice with chemical fertiliser or *Sesbania* incorporation. Similar results to those at Khon Kaen were found at Surin Rice Experiment Station in 1995. The grain yield of KDML105 obtained from the broadcast rice with rice straw mulching was higher than that from transplanted rice with chemical fertiliser or with incorporation of *Sesbania* into the soil (Table 5).

Table 2. Total rice planted area, percentage of different growing methods and average grain yields in four regions of Thailand, 1989–92.

Region	Growing methods	1989	1990	1991	1992	Average grain yield t/ha
Northeastern	Transplanting	94.8%	92.6%	87.6%	73.6%	1.80
	Dry seed, broadcast	4.4%	6.4%	11.3%	25.5%	1.37
	Germinated seed, broadcast	0.4%	0.5%	0.7%	0.3%	1.81
	Dibbling	0.4%	0.5%	0.4%	0.7%	1.36
	Total area (million ha)	**4.94**	**5.06**	**4.76**	**5.07**	**1.69**
Northern	Transplanting	64.7%	60.2%	51.9%	41.6%	2.44
	Dry seed, broadcast	24.0%	26.0%	33.4%	39.2%	1.91
	Germinated seed, broadcast	10.1%	12.7%	13.9%	17.8%	3.30
	Dibbling	1.3%	1.2%	0.7%	1.5%	1.29
	Total area (million ha)	**2.09**	**2.09**	**1.95**	**1.90**	**2.37**
Central Plain	Transplanting	31.4%	23.3%	17.2%	17.1%	2.12
	Dry seed, broadcast	29.2%	33.9%	39.2%	41.8%	2.02
	Germinated seed, broadcast	39.1%	42.4%	43.3%	40.9%	3.57
	Dibbling	0.4%	0.4%	0.3%	0.2%	1.34
	Total area (million ha)	**1.92**	**1.69**	**1.64**	**1.57**	**2.70**
Southern	Transplanting	62.7%	50.7%	56.8%	54.1%	1.94
	Dry seed, broadcast	27.4%	35.3%	33.5%	31.5%	2.00
	Germinated seed, broadcast	6.2%	8.8%	5.2%	9.7%	2.42
	Dibbling	3.6%	5.2%	4.6%	4.7%	1.44
	Total area (million ha)	**0.52**	**0.48**	**0.48**	**0.46**	**1.98**

Source: OAE (1994)

Table 3. Grain yield of broadcast and transplanted KDML105 rice as affected by rate of fertiliser, Roi-Et, Northeastern Thailand.

Fertiliser rate $N–P_2O_5–K_2O$ (kg/ha)	Grain yield (t/ha)		
	Broadcast rice	Transplanted rice	Difference
1994			
0–0–0	1.24b	1.80ab	
75–37.5–37.5	1.90ab	2.06a	
112.5–37.5–37.5	2.08a	2.26a	
Mean	1.74	2.09	ns
1995			
0–0–0	1.77d	2.04cd	
75–37.5–37.5	2.30c	2.86b	
112.5–37.5–37.5	2.33c	3.30a	
Mean	2.21	2.87	**

ns = not significant; ** = significant ($P < 0.01$)

Note: In each year yields followed by a common letter are not significantly different ($P < 0.05$ by DMRT).

Table 4. Effect of cultural practices on grain yield of KDML105 rice grown at Khon Kaen and Ubon, Northeastern Thailand (yield averaged from three years).

Treatment	Grain yield (t/ha)	
	Khon Kaen	Ubon
Transplant + chemical fertiliser	2.09	1.30
Sesbania before transplant	2.23	1.23
Mungbean before transplant	2.26	1.06
Mungbean + rice broadcast	2.41	0.87
Mungbean + rice broadcast + rice straw mulching	2.69	1.25

Notes:
1. Transplant spacing = 20 × 20 cm; rice seed rate in broadcasting = 62.5 kg/ha; seed rate of mungbean = 30 kg/ha
2. Ubon soil pH = 3.95, OM = 0.2%, available P = 14 ppm; Khon Kaen soil pH = 4.28, OM = 0.55%, available P = 34 ppm

Source: Khonthasuvon et al. (1994)

Table 5. Effect of cultural practices on grain yield of KDML105 rice, Surin, Northeastern Thailand, 1995.

Cultural practice	Grain yield (t/ha)
Dry-seed broadcast rice + straw mulching	3.96
Transplanted rice (at 20 × 20 cm spacing) + chemical fertiliser	3.31
50-day-old *Sesbania* incorporated into the soil before transplanting	3.48

Direct-Seeded Rice Production Technology

Land preparation and seed rate

Land preparation is the first step of direct-seeded rice production technology. It not only minimises the weed problem but also promotes establishment and growth of rice seedlings. The first ploughing should be done after heavy rain when weed seedlings have emerged. The second ploughing should be followed by the broadcasting of rice seeds and then harrowing. The second plough will uproot the weed seedlings to the soil surface, where they will dry out. If labour is available, a third plough is recommended to reduce the weed population.

In general, there are no clear-cut recommendations on the number of ploughing, harrowing and rotavating operations that are required for proper land preparation. The kinds of tillage operations selected and the number of operations depend upon soil type and condition, and the presence of stubble, trash or weeds.

Land should be ploughed at least 15 days before direct seeding to save the seedlings being exposed to the effects of a high concentration of harmful substances generated by decomposing organic matter ploughed into flooded soils, and to allow the plants to utilise the nutrients released during the decomposition of organic matter.

Romyen et al. (1996) reported that a higher yield of dry-seeded rice, in the clayey loam soil of Phimai Rice Experiment Station, was achieved when the first plough was done 15 days before seeding rather than at the time of seeding. If there was a second plough, and if dry seeds of KDML105 at the rate of 75 or 100 kg/ha were broadcast and then harrowed, grain yield was the highest, at 2.81–2.92 t/ha (Table 6).

Straw mulching and seed rate

A major problem for rice production in Northeastern Thailand, in addition to drought, is the nature of the sandy soils. The soil is infertile and water-holding capacity is very low. Straw mulching over the field of dry-seed broadcast rice may be introduced to improve soil fertility and also soil moisture retention.

Two experiments were conducted in 1992–94 at Surin and Roi-Et (Naklang et al. 1996b). Three rates of rice seeds and mulching straw were used. Surin soil is sandy loam, pH = 4.3, organic matter (OM) = 0.71%, available phosphorus (P) = 23 ppm and exchangeable potassium (K) = 40 ppm; Roi-Et soil is loamy sand, pH = 5.2, OM = 0.58%, available P = 5 ppm and exchangeable K = 18 ppm. Average grain yields of rice during the three years are shown in Table 7.

Table 6. Effect of land preparation and seed rate on grain yield (t/ha) of KDML105 rice, Phimai, Northeastern Thailand, 1995.

Land preparation	Seed rate (kg/ha)					Mean
	50	75	100	125	150	
First plough + broadcast + harrow	1.79b	2.46ab	2.35ab	2.59ab	2.76a	2.39
First plough 15 days before broadcast + harrow	2.78a	2.58a	2.56a	2.52a	2.75a	2.64
First plough + second plough 15 days after the first plough + broadcast + harrow	2.29a	2.81a	2.92a	2.67a	2.72a	2.68
Mean	2.29	2.61	2.61	2.60	2.74	

Note: Yields followed by a common letter within a row are not significantly different ($P < 0.05$).
Source: Romyen et al. (1996)

Table 7. Effect of rates of rice seed and rice straw mulching on grain yield (t/ha) of KDML105; average of three years, 1992–94, Surin and Roi-Et, Northeastern Thailand.

Seed rate (kg/ha)	Straw rate (t/ha)			Mean grain yield (t/ha)
	6.25	9.375	12.5	
Surin Rice Experiment Station				
50	1.94	2.00	2.62	2.29a
75	2.00	2.57	2.67	2.41a
100	2.19	2.35	2.74	2.42a
Mean grain yield (t/ha)	2.04C	2.41B	2.68A	2.37
Roi-Et Land Development Station				
50	1.41a	1.56ab	1.56a	1.52
75	1.53a	1.44b	1.75a	1.57
100	1.96a	1.71a	1.60a	1.55
Mean grain yield (t/ha)	1.42	1.57	1.64	1.54

Note: Yields followed by a common letter are not significantly different ($P < 0.05$); for Roi-Et experiment, comparison is for different seed rates.
Source: Naklang et al. (1996b)

Broadcasting the seeds at the rates of 50 to 100 kg/ha produced no significant difference in grain yield of KDML105. Using a larger amount of mulching straw tended to increase rice yield.

Sowing time

Farmers who wish to save on the cost of inputs such as labour and implements for transplanting will broadcast seeds earlier than for transplanting, in May–June. Some farmers broadcast during the drought period, around late July to mid-August, when they cannot transplant seedlings because the soil is too hard to transplant by hand or because seedlings are not available or are too old.

The results from an experiment at Surin Rice Experiment Station (Table 8) indicated that in some years dry seeds could not be sown in mid-June or at the end of July–August, because of heavy rain with subsequent flooding of the field. However, in some years we broadcast in June and obtained a grain yield of about 1.80–2.36 t/ha. During the three years at Surin, broadcast rice grain yield varied from 1.43 t/ha to 2.69 t/ha; higher yields were obtained when rice was sown between June 30 and August 15.

At Chum Phae Rice Experiment Station, seeding in June gave a higher yield than did seeding in July–August. In 1995 at Chum Phae, the seeds broadcast at 30 July and 15 August rotted due to heavy rain that flooded the plots after the seeds were broadcast.

Table 8. Effect of sowing date on grain yield of rice (t/ha), average of three cultivars (KDML105, RD15 and RD6), Surin and Chum Phae, Northeastern Thailand.

Location	Year	Date of sowing							
		June			July			August	
		15	24	30	5	15	30	15	30
Surin	1993	a	–	a	2.69	1.97	2.04	1.44	1.51
	1994	a	1.81	a	1.43	1.83	2.18	2.49	–
	1995	1.80	–	2.36	–	2.11	a	a	–
Chum Phae	1993	2.39	–	2.09	–	1.59	1.16	0.89	–
	1994	1.34	–	1.29	–	0.87	0.89	0.52	–
	1995	2.41	–	2.39	–	2.41	b	b	–

a = cases in which the land was flooded on the due date for broadcasting (15, 30 June; 15, 30 July; and 15 August) and then drained, thus delaying the sowing date

b = seeds were rotten due to heavy rain and flooded water after broadcasting

Rice cultivar

Farmers in the northeast prefer to dry-seed broadcast cultivars that they wish to sell but not use for their own consumption. The cultivars that are commonly dry-seed broadcasted include KDML105, RD15, RD6 and some local cultivars. Grain yield of RD6 (glutinous rice) was slightly higher than KDML105 and RD15 (both non-glutinous) in Surin and Chum Phae (Table 9).

Fertiliser application

For broadcast rice, the recommended basal application of fertiliser is compound grade 16–16–8 (N-P_2O_5-K_2O) for sandy soil and 16–20–0 for clayey soil, at the rate of 156 kg/ha at 30 days after emergence. Common top-dressing fertiliser is ammonium sulfate at the rate of 94 kg/ha or urea at the rate of 44 kg/ha, and this would be applied around the time of panicle initiation. If the field has some standing water at the time for fertiliser application, the farmer will apply fertiliser without hesitation. If the field is dry, however, the application of fertiliser is not good practice.

In an experiment at Roi-Et, seeds were broadcast on infertile, loamy sand soil under rainfed condition, and compound fertiliser (16-16-8) at the rate of 0, 187.5, 250 and 312.5 kg/ha was applied 32 days after emergence. Ammonium sulfate at the rate of 62.5 kg/ha was applied at panicle initiation stage. The grain yield increased with the rate of compound fertiliser up to 250 kg/ha, then decreased at the highest rate (Table 10). Rice plants receiving a high rate of fertiliser showed physiology disorder symptoms. The older leaves were dark green and droopy; leaves turned to yellow, then brown, from the tip of the leaf. The rice plants were short but tillering was normal. Visual observation could not be used to identify whether the symptoms were due to imbalance, deficiency or toxicity of the nutrients.

Table 9. Grain yield of three rice cultivars averaged from three to five broadcasting dates during June to August.

Location	Year	Grain yield (t/ha)			Mean
		KDML105	RD15	RD6	
Surin	1993	1.86	1.92	2.01	1.93
	1994	1.91	1.82	2.12	1.95
	1995	2.02	1.86	2.39	2.09
	Mean	**1.93**	**1.87**	**2.13**	**1.99**
Chum Phae	1993	1.73	1.53	1.62	1.63
	1994	0.99	0.88	1.07	0.98
	1995	2.28	2.17	2.78	2.41
	Mean	**1.67**	**1.53**	**1.82**	**1.67**

Table 10. Effect of rate of fertiliser on grain yield of dry-seed broadcast rice, Roi-Et, Northeastern Thailand, 1994.

Treatment	Grain yield t/ha
No fertiliser	1.20c
187.5 kg/ha of compound fertiliser grade 16–16–8 + 62.5 kg/ha of AS	1.54b
250 kg/ha of compound fertiliser grade 16–16–8 + 62.5 kg/ha of AS	1.86a
312.5 kg/ha of compound fertiliser grade 16–16–8 + 62.5 kg/ha of AS	1.24c

Note: Compound fertiliser was used as basal fertiliser and ammonium sulfate (AS) was used as a top-dressing. Yields followed by a common letter are not significantly different ($P < 0.05$).

Weed Control Technology

The weed problem is the bottleneck of direct-seeded rice technology in the northeast. Weeds compete with rice for nutrients, light, water and space, and also act as a host of other pests. Weeds cause yield losses of about 30% in broadcast rice at Surin (Vongsaroj et al. 1993). Weed control can be integrated with all stages of the direct-seeded rice-growing process from sowing to harvesting. Knowledge of the weeds involved and of direct-seeded rice production technology is an advantage in weed control. The methods used should be safe for both the environment and users.

Vongsaroj et al. (1993) reported results from an experiment conducted at Surin Rice Experiment Station during 1990–1992. Weed control by hand-weeding and use of post-emergence herbicides (2,4-D or propanil) reduced the dry weight of weeds and the grain yield of rice was increased (Table 11).

Table 11. Effect of weed control on grain yield of dry-seed broadcast rice, Surin, Northeastern Thailand, 1990–92.

Treatment	Grain yield (t/ha)		
	1990	1991	1992
No weeding	2.05	2.63	2.25
Hand-weeding 45 days after emergence of rice	2.60	3.66	3.18
2,4-D	2.86	3.84	3.30
Propanil	3.10	3.78	3.52

Source: Adapted from Vongsaroj et al. (1993)

There are many weed species in dry-seeded rice, which can be classified into five groups:

- grasses— *Echinochloa colona* (L) Link, *Paspalum scorbiculatum* L., *Eschaemum rugosum* Salisb., *Leptochloa chinensis* (L) Nees
- broadleaves — *Jussiaea linifolia* (L) Vahl, *Melochia carchorijolia* L., *Lindernia* spp., *Xyris indica* L., and *Richaria brazilensis*
- sedges — *Fimbristylis miliacea* (L) Vahl., *Cyperus difformis* Linn., *Cyperus iria* L., and *Cyperus rotundus* L.
- fern — *Marsilea crenata* Presl.
- algae — *Chara zeylanica* Kl. ex Wild.

Dry-seed broadcasting is possible only if good weed management is practiced, involving:

- prevention — rice seed should be clean and free from weed seeds and other propagules of weeds (this can be done either manually or by machine winnowing);
- land preparation — a system of year-round tillage should be developed with the objective of preparing a weed-free seedbed to facilitate early sowing for establishment of good rice stands;
- seed rate — high population density of rice plants will cover most of the space and will reduce weed growth (it is recommended that 100–125 kg/ha of seed be used to minimise the weed problem);
- time of seeding — direct dry-seeded rice is normally seeded in the first shower of rain, but weeds will emerge from the soil for a long time; seeding of rice late in July or early in August results in fewer weeds than earlier seeding;
- chemical weed control — chemical weed control will be achieved with good land preparation; herbicides can be applied at pre-emergence or post-emergence.

Use of herbicides

Pre-emergence herbicide is applied after seeding, with harrowing. The herbicide will cover the soil surface as a layer or diffuse to a certain level of soil. When weed seedlings emerge, either the shoot or root of weed seedlings will take up the herbicide and the weed will be killed. Weeds that sprout from the vegetative part, such as *P. scorbiculatum*, cannot be controlled. Pre-emergence herbicides are: oxadiazon, bifenox and pedimethalin at the rate of 0.75, 2.0 and 2.0 kg active ingredient (a.i.)/ha, respectively. Each herbicide controls grasses, broadleaves and sedges effectively.

Post-emergence herbicides are sprayed after the establishment of rice seedling and when the weed is at the 3–4 leaf stage or 15–20 days after the emergence of rice seedling. The advantage of the post-emergence herbicides is that spot spraying can be used only in the places where there is weed infestation.

Many herbicides that can be used for direct-seeded rice are shown in Table 12 (P. Vongsaroj, Botany and Weed Division, Department of Agriculture, Bangkok, personal communication).

Root and Shoot Development under Different Planting Methods

Roots are believed to play a critical role when there are environmental stresses, since many of the stresses occur in the soil. A greater understanding of root development is now needed to support efforts to increase rice yield. It is common for soil moisture conditions to fluctuate between deficit and excess during a life cycle of rice crops in rainfed lowland. Root systems differ greatly among cultivars, soil conditions and hydraulic regimes (Sharma et al. 1994; Samson et al. 1995).

Lilley and Fukai (1994) found consistent cultivar differences in root growth in different water-availability conditions; cultivars differed in their inherent rooting pattern, with total root length ranging from 1-3 to 33.7 km/m^2. These inherent differences in rooting pattern are of vital importance to the cultivar's ability to extract water during water deficit. Extractable soil water and water extraction rate were related to root-length density. Cultivars with deeper root systems would be able to extract more soil water from the deeper layer of the soil profile and therefore are more drought resistant (Lilley and Fukai 1994; Fukai and Cooper 1995; Wade et al. 1996).

In one experiment the length and weight of roots were higher in dibbled and drilled rice than in transplanted rice (Katare and Upadhyay 1981). The ratios of root to shoot (R/S) of dibbled, drilled and transplanted rice were 0.23, 0.24 and 0.28, respectively. Root volume and root dry weight were higher under continuous submergence or soil saturation than under drier upland moisture regimes (Yellamanda Reddy and Kuladaivelu 1992).

Direct-seeded rice had more total root length than transplanted rice (Ingram et al. 1994). The same results were found in our nine experiments at Surin from 1992 to 1994 (Naklang et al. 1996a). Dry-seeded rice (broadcasting and dibbling methods) had higher root dry matter than transplanted rice except in 1992, when lower root dry weight was seen in upland direct-seeded rice due to drought and rice plants dying around the panicle initiation to flowering stage (Table 13). The highest shoot dry weight was obtained from direct-seeded rice in the lowland. R/S ratios of direct-seeded rice were also higher than those of transplanted rice. Grain yield of the direct-seeded crop in lowland conditions was similar to, or even higher than, that in the transplanted crop. Under upland conditions, severe drought caused no yield in 1992 and 1993, and produced a very low yield in 1994.

Table 12. Herbicides used for control of weeds in direct-seeded rice.

Herbicides	Rate (kg a.i./ha)	Target weeds	Remarks
2, 4-D	0.75–1	Broadleaves and sedges	–
Propanil	2–3	Grasses and sedges	Carbamate insecticide should not be sprayed 7 days before or after Propanil application
2, 4-D/Propanil	2	Grasses, broadleaves and sedges	as above
Thiobencarb/propanil	2	Grasses, broadleaves and sedges	as above
Butachlor/propanil	2	Grasses, broadleaves and sedges	as above
Molinate/propanil	2	Grasses, broadleaves and sedges	as above
Bensulfuran-methyl	0.05	Broadleaves, sedges	–
Metsulfuran-methyl	0.05–0.08	Broadleaves, sedges and ferns	–

a.i. = active ingredient

Table 13. Root and shoot dry weight (g/m^2) and root/shoot (R/S) ratio at maturity and grain yield (g/m^2) in different conditions.

Year	Upland (U)			Lowland (L)						Grain yield (g/m^2)		
	Direct- seeded (D)			Direct- seeded (D)			Transplanted (T)					
	Root	Shoot	R/S	Root	Shoot	R/S	Root	Shoot	R/S	U–D	L–D	L–T
1992	92	642	0.14	304	1791	0.17	163	1370	0.12	–	540	289
1993	205	507	0.40	237	968	0.24	150	800	0.19	–	345	358
1994	172	745	0.23	320	1268	0.25	161	700	0.23	145	357	414

Note: In 1992, U-D samples were done at around flowering stage. Grain yield of upland direct-seeded rice was not obtained due to drought stress during grain filling.
Source: Naklang et al. (1996a)

Table 14. Different rice-growing technologies for rainfed lowland areas of Northeastern Thailand.

Components		Transplanting	Broadcasting		
			Dry-seed dry soil	Dry-seed moist soil	Germinated-seed (24 h soaking + 24 h incubation)
Cultivar		RD6, KDML105, RD15	Same	Same	Same
Land preparation		2 ploughings + 1 harrowing	2 ploughings + 1 harrowing	2 ploughings + 1 harrowing	2 ploughings +1 harrowing + smoothed surface
Time of seeding		June–August	May–mid-August	May–mid-August	May–mid-August
Soil surface at seeding or transplanting time		Standing water preferred	Dry	Moist	Saturated
Seeding rate		25–30 kg/ha	50–100 kg/ha	50–100 kg/ha	50–100 kg/ha
Spacing		20 × 20 cm (3 seedlings/hill)	Scattered	Scattered	Scattered
Labour		25–30 man-day/ha	1 man-day/ha	1 man-day/ha	1 man-day/ha
Weed management		Hand-weeding or post-emergence herbicide	Pre- or post-emergence herbicide	Same as dry soil	Same as dry soil
Fertiliser	Basal rate:	150–185 kg/ha of fertiliser grade 16–16–8 for sandy soil or grade 16–20–0 for clayey soil	Same	Same	Same
	Time:	Transplanting	30 DAE	30 DAE	30 DAE
Top-dressing at panicle initiation stage		45 kg/ha of urea or 100 kg/ha of ammonium sulfate	Same	Same	Same
Insect pest management		Apply insecticide if necessary	Same	Same	Same
Time of harvest		Nov–Dec	Same	Same	Same
Rice stubble and crop residue management		Plough under after harvesting or at the first ploughing	Same	Same	Same
Rice straw management		Feed cattle, mulching field crops or incorporate into soil after harvesting	Scatter over the area after dry rice seed is broadcast	Same as dry soil	Same as transplanting

DAE = Days after emergence

Conclusion

In Thailand, the largest area of rainfed rice is in the northeast. In recent times, the traditional transplanting method has been increasingly replaced by dry-seed broadcasting onto dry or moist soil. Farmers spend less time and labour by broadcasting and they can broadcast any time from May until August, thus avoiding the risk of lack of seedlings for transplanting and the difficulty of transplanting old seedlings into dry and hard land resulting from drought.

Farmers can increase grain yield from broadcasting by using appropriate cultural practices as shown in Table 14. They must start with good land preparation and then broadcast a suitable cultivar, at the appropriate seeding rate to obtain the best plant density. Weed, insect pest and disease control have to be undertaken if necessary. Mulching straws over the broadcast dry seed, and the appropriate rate and time of chemical fertiliser application, are necessary to promote rice growth.

The development of dry-seed broadcasting technology is still at an early stage, and although the method of sowing has been changed from transplanting to broadcasting in many areas, the rice cultivar and some technologies, such as fertiliser management, have not been changed to accommodate the new seeding method (Table 14). Breeders' efforts have been directed to developing a new rice type for direct seeding in the rainfed lowlands which:

- has a good root system;
- is resistant to drought, blast and nematodes ;
- has low tillering but a high proportion of bearing tillers;
- shows good weed competition; and
- performs well in soil with low fertility.

More studies of land preparation and weed, fertiliser and crop residue management are needed for dry-seeded rice grown under rainfed conditions. To improve fertiliser efficiency, soil properties and grain yield, introduction of legumes, which can be grown before or after rice, and/or leaf litter addition, are necessary to sustain crop production in this area. As labour shortages and the cost of labour increase, technologies that promote early rice seedling growth, and reduce or eliminate weed competition after sowing, will become increasingly necessary. Such technologies might include coating of rice seeds with small quantities of fertiliser and selective herbicide. This could potentially reduce inputs to ecologically and economically sustainable levels.

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Genotype Requirements for Direct-Seeded Rice

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Abstract

Cultivars developed for transplanted systems may perform well under direct seeding, but specific traits, such as seedling vigour, submergence tolerance, and drought resistance, are highly desirable for direct-seeded systems. Seedling vigour is essential for good stand establishment and competitive ability against weeds. Tolerance to submergence and drought, on the other hand, are important in rainfed areas that are often subjected to flash flooding or long spells of dry weather. Quantitative trait loci for all these traits have been identified via linkage to molecular markers. Seedling vigour and drought resistance are complicated traits that involve many loci and genotype-by-environment interactions. Submergence tolerance is simply inherited and has been transferred from traditional cultivars into high-yielding breeding lines. Changes in plant type have been advocated, but the effects of these changes on performance are still tentative. Breeding nurseries should grow plants under direct-seeded conditions to intensify selection for adaptation to this system.

TRADITIONAL Asian rice culture involves both transplanting and direct seeding, but tropical lowland cultivars tend to be associated with the transplanting system. Due to increased labour costs, the transition to direct seeding is being pursued urgently in many countries. In the Philippines, for example, key rice production areas have totally shifted to direct-seeded culture. Direct seeding has long been the norm in the Americas, Europe and Australia, where labour costs have been high over the last century. Cultivars and management practices have, therefore, been oriented toward this method of crop establishment (Hill et al. 1991). In California, the rice breeding program at Biggs has developed cultivars that are highly adapted to an aerial seeding (or 'water seeding') system, which provides superior weed control (McKenzie et al. 1994). Genetics research has focused on traits relevant to this system (Mackill 1995).

The relation between genotypic performance under direct seeding and transplanting is not well understood. Cultivars developed for transplanting often perform well when grown under direct seeding, but it has been recognised that certain traits are specifically advantageous for direct seeding. These include seedling vigour (for improved stand establishment and competitive ability against weeds), submergence tolerance, and drought resistance. A new, low-tillering plant type has also been advocated for direct seeding (Dingkuhn et al. 1991). The present paper will discuss the genetics of these traits and the implications for breeding strategies in direct-seeded rice.

Stand Establishment and Weed Competition

Intense weed competition is an overriding feature of all direct-seeded environments. In the absence of herbicides, a minimum plant height is essential to ensure suppression of weed competition (Garrity et al. 1992). In traditional Asian direct-seeded systems, farmers grow tall, highly vigorous cultivars. These cultivars compete well with weeds, but their productivity is generally low. Even when herbicides are used, competitive ability with weeds is a desirable attribute (Hill et al. 1991). Competitive ability involves seedling vigour traits such as rapid emergence and shoot growth, and rapid canopy development (Hill et al. 1991).

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In the water-seeding system practiced in California, weed competition is reduced by sowing pregerminated seed into standing water (10 cm). In this system, seedling vigour is not only directly related to weed competition, but essential to ensure emergence of a sufficient number of plants to establish an optimum stand. The seedling vigour characteristics must be manifested under stresses such as submergence and low water temperature. Both shoot and root elongation are important in a water-seeded system, while mesocotyl elongation is desirable for drill seeding (Dilday et al. 1990). A slantboard test performed under aerobic conditions has been used to measure these seedling vigour traits (Jones and Peterson 1976). This test appears to provide a fairly reliable prediction of seedling vigour in both the water-seeded and drill-seeded systems (Redoña and Mackill 1996a) and is currently being evaluated for suitability under tropical conditions.

While improved seedling vigour has been obtained in the California semidwarf rice cultivars (McKenzie et al. 1980), higher levels are desired to improve stand establishment and allow deeper water levels for increased weed suppression (Williams et al. 1990). In a study of seedling vigour traits in 27 diverse cultivars, temperate japonica and indica cultivars were generally superior to tropical japonicas (Fig. 1a). Overall, the best level of seedling vigour was found in the Italian japonica cultivar Italica Livorno, which has been a major donor for this trait in the Californian breeding program, but the indica-aus cultivar Black Gora also had superior vigour. These cultivars, however, are agronomically poor, and it has been difficult to exploit this improved seedling vigour in breeding programs (McKenzie et al. 1994). Tropical japonica cultivars were relatively poor in seedling vigour under both temperature regimes, but this was particularly noticeable under lower temperature (Fig. 1a). In the field under dry seeding, temperate japonica cultivars were superior in seedling vigour, and indica cultivars had relatively low vigour (Fig. 1b).

A possible means of overcoming the linkage of positive seedling vigour genes to undesirable traits, thereby facilitating breeding for high-vigour genotypes, is to genetically map the quantitative trait loci (QTL) through linkage to molecular markers. We have mapped seedling vigour QTL (length of shoot, root, coleoptile and mesocotyl) in two crosses using the slantboard screening method (Redoña and Mackill 1996b, c). Both crosses involved the tropical japonica cultivar Labelle as the low-vigour parent. The high-vigour parents were Black Gora (indica-aus) and Italica Livorno (temperate japonica). Restriction fragment length polymorphism (RFLP) markers were used in the Black Gora cross, and random amplified polymorphic DNA (RAPD) markers were used with Italica Livorno due to lower polymorphism for RFLPs. Measurements were taken at both 18°C (representing the typical temperate environment) and 25°C (for tropical environments, in the Black Gora cross only). Results for both crosses indicated that seedling vigour traits were under complex genetic control (Fig. 2). No significant positive QTL from the high-vigour Black Gora were identified for shoot length, the most important seedling vigour trait under water-seeded conditions. On the other hand, the low-vigour parent Labelle had shoot length QTL on chromosomes 1, 3, 5 and 9. One shoot length QTL linked to the RAPD marker $OPAD13_{720}$ on chromosome 3 was identified from the high-vigour Italica Livorno (Fig. 2). Several QTL exhibited overdominant gene action, indicating that the heterozygote had improved vigour over the two homozygotes. (True overdominance could not be distinguished from multiple QTL closely linked in repulsion phase.) Heterosis for seedling growth has been observed previously (Akita 1988).

It is clear from the genetic map (Fig. 2) that seedling vigour QTL from the two populations were usually different, and that very few QTL were effective under both temperature regimes. These observations underscore the complexity of breeding for improved seedling vigour. Nevertheless, individual markers such as $OPAD13_{720}$ may have utility for selection in specific crosses. The application of QTL tagging to applied plant breeding is still problematic, although this has received considerable attention. The use of markers is prohibitively expensive for routine breeding work, but the costs will probably decrease with development of improved technology. Use of markers to introgress QTL from a specific exotic source into a highly adapted cultivar appears feasible. In general, traits that have a low heritability or are relatively difficult or costly to measure are the best candidates for marker-assisted selection (Dudley 1993).

Submergence Tolerance and Drought Resistance

In broadcast or drilled systems, young seedlings may be subjected to temporary submergence after inundation from heavy rains. In water-seeded systems, seedlings are always submerged for a period of 10–20 days. Submergence tolerance may, therefore, be a desirable trait in many direct-seeded environments. Rice cultivars can cope with submergence through either rapid shoot elongation, or tolerance and recovery when the water level drops. Rapid seedling elongation is probably related to the seedling vigour characteristics mentioned above, and is likely to be complexly inherited. True tolerance to submergence is simply inherited, and improved tolerant cultivars have been developed (Mackill et al. 1993). We have recently mapped a major locus, designated *Sub1*, on rice chromosome 9 (Xu and Mackill 1996). This locus is responsible for submergence tolerance in the breeding line IR40931-26, which inherits tolerance from the cultivar FR13A. Having markers for this locus will aid in its incorporation into high-yielding cultivars. It is still not clear if submergence tolerance will be useful for water-seeded rice, because submergence-tolerant genotypes tend to have reduced leaf elongation under flooding, and emergence of seedlings from the water may be delayed.

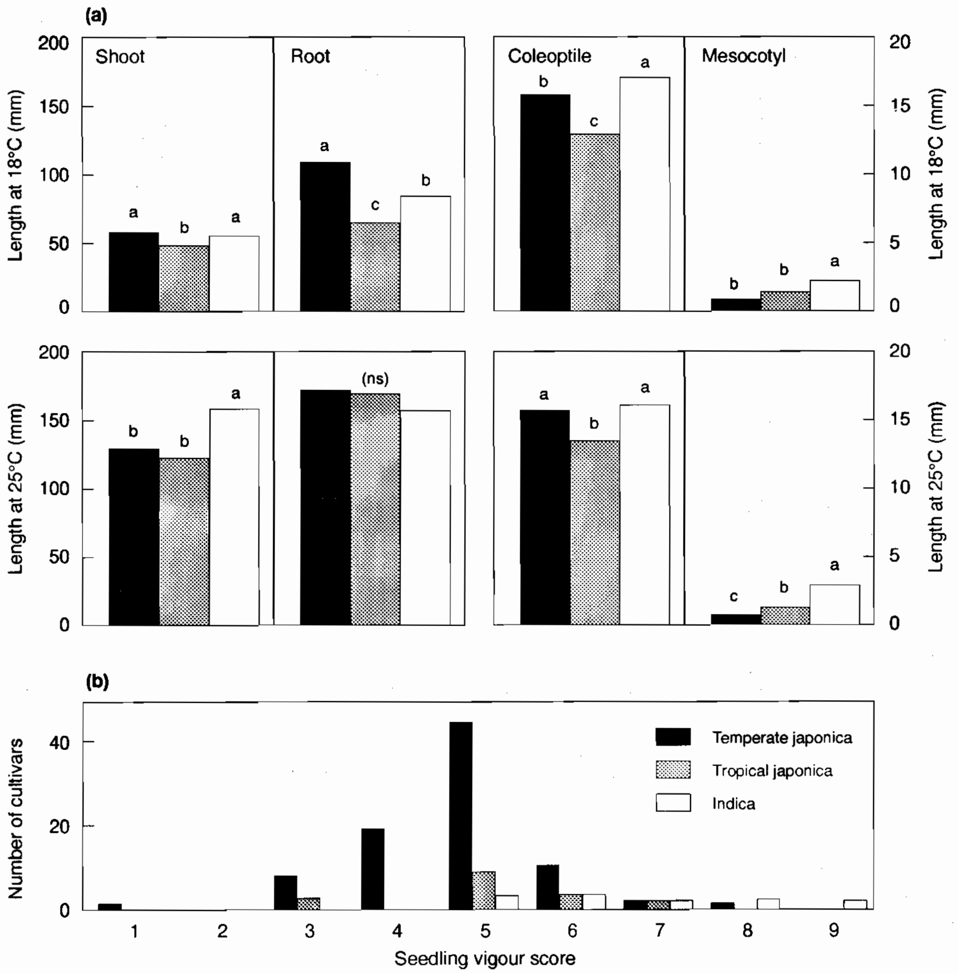

Figure 1. (a) Average values of three cultivar groups for four seedling vigour traits at 18 and 25°C measured in slantboard tests. Coleoptile and mesocotyl lengths follow the scale on the right. Total number of cultivars in each group was 12 for temperate japonica, 7 for tropical japonica, and 8 for indica (Redoña and Mackill 1996a). (b) Distribution of seedling-vigour score (on a scale of 1 = highly vigorous to 9 = poor vigour) under dry seeding at Davis, California, USA, for 117 rice accessions classified into three rice groups by RAPD analysis (Mackill and Lei, in press). Different letters next to the bars indicate a significant difference ($P < 0.05$) (ns = not significant).

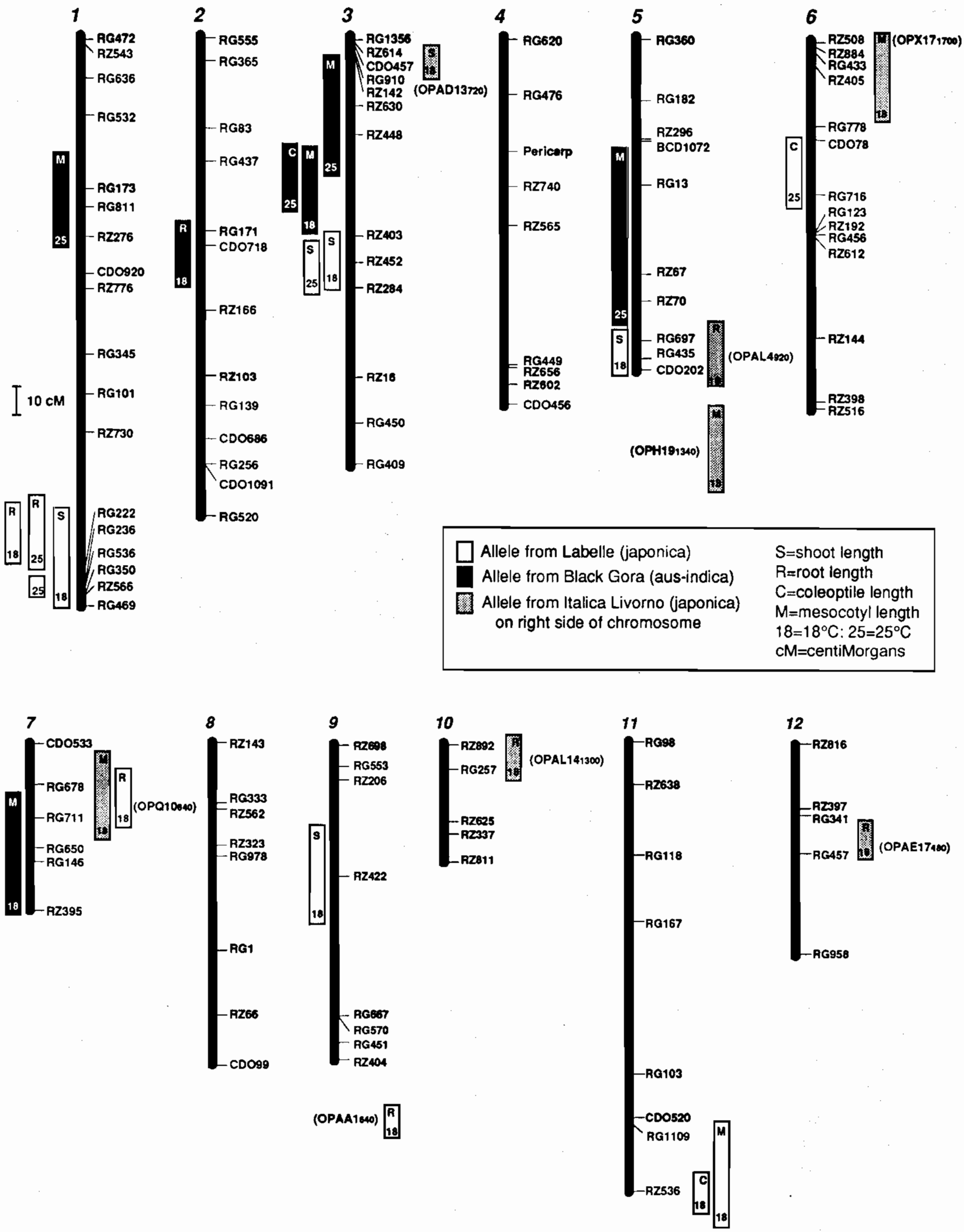

Figure 2. RFLP map of rice cross Labelle (japonica) × Black Gora (indica-aus) showing QTL for four seedling-vigour traits (length of shoot, root, coleoptile and mesocotyl) at two temperatures (18 and 25°C) (Redoña and Mackill 1996b). Bars at the right of specific chromosomes show the approximate location of QTL identified in the cross Labelle × Italica Livorno by linkage to RAPD markers (Redoña and Mackill 1996c).The length of the bars indicates the most likely position of QTL. Bars indicated below the chromosome were located on that chromosome but were not mapped to a specific position.

Drought stress is not common in water-seeded or irrigated environments. Under water seeding, root growth is inhibited, and some farmers practice 'pin-point' drainage to increase root growth. Dry seeding under rainfed lowland conditions may either enhance or mitigate drought stress compared with transplanting. In a transplanted system, root systems are damaged during the uprooting process and are further inhibited by the hardpan that forms in puddled soils. Root growth is typically limited to shallower soil levels. Dry seeding can promote rapid root development and early vegetative growth, because transplanting shock is avoided and roots tend to grow deeper in aerobic conditions. On the other hand, in a transplanted system, seedlings are often protected from drought by being kept in the seedbed until sufficient water has accumulated in the field. Puddling helps to reduce water loss through seepage. In dry-seeded rice, inadequate rainfall will expose the young plants to drought stress.

A deep root system with thick roots is considered the most important trait required for improved drought resistance under upland conditions (O'Toole and Chang 1979). The relevance of the root system to drought resistance under lowland conditions is less clear (Chang et al. 1982; Fukai and Cooper 1995; Mackill et al. 1996). The increased penetration resistance caused by the formation of a hardpan reduces root development under lowland conditions. Drought screening under transplanted lowland conditions usually gives different results from screening under upland conditions (IRRI 1985). However, there is evidence that genotypic differences in root growth are relevant to rainfed lowland rice. Root-length density was found to be linearly related to yield in a lowland experiment conducted under a sprinkler gradient (Thangaraj et al. 1990). Root pulling force has been used to measure root growth differences under lowland conditions (O'Toole and Soemartono 1981). Genotypic differences in root pulling force are related to the proportion of the root system in deeper soil levels (Ekanayake et al. 1986). Root pulling force has been shown to be related to yields under drought stress in lowland conditions (Ingram et al. 1990). The correlation of canopy temperature based indices with drought resistance also suggests a role for roots in lowland drought resistance (IRRI 1986; Ingram et al. 1990). Under direct seeding, root growth may play a more important role for drought resistance, because the penetration resistance may be lower due to absence of puddling, and the initial growth conditions approximate those of upland rice (Mackill et al. 1996).

Champoux et al. (1995) identified QTL controlling root characteristics in a cross between Moroberekan (deep-rooted japonica) and CO39 (shallow-rooted indica), and these loci were also shown to confer improved drought resistance. We identified QTL for seedling root growth in two populations (Fig. 2) (Redoña and Mackill 1996b, c). Three of these QTL may correspond to those identified by Champoux et al. (1995): one on chromosome 2 near CDO718, one on chromosome 5 linked to $OPAL4_{920}$, and one on chromosome 12 linked to $OPAE17_{480}$. An additional locus on chromosome 9 was not placed on the RFLP map in our populations (Fig. 2), but Champoux et al. found on this chromosome at least two QTL controlling several root-related traits. Root penetration ability may be a more important attribute in rainfed lowland situations, and genotypic differences exist for this trait (Yu et al. 1995). Six QTL for penetration index were mapped in the recombinant inbred populations CO39/Moroberekan, and preliminary evidence indicates these QTL are associated with higher root number and thicker roots (Ray et al. 1996). The implications of these QTL studies for breeding for improved drought resistance are not yet clear.

Selection Strategies

In a breeding program for direct seeding, cultivars or breeding lines that are known to possess the desirable attributes discussed above can be selected as parents for crossing. Obviously, choice will depend on local factors, but it is usually observed that the wider the cross (i.e. intersubspecific or interspecific), the more difficult it is to obtain superior plants. Thus, breeders might consider the highly vigorous indica-aus cultivars or japonicas like Italica Livorno as good sources of seedling vigour, but they will be extremely poor combiners with improved indica cultivars. For submergence tolerance, a number of improved indica lines are available that are agronomically superior to the original sources. For drought resistance, the upland japonica cultivars have excellent levels, but will be difficult to exploit where indica cultivars are the major varietal type. It is much easier to use the best sources from more adapted donors.

If breeders want to change their emphasis from transplanting to direct seeding, then they should apply direct seeding in their breeding nurseries. Continued selection under transplanted conditions can produce plants that are prone to excessive lodging. Breeders at the California Rice Experiment Station have found that use of drill seeding is not effective in breeding for a water-seeded system (McKenzie et al. 1994). One serious shortcoming of breeding lines developed under drill seeding is higher susceptibility to lodging. In addition, rapid emergence of seedlings from the water is a critical requirement for the water-seeded system, and breeders begin selecting for this trait in early generations. Genotypic differences may vary in drill vs water seeding, although there is evidence they are related (Redoña and Mackill 1996a). As mentioned above, the slantboard test procedure may be used for culling out breeding lines based on seedling vigour characteristics. In the USA, F_2 populations are usually drill-seeded with precision planters, which are relatively expensive. Where labour is sufficient, F_2 populations can be planted directly into furrows by hand. It is relatively easy to plant pedigree nurseries by broadcasting into 1–2 m rows. Individual panicles can be selected from superior rows, and each panicle provides sufficient seed for a single row in the next generation. Selection under these conditions is more likely to produce plants that are adapted to the stresses found under direct-seeded conditions. Direct-seeded nurseries can also reduce the labour costs of managing breeding nurseries, although appropriate herbicide use is essential.

The genetic and physiological understanding of the traits necessary for improving productivity under direct-seeded conditions should provide valuable input into breeding programs. But utilisation of this information will depend on application of appropriate selection methods in the appropriate environments to develop improved rices. For practicing breeders, the most important consideration is to make selections in an environment that approximates the most likely farm conditions. This may be problematic for rainfed rice, considering the wide fluctuations that occur over years and locations, so breeders may need to spend considerable effort in defining optimum selection environments.

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Oryza sativa and *O. glaberrima* Genepools for High-Yielding, Weed-Competitive Rice Plant Types

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Abstract

Rainfed rice systems in West Africa, in which labour is a major production constraint, require rice cultivars that resist multiple stresses and require minimal management interventions from farmers. Weeds are the most important yield-reducing factor, and weeding is very labour intensive. A plant-type concept was developed to minimise the tradeoffs between rice–weed competitiveness and yield potential. The concept is based on two main components: the combination of weed suppressive traits from African rice *Oryza glaberrima* and the high-yielding characteristics of Asian rice *O. sativa*; and the development stage specific expression of these traits during periods when they are most needed. The resulting rice plants should have many of the 'weedy' characteristics of *O. glaberrima* during vegetative growth but resemble *O. sativa* during later growth stages. *O. glaberrima* will contribute superior seedling vigour and early groundcover, along with several other stress adaptations.

Upland field trials in 1994 and 1995 confirmed the superior weed competitiveness of *O. glaberrima* landraces. This was associated with rapid vegetative growth, tillering and leaf area production. During the wet season of 1995, growth analyses for four F_8 interspecific groups of progenies and their parents were conducted under differential nitrogen (N) resources in an upland field in Cote d'Ivoire. The superior vigour and leaf area index (LAI) of the *O. glaberrima* landrace CG14, compared to those of the tropical japonica *O. sativa* line WAB56-104, could be explained by higher specific leaf area (SLA) and assimilate partitioning ratios to leaf-blades. The interspecific hybrids had intermediate LAI, SLA and partitioning ratios. The pale appearance of the foliage of CG14 and the hybrids was due to lower leaf N content per unit leaf area, but their N concentration per unit dry weight was higher than that of WAB56-104. Marked differences in canopy architecture were observed, which affected light interception. Grain yields were similar in the hybrids and their *O. sativa* parent, but they were much lower in the *O. glaberrima* parent, a result of the panicle architecture, lodging and grain shattering that are typical of this species. Crop simulation studies are under way to design interspecific plant types with minimal tradeoffs between traits for yield potential, drought resistance and weed competitiveness in specific African environments.

A RECENT breakthrough in hybridising Asian rice *Oryza sativa* L. with African rice *O. glaberrima* Steud. gave rise to a major thrust in cultivar improvement research at the West Africa Rice Development Association (WARDA): the development of weed-competitive upland rices for resource-poor farmers and stress-prone environments (WARDA 1994, 1995 and 1996).

Average yields on West Africa's 2 million ha of upland rice fields are only 1.0 t/ha (WARDA 1996). As the most commonly grown cultivars can yield up to 4.0 t/ha, the yield gap is substantial. It reflects two major constraints to production:

- the multiple stress factors that affect the crop and are largely beyond the control of resource-poor farmers; and
- the labour-limited nature of most African rice production systems, which frequently does not permit sustained crop and land management efforts.

Weed competition is the most important yield-reducing factor, followed by drought, blast and soil acidity. Traditionally, farmers manage these stresses through long periods of bush fallow. However, popu-

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lation growth has led to a dramatic reduction of fallow periods in many areas, thereby aggravating weed pressure and soil infertility.

Despite sustained efforts to improve upland rice cultivars on the basis of *O. sativa*, their resistance to weed competition and drought remains poor. By contrast, many African indigenous *O. glaberrima* cultivars are highly weed competitive, and many resist drought, blast and other stresses (Koffi-Goli 1979; WARDA 1996). However, they have been marginalised by Asian rice *O. sativa*, which has a higher yield potential. *O. glaberrima*, of which only cultivated forms are known, is now sporadically grown in upland areas for its superior grain quality, and in deepwater ecosystems where flood-tolerant landraces have a comparative advantage. The species has never been used systematically in rice breeding because of the sterility barrier to crossing with *O. sativa*; its panicle type, with no or few secondary branches; its weak stems, which easily lodge; and its tendency to shatter grain. The marginalisation of *O. glaberrima* has resulted in a major loss of biodiversity.

The present study aims at developing a detailed concept for high- and stable-yielding upland rice types, drawing on traits of African and Asian rice and based on a systems approach involving breeders, plant physiologists and weed scientists. The plant-type concepts, once refined and validated, will give direction to a long-term interspecific rice breeding program for low-input, rainfed and labour-limited environments.

Materials and Methods

Parent selection and hybridisation

During 1991–92, 316 improved and 275 traditional *O. sativa* and 1130 *O. glaberrima* accessions were evaluated for morphological and agronomic traits in an upland field at Mbe (7°52'N, 5°6'W), Cote d'Ivoire using the standard evaluation system of the International Rice Research Institute (IRRI). Eight *O. glaberrima* parents were selected on the basis of vigour and tiller number, including CG14 and IG10. Improved tropical japonica upland rices such as WAB56-104 and WAB181-18 were selected as sources of high yield potential. Out of 48 *O. sativa* × *O. glaberrima* crosses, seven produced fertile grains. The F_1 progenies were backcrossed twice to the *O. sativa* parents, followed by pedigree selection. Traits were fixed after six generations. Anther culture was used in a subset of crosses. Anthers were removed from the F_2 generation at booting and placed in a modified N_6 growth medium with 0.5 mg/L Kinetin, 2 mg/L 2,4D, 5% maltose and 150 mL/L coconut milk. After 3–8 weeks, calli were transferred to Murashige and Skoog (MS) medium. They developed in 3–4 weeks into plantlets, which were treated with a hardening chemical to condition them for transfer to the soil.

Field experiment I

During the 1994 wet season, 12 *O. glaberrima* and *O. sativa* lines were studied for competitiveness with a natural weed flora on an upland field at Mbe (2-factorial randomised complete block (RCB) with three replications). Weed management was either clean weeding throughout, or one weeding at 43 days after emergence (DAE). Fertiliser inputs were 14 kg nitrogen (N) per ha and 20 kg phosphorus (P) per ha. Observations on only two lines, CG14 (*O. glaberrima*) and WAB56-104 (*O. sativa*, tropical japonica type), are reported here. Details of the study were reported by Fofana et al. (1995).

Field experiment II

During the 1995 wet season, a detailed study of the interaction between weeds and *O. glaberrima* (IG10) and improved (IDSA6) and 'traditional' (Moroberekan) *O. sativa* was conducted. The weed treatments were clean weeding throughout, clean weeding during the first 14 DAE, and weeding once at 28 DAE. Fertiliser inputs were 46 kg N (2-split), 40 kg P and 50 kg potassium (K) per ha.

Field experiment III

During the 1995 wet season, 22 fixed *O. sativa* × *O. glaberrima* progeny derived from conventional breeding and anther culture were evaluated in a yield trial with four replications under high- and low-input management on an infertile upland field. The parents (CG14 and WAB56-104) and the improved *O. sativa* checks IDSA6 and WABC165 were also sown. High-input plots were ploughed and harrowed. In low-input plots, vegetation was slashed and the soil scarified by hand hoe. High-input plots were fertilised with 100 kg N/ha (3-split), and 36 kg/ha each of P and K. Low-input plots received only 40 kg N/ha as 2-split. High-input plots were kept weed free, and low-input plots were hand-weeded at 21 and 42 DAE. Seedling vigour was scored at 30 DAE. Details of the breeding approach that resulted in the progenies were published elsewhere (WARDA 1994, 1995).

Field experiment IV

Growth and yield analyses of four *O. sativa* (upland-adapted improved tropical japonica) × *O. glaberrima* (upland-adapted landrace from Senegal) interspecific F_7 progenies and their parents were conducted during the 1995 wet season on WARDA's research station at Mbe. The male parent material was CG14 (*O. glaberrima*) (V1) and the female parent WAB56-104 (*O. sativa*) (V2). The progenies were WAB450-1-B-P-160-HB(V3), WAB450-24-3-2-P18-HB(V4), WA B450-24-2-3-P33-HB(V5) and WAB450-1-B-P31-HB(V6). In the following, unless specified otherwise, we refer to V4, the progeny with the most pronounced intermediate characteristics, when discussing the progenies' behaviour.

The materials were grown on a comparatively fertile, well-drained Alfisol following one crop of maize and six years of fallow, using a 2-factorial RCB design with three replications. The factors were variety and N levels (0, 40, 80, and 120 kg/ha). Half of the N was applied basally and the other half top-dressed at 40 days after sowing (DAS). Triple superphosphate (100 kg P/ha) and potassium chloride (KCl; 50 kg K/ha) were applied basally to all plots. The soil was well drained, and moisture was not limiting, due to supplementary boom irrigation. Plots measured 3 × 5 m, including a yield sampling area measuring 2 × 2.5 m. Weather data are presented in Table 1.

On 26 June 1995, dry seed was dibbled at a rate of three seeds per hill with a spacing of 0.25 × 0.25 m. Seedlings emerged about five days later. Upon seedling establishment, seedlings were thinned to two plants per hill. Maturity was observed on 11 October (V1), 30 September (V2), 8 October (V3), 12 October (V4), 26 September (V5) and 7 October (V6). The following parameters were measured at 14-day intervals:

- bulk leaf, stem and panicle dry weight based on four hills (destructive);
- specific leaf area (SLA) of randomly sampled (with the exception of flag leaves, which were systematically sampled at flowering), fully expanded, healthy leaves (destructive), based on in-situ leaf area measurement with a LiCor LI-3000 (Lincoln, Nebraska) and subsequent dry weight measurement;
- tiller number and plant height; and
- area-based chlorophyll content of randomly sampled (except flag leaves, see above), fully expanded, healthy leaves using a SPAD chlorophyll meter (Minolta). The leaf chlorophyll content was converted into area and weight-based N content according to Peng et al. (1993).

Table 1. Weather data recorded at the experimental site, Mbe, Cote d'Ivoire, 1995 wet season.

Month	10-day period	Temperature (°C)			Rs (MJ/m^2/day)	E(pan) (mm/day)	Wind (m/second)	Rainfall (mm)
		Mean	Min.	Max.				
June	1	25.2	22.3	29.3	18.4	4.95	0.99	49.9
	2	25.7	22.5	29.8	16.9	4.09	1.27	13.8
	3	25.3	22.5	29.2	16.4	4.27	1.25	13.5
July	1	24.5	21.8	28.0	14.0	3.53	0.87	2.6
	2	24.3	22.0	27.7	17.5	2.98	0.83	25.2
	3	24.4	22.3	27.2	15.8	3.48	1.27	10.0
August	1	24.2	22.0	27.3	13.0	2.81	1.00	24.4
	2	24.2	21.0	29.1	15.6	2.59	0.11	128.7
	3	24.6	21.6	29.3	15.2	2.97	0.18	28.0
September	1	24.9	21.7	29.8	16.4	3.42	0.11	102.0
	2	24.5	21.3	29.4	17.7	3.08	0.22	74.2
	3	24.1	21.1	29.3	16.3	3.26	0.25	19.9
October	1	24.6	21.2	31.0	16.1	3.72	0.81	27.0
	2	24.9	20.9	32.0	15.5	3.73	0.65	22.0
	3	24.9	20.9	32.3	16.3	3.40	0.62	23.0

Rs = daily solar radiation; E(pan) = Class A pan evaporation

At maturity, grain yield and yield components were measured as described by Dingkuhn and Le Gal (1996). In addition, we counted the number of primary, secondary and tertiary branches and estimated the degree of shattering by counting the number of attached and missing spikelets for a random sample of 10 panicles per plot at maturity.

Results and Discussion

Genetic sources in Africa for weed-competitive rice plant types

Success in crop improvement depends on available genes for useful traits. Field evaluations of African rice germplasm during 1991 and 1992 showed that many landraces of *O. glaberrima* mature extremely early. The species also possesses many adaptations to traditional shifting cultivation, including early groundcover through profuse vegetative growth and droopy lower leaves, which help suppress weeds. *O. glaberrima* is also a rich source of genetic resistance to blast, African rice gallmidge, rice yellow mottle virus, root-parasitic weeds and nematodes, and drought (WARDA 1994).

Some *O. glaberrima* types produce many tillers and panicles. In experiment I, the *O. glaberrima* accessions CG14, IG10 and ACC 102257 had between 220 and 307 tillers/m^2 (mean 268), and nine *O. sativa* lines of diverse origin had between 119 and 240 tillers/m^2 (mean 179).

The most crucial weakness of *O. glaberrima* as a crop is its low yield potential, resulting from its specific panicle type, and tendency to lodge and shatter grains. All *O. glaberrima* accessions tested had no or few secondary branches on the panicles. In experiment IV, the landrace CG14 had between 11.0 and 12.2 primary and between 15.2 and 24.0 secondary branches, depending on N treatments. By contrast, the *O. sativa* line WAB56-104 had 12.2–12.6 primary and 37.5–41.0 secondary branches. As a result of panicle architecture, most *O. glaberrima* materials produce only 75–150 grains per panicle, as compared to 250 or more grains in *O. sativa*. The low yield potential of *O. glaberrima* has motivated many farmers to replace it with *O. sativa* cultivars.

The weed competitiveness of *O. sativa* and *O. glaberrima* cultivars

The *O. glaberrima* cultivar IG10 grew twice as fast as the improved upland rice IDSA6 and the traditional cultivar Moroberekan, when competing with a natural weed population (Fig. 1; experiment II). This rapid growth was associated with a strong suppression of weed growth. Only half the weed biomass was observed at mid-season in the IG10, *O. glaberrima,* compared to IDSA6 plots. Consequently, aggregate biomass in the plots was about the same for the three cultivars, but weeds accounted for only one-third of biomass in IG10 plots, and about two-thirds in IDSA6 and Moroberekan plots. The superior suppression of weed growth by *O. glaberrima* types is thought to be due mainly to vigorous early growth. Seedlings of IG10 tillered more and earlier than Moroberekan and IDSA6. This vigour continued, with IG10 developing a greater leaf canopy compared to either Moroberekan or IDSA6 (leaf area index, LAI, 2.4, 0.7 and 0.8 respectively; SE ± 0.14) at 49 days after emergence in the presence of weeds.

Weed competition reduced the LAI of the *O. glaberrima* cultivar at 49 DAE by 36% (SE ± 7.4), compared to 33% for Moroberekan and 56% for IDSA6. Reduction in dry matter and tiller numbers were similar, indicating a marked effect of weeds on the vegetative growth of rice, particularly in the improved cultivar IDSA6. At harvest, IG10 showed considerable yield stability between the clean and weedy plots, with mean yield of 2.6 vs 2.1 t/ha, compared to Moroberekan (3.9 vs 1.5) and IDSA6 (3.9 vs 1.4; SE ± 0.25). The weed competitiveness of IG10 was due more to weed suppression than tolerance. IDSA6 and Moroberekan are commonly grown by upland rice farmers in Cote d'Ivoire. IG10 originates in the same environment but has been largely replaced by *O. sativa* cultivars.

The weed competitiveness of the most extensively used parents in WARDA's interspecific breeding program was studied in experiment I. The *O. glaberrima* parent, CG14, competed much better with weeds than the *O. sativa* parent, WAB56-104 (Fig. 2). In clean weeded plots, CG14 showed superior vegetative growth, but had lower yields than WAB56-104. In the presence of weeds, however, CG14 produced four times the biomass and eight times the yield of WAB56-104. Weeds reduced the grain yield of CG14 by 39%, as compared to 94% for WAB56-104.

Generating and testing interspecific hybrids

During the past five years, large numbers of interspecific progenies have been generated and field-tested. The yield potentials of many progenies were similar to, or higher than, either of their parents and several improved check cultivars. After eliminating progenies that had the panicle type and some other undesirable traits of *O. glaberrima*, the majority of the remaining progeny were high yielding under high-input conditions, but only a few showed yield stability across input levels. Consequently, the selection pressure for high yield under low-input conditions will now be increased.

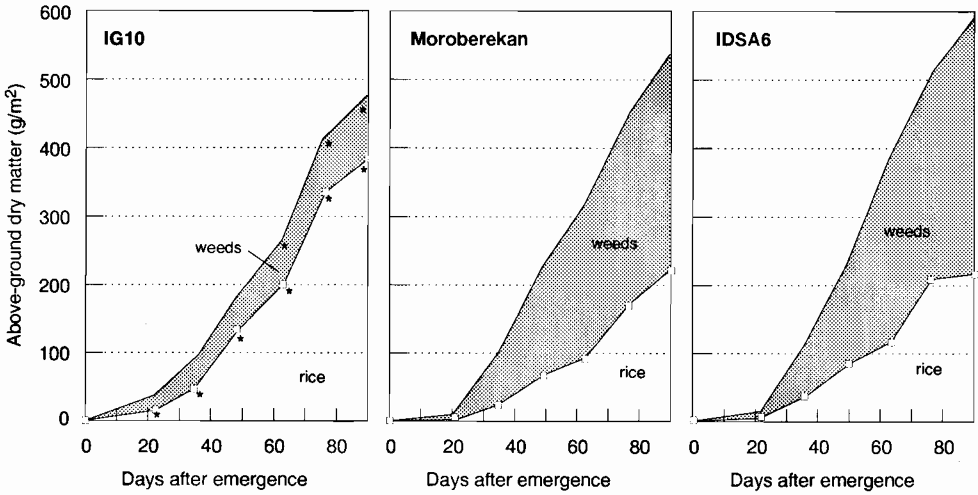

Figure 1. Time courses of rice plant and weed biomass for *O. glaberrima* (IG10), and 'traditional' (Moroberekan) and improved (IDSA6) *O. sativa* cultivar. Weed growth was not controlled after 14 days after emergence (DAE) Mbe, Cote d'Ivoire, 1995 wet season. (Asterisks on the IG10 graph indicate significant differences ($P < 0.05$) from Moroberekan and IDSA6.)

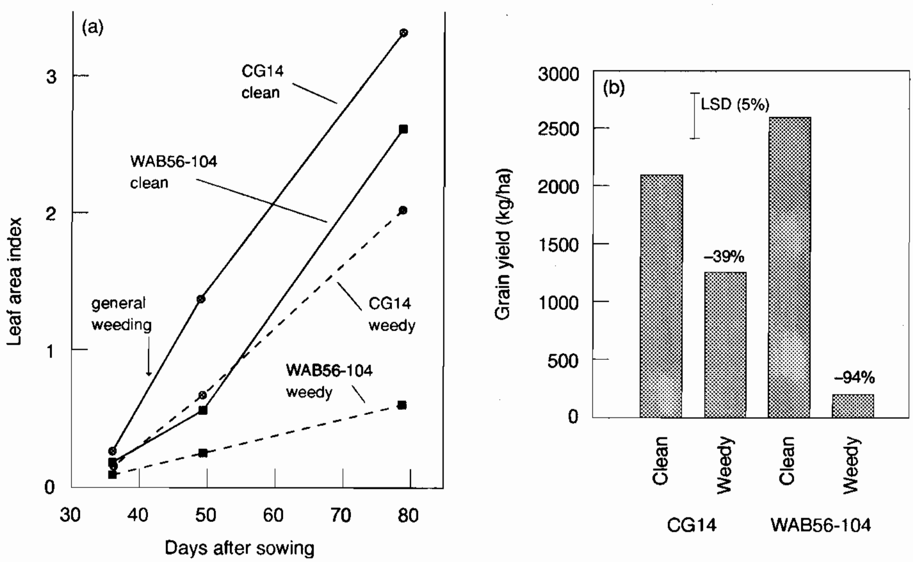

Figure 2. Leaf area index (a) and grain yield (b) of the *O. glaberrima* cultivar CG14 and the *O. sativa* line WAB56-104 grown with differential weed management ('clean' weeding) or one single weeding ('weedy') under non-water limited upland field conditions. The LSD (5%) is based on the factor 'weed management'. Mbe, Cote d'Ivoire, 1994 wet season.

Although only seven out of 48 crosses produced more than 5% fertile seeds in the first generation, a remarkable diversity of plant types evolved. The highest fertility was obtained in F_1 hybrids that had the *O. glaberrima* CG14, CG20, T2, YG230 or YG170 as parents. The F_1 plants resembled *O. glaberrima*, including infrequent secondary branching of the panicle, early seedling vigour and a short ligule. Two backcrosses to the *O. sativa* parents raised fertility to 30–65%, and helped combine the *O. sativa* and *O. glaberrima* features. Traits appeared that had been absent in the parents, such as purple leaf sheath, awns and apiculae.

Morphological intermediates between *O. sativa* and *O. glaberrima* were frequent in some populations, such as WAB449 (WAB56-104 × T2) and WAB450 (WAB56-104 × CG14). Some of these had an intermediate ligule length, a trait that distinguishes the two species. Most importantly, some intermediates combined the high yield potential of *O. sativa,* a result of high spikelet number caused by secondary branches on the panicle, with useful vegetative traits of *O. glaberrima* such as rapid vegetative growth, droopy lower leaves, high tillering, short growth duration between 75 and 100 days, and good grain quality.

Using conventional breeding methods, fixation and full fertility was achieved in the course of seven generations, during which useful introgressed traits were retained. Seed shattering was greatly reduced, and the selection of plants with thick culms solved the problem of lodging. Anther culture was used as an alternative path to achieve early fixation and high fertility. Two-fifths of the regenerated green plantlets were doubled-haploids, and the othpers haploids and polyploids. Some of the F_1 and F_2 doubled-haploids had 96–100% fertility. Rapid genetic fixation through double-haploidisation has the additional advantage of retaining genes which would otherwise be lost through repeated selection. On the other hand, in a first set of regional trials conducted by task forces, many lines succumbed to diseases at some sites, probably due to the expression of many recessive genes. The most interesting morphological plant types were so far obtained with anther culture.

A subset of progenies from CG14 (*O. glaberrima*) × WAB56-104 (improved tropical japonica) crosses was evaluated during 1995 using high- and low-input management packages. CG14 was among the top yielders under low inputs, although its yield did not respond to increased inputs (Fig. 3). By contrast, WAB56-104 and the local improved check IDSA6 had low yields under low input, but yields more than doubled under high inputs. Another improved check cultivar, WABC165 from Latin America, had relatively high yields in both treatments.

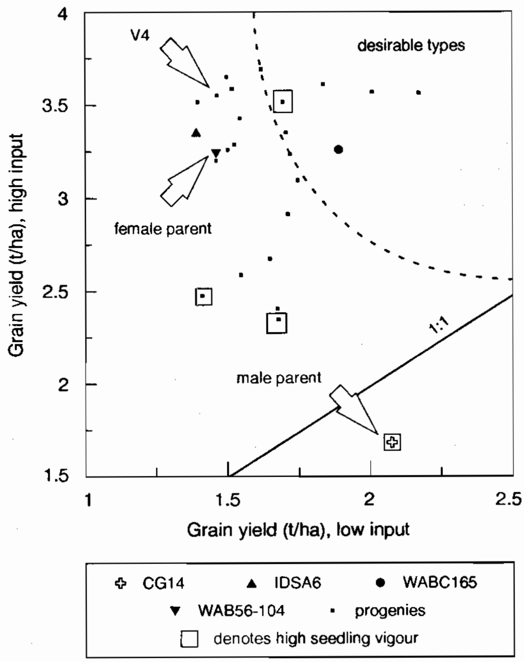

Figure 3. Relationship between grain yields obtained under high- and low- input management for 22 interspecific progenies, the *O. glaberrima* parent CG14, the *O. sativa* parent WAB56-104, and two improved *O. sativa* upland rices. Mbe, Cote d'Ivoire, 1995 wet season.

A cluster of interspecific progenies had slightly higher yields than WAB56-104 and IDSA6 under both high and low inputs, indicating a high yield potential and a very strong yield response to inputs. A smaller cluster of progenies had a similar yield to that of WAB56-104 and IDSA6 under low inputs, but was less responsive to increased inputs. None of the progenies followed the yield pattern of CG14, the *O. glaberrima* parent, probably because none had the *O. glaberrima* panicle type, which had been selected against. However, two progenies (top right in Fig. 3) combined the high yields of CG14 under low inputs with the high yields of WAB56-104 under high inputs. These entries, as well as one that had outstanding seedling vigour and good yield potential, will be further studied.

Detailed morphophysiological characterisation of parents and selected progenies

During the 1995 wet season, we initiated a series of detailed growth analyses for selected interspecific progenies and their parents. The results will serve to develop crop models that predict the effect of various trait combinations on yield potential and stability in stress environments, particularly under weed competition. We report here the results of a first such upland experiment (IV), conducted under non-limiting water but variable N resources, for four progenies and their parents, CG14 and WAB56-104. Subsequent studies will introduce, in steps, additional stress factors, such as weed competition and drought, along with an expansion of model sensitivities to these stress factors.

Grain yield and yield components

The *O. sativa* parent and the progenies showed very similar yields and yield responses to N application, the progenies having consistently (but not statistically significantly) higher yields across N levels (Fig. 4). When comparing pairs of means, however, the progeny V4 significantly outyielded its parents in the 80 kg N treatment. Yields of the *O. glaberrima* parent did not respond to N application, probably due to lodging, which occurred in all treatments but occurred earlier at higher N rates. For all N levels, the *O. glaberrima* parent had the same grain loss of about 1 t/ha due to shattering (30–40% of the grain produced). Neither the *O. sativa* parent nor the progeny lodged or shattered. When considering both attached and shattered grains, all parents and progenies had precisely the same yield at zero N inputs (3.7 t/ha), and varietal differences only materialised as N was applied.

The similarity among the yields of the progenies and their *O. sativa* parent was partly due to the high incidence of secondary panicle branches (1.53 secondary branches per primary branch in the *O. glaberrima* parent, 3.16 in the *O. sativa* parent, and between 3.22 and 3.46 in the progenies). The progeny had comparatively open panicles, most of which were larger than those of either parent.

Dry-matter accumulation and leaf area growth

The seedling vigour of the *O. glaberrima* parent and progeny was superior to that of the *O. sativa* parent, resulting in rapid biomass accumulation during exponential growth (Fig. 5). For the 80 kg N treatment, relative growth rates (RGR) of 18.7% per day were observed for the V4 progeny between 26 and 39 days after sowing (DAS), as compared to 18.4% for the *O. glaberrima* and 14.8% for the *O. sativa* parent. At the onset of linear growth between 39 and 53 DAS, the RGR was 12.0% for V4, as compared to 11.6 % for the *O. glaberrima* and 9.8% for the *O. sativa* parent. Consequently, at any given amount of biomass on the plot, the *O. glaberrima* parent and the V4 progeny grew faster than the *O. sativa* parent.

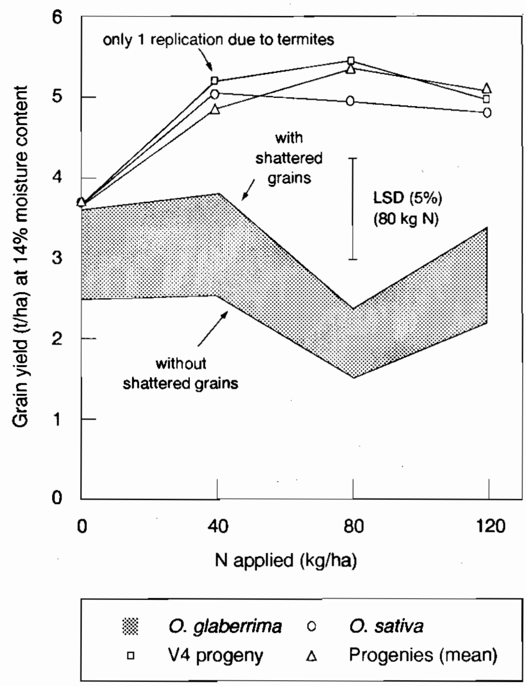

Figure 4. Grain yield as a function of N rate of the *O. sativa* cultivar CG14, the *O. sativa* line WAB56-104 and four interspecific hybrids. Mbe, Cote d'Ivoire, 1995 wet season.

These differences might have been due to access to resources, resource use efficiency within the plant, or both. Preliminary evidence from an ongoing repetition of experiment IV, during the 1996 wet season at the same site, points to superior N uptake (access) and canopy architecture, and related light-use efficiency, as major determinants of the observed genotypic differences. *O. glaberrima* CG14, with its droopy lower leaves, achieved a high light interception at mid-height of the leaf canopy, whereas WAB56-104, with its more erect and sparser foliage, had a more uniform light interception profile and lower overall light interception due to its uniformly erect leaves (Fig. 6). In addition, CG14 intercepted significantly ($P < 0.05$) more photosynthetically active radiation at any given level of global light interception (Fig. 7). This observation has been verified in independent studies, but its causes are as yet unknown.

The V4 progeny resembled the *O. sativa* parent more closely. Weed competitiveness of rice is not only a function of total light interception and the canopy's light extinction coefficient, which determine light use and light-use efficiency of the crop. It also depends on the quantity and quality of light available to weeds associated with rice. CG14 and WAB56-104 differ in this regard, but more research is needed to understand how light interception profiles affect weed competition.

The rapid initial growth of the progenies and their *O. glaberrima* parent was associated with faster leaf growth (Fig. 8). The *O. glaberrima* parent developed more than twice the leaf area of the *O. sativa* parent under zero N inputs, and 3.5 times its leaf area in the 80 kg N treatment. The progenies were generally intermediate. Rapid biomass and leaf area growth, as in CG14 and the progeny, are major components of weed competitiveness. Again, however, we noted that these traits were more strongly expressed in the progeny under high inputs, indicating that more emphasis must be placed on low-input selection environments.

Specific leaf area

Specific leaf area (SLA) was in part responsible for the large difference in LAI observed among genotypes. The SLA was strongly affected by genotype and phenological stage (Fig. 9). At any given phenological stage and genotype, however, SLA was remarkably stable across replications and N treatments. The *O. glaberrima* parent had a high SLA throughout its development. By contrast, the *O. sativa* parent had a much lower initial SLA, which even decreased significantly in the course of development, indicating that leaves were getting thicker.

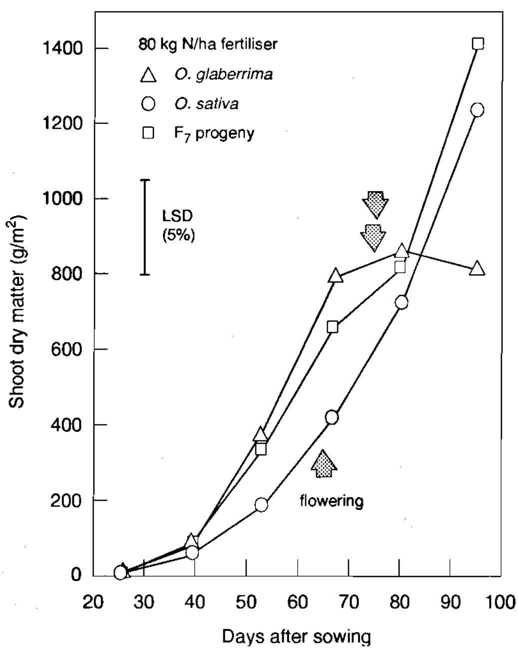

Figure 5. Time courses of above-ground (shoot) dry-matter growth for the *O. glaberrima* cultivar CG14, the *O. sativa* line WAB56-104 and the interspecific F_7 progeny V4 (details in Materials and Methods) in an upland field fertilised with 80 kg N/ha. Mbe, Cote d'Ivoire, 1995 wet season.

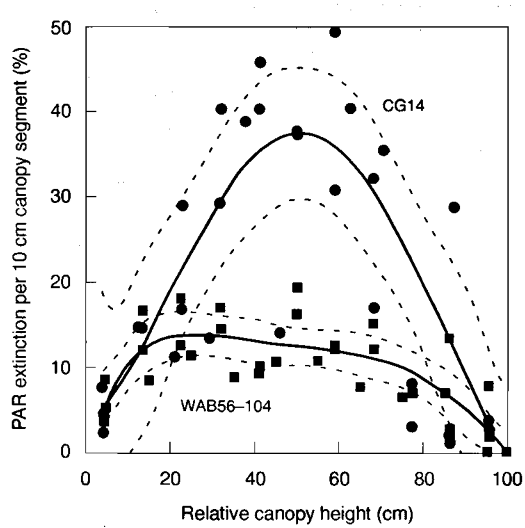

Figure 6. Interception profiles for photosynthetically-active radiation (PAR) of a CG14 (*O. glaberrima*) and WAB56-104 (*O. sativa*) canopy at mid-season, measured at 10-cm intervals and normalised for plant height. At each 10-cm layer, extinction ratios were calculated on the basis of PAR reaching the top of that layer. Broken lines indicate the confidence interval for 5th order regressions (sigma plot), based on data from three lumped replications. Mean plant height was 110 cm for CG14 and 107 cm for WAB56-104. Total light interception and leaf area index were 0.93 and 5.8 for CG14, and 0.66 and 1.4 for WAB56-104, respectively, Mbe, Cote d'Ivoire, 1996 wet season.

The progeny had generally intermediate SLA during early growth stages, followed by a decrease at least as sharp as that of the *O. sativa* parent.

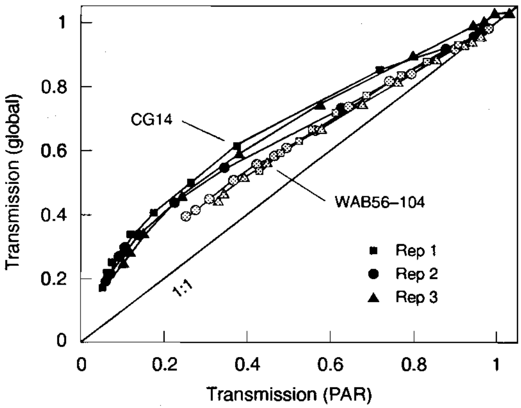

Figure 7. Relationship between light transmission patterns for photosynthetically active radiation (PAR, 400–700 nm) and global radiation (ca. 350–1100 nm), measured simultaneously, for the CG14 and WAB56-104 rice canopies shown in Figure 6. Mbe, Cote d'Ivoire, 1996 wet season.

There were linear correlations between LAI and SLA across genotypes at any given sampling date (example shown for 52 DAS in Fig. 9). The slope of these relationships, however, depended on N inputs. The most likely explanation is that LAI was mainly limited by resources (light and N) and the physiological cost of producing leaf area. Genotypes with high SLA achieved a high LAI because fewer resources were invested per unit area. This, in turn, enabled a higher light harvest and more rapid growth, as confirmed by preliminary modelling studies based on the rice growth model ORYZA 1 (Kropff et al. 1994). More recent studies at WARDA show a positive correlation between SLA and LAI across diverse rice cultivars.

Tradeoffs between leaf area and nitrogen content

Leaf N content is a major determinant of crop photosynthesis, and, therefore, growth rate, for a given canopy architecture. There is generally a tradeoff between leaf area and leaf N concentration if N resources are limited. Therefore, it is likely that the best compromise between weed competitiveness and yield potential is achieved if leaf area is maximised during the early stages of growth, and leaf N concentration maximised during reproductive stages.

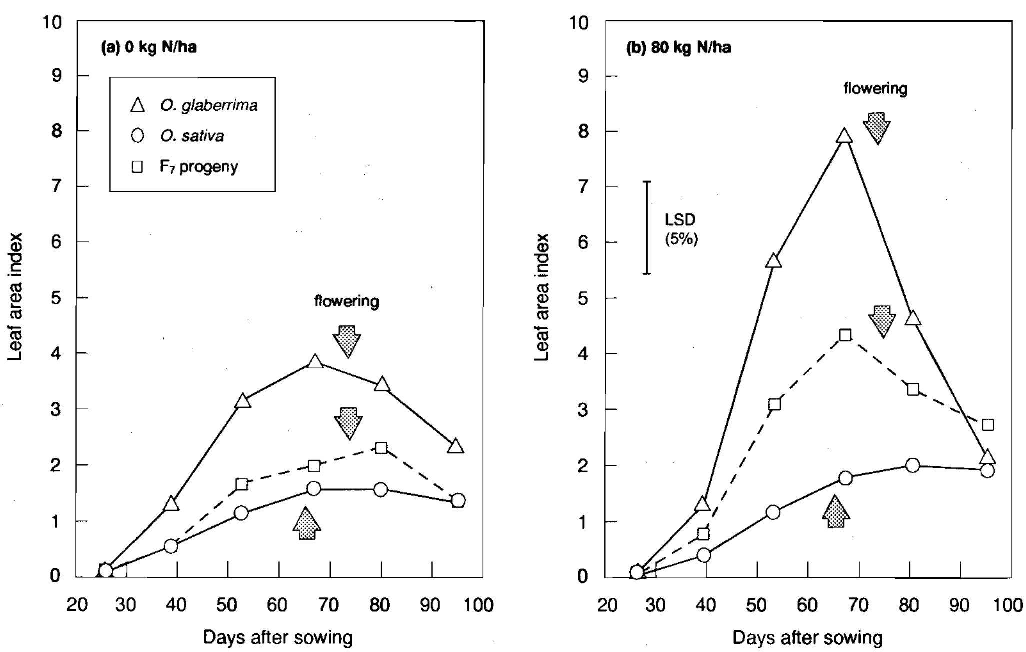

Figure 8. Time courses of leaf area index observed in an upland field fertilised with (a) 0 and (b) 80 kg N/ha for the interspecific progeny WAB450-24-3-2-P18-HB and its parents WAB56-104 (*O. sativa*) and CG14 (*O. glaberrima*). Mbe, Cote d'Ivoire, 1995 wet season.

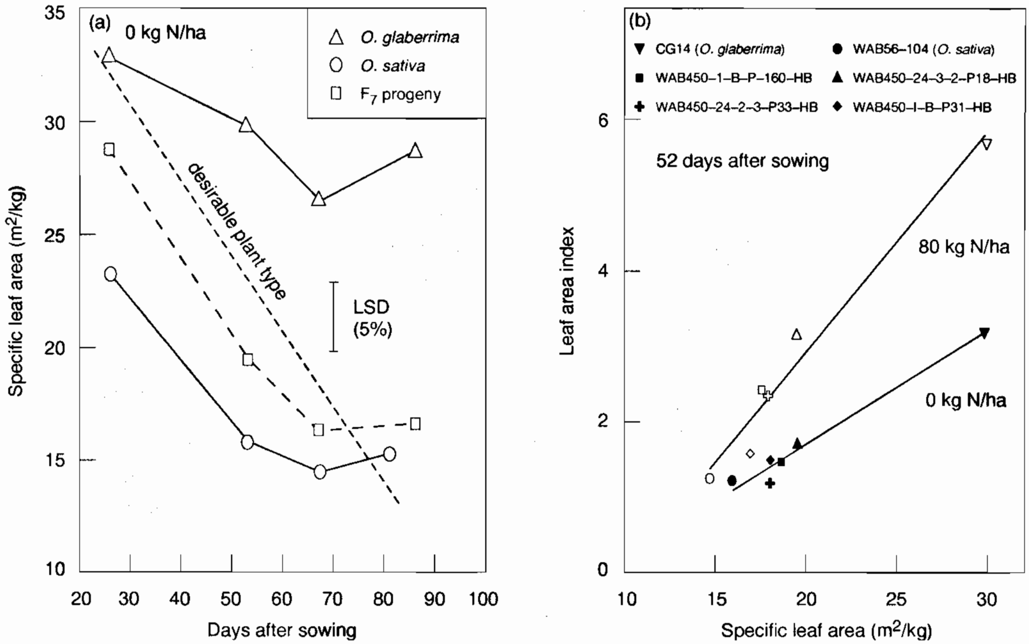

Figure 9. (a) Time courses of specific leaf area (SLA) for the interspecific progeny WAB450-24-3-2-P18-HB and its parents WAB56-104 (*O. sativa*) and CG14 (*O. glaberrima*). The broken line indicates the 'ideal' SLA for a high-yielding, weed-competitive plant type. (b) Relationship between leaf area index (LAI) and SLA across interspecific progeny and their parents, during the late vegetative stage in an upland field fertilised with 0 (solid symbols) or 80 (open symbols) kg N/ha. Mbe, Cote d'Ivoire, 1995 wet season.

All test genotypes showed the phenological decrease in dry-weight based leaf N concentration characteristic of cereals (Fig. 10: observations for the zero N treatment). The *O. glaberrima* parent, however, had a higher N concentration than the *O. sativa* parent throughout the season. The V4 progeny was intermediate during early vegetative growth, followed by a dramatic decrease in N concentration which was probably caused by dilution through rapid growth (Dingkuhn et al. 1990). In the N-fertilised treatments, the drop in N concentration was less pronounced and the interspecific progeny showed intermediate behaviour throughout the season (data not presented).

When calculated on a per-area basis, the lowest leaf N content was observed in the *O. glaberrima* parent and the highest in the *O. sativa* parent (Fig. 10). This seemingly inverted situation was due to the thinner leaves (higher SLA) of the *O. glaberrima* parent and its progenies. It follows that the generally pale appearance of *O. glaberrima* leaf canopies in this study was not caused by N deficiency (because the weight-based N concentration was high), but rather by the thin and translucent leaves. It also follows that, when genotypic variability in SLA is high, selection for dark green leaves results in the selection of plants with high N content on a per area basis, but also in thicker leaves (low SLA). This may unintentionally favour plants with poor initial vigour and groundcover, and consequently, poor weed competitiveness.

We know little about the relationship between SLA and photosynthetic rates, particularly for genotypes drawing traits from two different species. A study by Furuya et al. (1994) indicated that two *O. glaberrima* cultivars had lower photosynthetic rates than two *O. sativa* cultivars. This observation is consistent with the low per-area N content measured in the *O. glaberrima* parent, but needs further study.

Dry-matter partitioning

Time courses of dry-matter partitioning among leaves, stems and panicles were generally similar among the test genotypes and reflected the patterns usually found in rice (Dingkuhn and Kropff 1996). Details of the results have been reported by Dingkuhn et al. (1996) and are not presented here. In contrast to results obtained with high-yielding indica rice (Dingkuhn 1996), effects of N nutrition on partitioning were small in this study. Comparing genotypes, the *O. glaberrima* parent partitioned more dry matter to leaf blades than the *O. sativa* parent during early growth, with the V4 progeny being intermediate. These trends were consistent across N treatments but have not yet been ascertained statistically.

If validated, the partitioning patterns of *O. glaberrima* would indeed be of considerable general interest. High initial assimilate partitioning rates to leaves, and low rates from mid-season onwards, have been identified as being major components of a high-yielding plant type for direct-seeded irrigated conditions (Dingkuhn et al. 1991). The same pattern would improve potential yields for rice cultivars with extremely short duration, because it would enable an earlier onset of linear growth. The specificity of partitioning patterns according to stage of development would also reduce tradeoffs between weed competitiveness at early growth stages and yield potential, which is mainly determined at later stages. However, partitioning patterns are technically difficult to measure and, therefore, not readily accessible to mass screening in breeding programs.

Tillering

The *O. glaberrima* parent CG14 produced twice as many tillers as the *O. sativa* parent in the zero N treatment. The progeny had slightly fewer tillers than the *O. sativa* parent, and thus did not show intermediate behavior. Tillering of both CG14 and the progenies, however, responded more strongly to N inputs as compared to the *O. sativa* parent. There are clearly tradeoffs between tall, sturdy stems and high tiller numbers, and the present set of progenies was probably excessively sturdy and tall. We observed in various weed competition experiments that profuse and early tillering is a major varietal determinant of weed suppression. Tallness, on the other hand, primarily increases weed tolerance through 'outgrowing'. The *O. glaberrima* cultivars IG10 and CG14 are highly weed-competitive despite their moderate height.

The particular interspecific progenies characterised in this study, although combining many desirable traits from both parents, still lacked the high tillering ability of *O. glaberrima* under low inputs. Other progenies carrying this trait have, however, been identified during 1995 and will be evaluated in 1996. We will also study in more detail the role of tillering

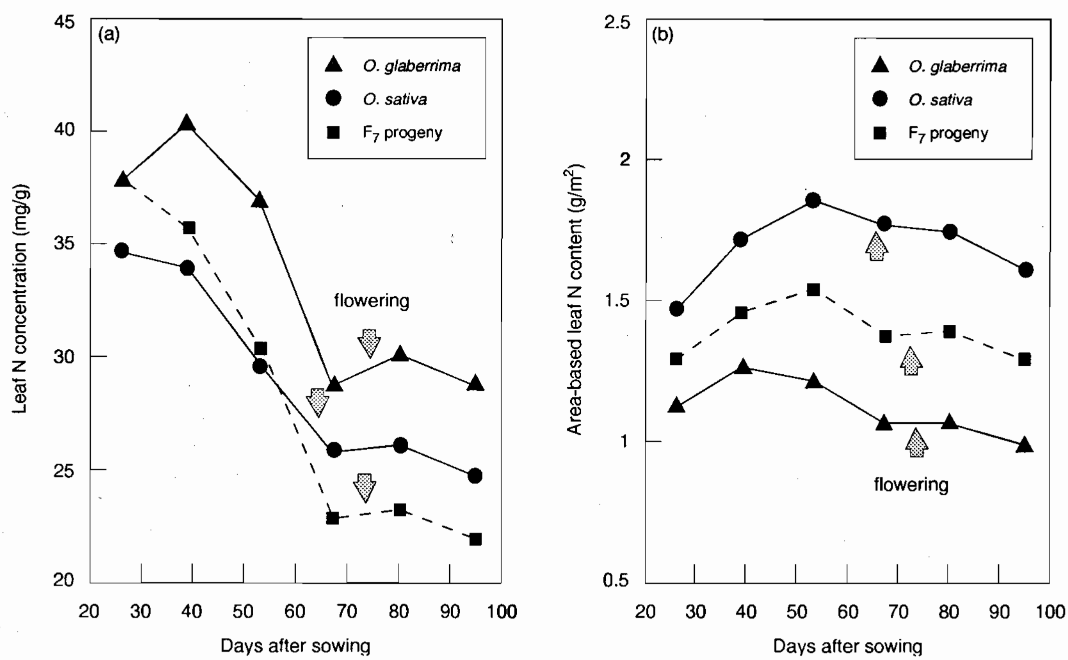

Figure 10. Time courses of (a) weight-based and (b) area-based leaf N content for the *O. glaberrima* cultivar CG14, the *O. sativa* line WAB56-104 and the interspecific hybrid V4 under zero N inputs. Mbe, Cote d'Ivoire, 1995 wet season.

in rice–weed competition, particularly the ability of cultivars to tiller at very early stages, and to rapidly fill the space created by weeding at later stages.

Conclusion and Outlook

We found strong morphophysiological evidence for trait introgressions from *O. glaberrima* into an *O. sativa* background. Most of the introgressions are of adaptive value in a resource-limited production environment, particularly in weed-prone upland fields. They include: rapid vegetative growth and leaf area development, at least in part caused by high SLA and partitioning of much assimilate to leaves; and droopy leaves during early growth stages, resulting in a high light extinction coefficient and thus a high level of light interception and groundcover. Combined with useful traits from *O. sativa*, such as large panicles, sturdy stems and erect foliage during reproductive stages, these traits are expected to improve yield stability at a high level of potential yield. More work needs to be done, however, to combine these traits with a high and early tillering ability, and to express them in low-input environments.

Weed competitiveness is not the only adaptation that new plant types can draw from *O. glaberrima*. Although the underlying mechanisms are unknown, it is already evident that the *O. glaberrima* parent in this study, CG14, is drought resistant. Many *O. glaberrima* landraces resist blast, rice yellow mottle virus and the African rice gallmidge. Studies have been initiated to characterise these traits, trace introgressions through molecular markers, and develop models to compose and test environment-specific plant-type concepts.

The new plant types, and the screening tools to be used to realise them, will emphasise the dynamic expression of morphological traits. Plants will be screened for a droopy, profuse foliage with high SLA during early growth stages, and for erect leaves with much lower SLA during reproductive stages. In other words, the new plant types will resemble *O. glaberrima* during early and *O. sativa* during later growth stages. Some new selections from the CG14 × WAB56-104 cross, evaluated during 1996, already show this phenological transition. The plants have generally vertical tillers, whose early-appearing leaves are uniformly droopy. At mid-season, the first erect leaves appear, and at flowering the majority of leaves are fully erect, resembling a 'modern' high-yielding rice cultivar. These selections are now being evaluated for their yield potential and weed competitiveness.

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Synthesis of an Effective Yield Evaluation Strategy for Wheat

P.S. Brennan*

Abstract

The wheat-growing area of Queensland is characterised by substantial variation in long-term rainfall distribution and frost probability. There is also substantial yearly variation among locations in rainfall and frost incidence and distribution. This translates into substantial genotype-by-environment interactions for wheat cultivars. There has been a long-term research program to develop a yield evaluation program that takes account of these interactions and thus facilitates the development of wheat cultivars that are well adapted to the majority of the production environments likely to be encountered. These breeding strategies were evaluated in 1993, after they had been in place for over a decade, during which period a number of cultivars were developed using this technology. The re-evaluation demonstrated that some of the regional differences identified in the initial study were no longer evident. Unlike similar material developed before the implementation of the current yield evaluation strategy, recently developed cultivars and late generation breeding lines did not perform relatively differently between regions and also performed better than the cultivars they replaced. This strongly suggests that the yield evaluation strategy has been effective in identifying cultivars that were more widely adapted.

GENOTYPE-by-environment (G×E) interactions are estimated as the sum of all the factors that contribute to changes in relative performance of cultivars for target attributes when assessed in different environments. However, for this paper a more limited definition has been applied with the focus on yield alone. This definition excludes all the effects that are, or should be, manipulated more simply than by conducting expensive yield trials, or effects for which no breeding solution is contemplated.

Attributes that should be manipulated using alternative breeding strategies include effects such as variation in phenological development patterns (particularly flowering in the case of wheat in Queensland) and disease resistance. For wheat, variation in time to flowering regularly contributes significantly to variation in ranking for yield. This is due to cultivars experiencing different environmental conditions at the same phenological developmental stage. Consequently, variation in the phenological developmental pattern can and does contribute to and inflate estimates of G×E interaction. It also tends to confound that portion of the interaction we need to understand in order to develop effective breeding strategies. Targeted manipulation of the phenological development pattern of crops to match their development with environmental resources is arguably the greatest contribution of plant physiology to maximising yield. This crop improvement strategy should not be discounted because of the strong influences of variation in flowering time on yield variation. There are alternative, less costly ways of manipulating phenological development pattern than conducting multienvironment yield trials. The way in which this is handled in the Queensland Wheat Research Institute (QWRI) wheat breeding program is to group breeding lines and cultivars for yield evaluation on the basis of similarity in their phenological development pattern. The group is planted at a time or times that will maximise yield by matching their development with limiting and critical environmental resources for wheat in Queensland, namely water, frost risk, temperature and radiation balance. When compar-

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ing the yields of different trial entries, there should be rigour in only comparing those entries that exhibit similar development patterns.

Also, to obtain strategic information, prospective cultivars and standards are planted in replicated trials in a few widely separated locations and at four different planting times to thoroughly document phenological development patterns.

Variation in disease resistance may also inflate G×E interaction estimates. In most circumstances multienvironment yield trials are not the most appropriate way to select for disease resistance. Indeed, there are usually far cheaper alternatives to determine resistance to a particular disease that is known to be important for the target region of a breeding program. It is, therefore, not appropriate to address disease resistance through multienvironment trials or to consider varietal variation in disease resistance as a legitimate component of the G×E interaction that has to be analysed in order to synthesise a relevant yield evaluation program.

Finally, there are abnormal, often traumatic, events that will inflate G×E interaction estimates that may be rare and for which no effective breeding is contemplated. Such events in my experience include severe frosts, weed growth and very high temperatures in early grain filling. Experiments where such events have been experienced should not be included for G×E interaction analysis or, at the very least, should be partitioned as specific G×E interaction components, because of their relatively low frequency and because no breeding is contemplated. Again my experience is that inclusion of such effects tends to mask systematic effects whose resolution may contribute to the synthesis of an effective yield evaluation strategy.

The contribution of the above effects to G×E interaction are graphically demonstrated by plotting the relative yield (cultivar yield expressed as a percentage of trial mean yield) of two cultivars (Cook and Gatcher) for 60 trials sampled over four years (Fig. 1). The distribution was random about the mean for each cultivar over all trials. However, many of the trials that were furthest from the mean had experienced either significant levels of disease and/or relatively rare traumatic events, for which no breeding effort is contemplated or warranted.

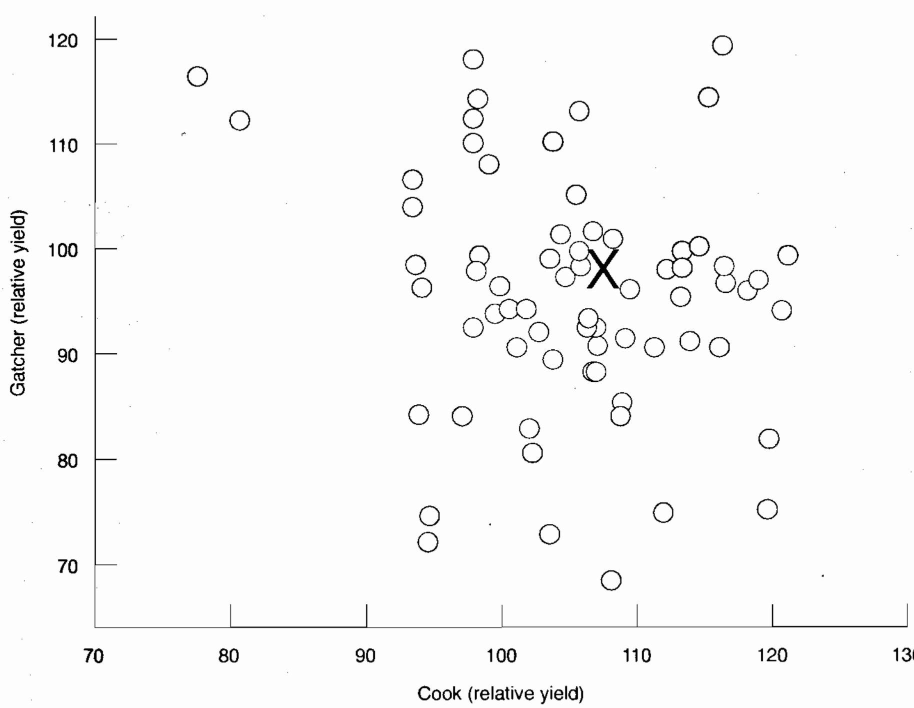

Figure 1. The relative yields of the cultivars Gatcher and Cook in each of the environments from 1975 to 1978 (× marks the centre point of the joint distribution and represents the mean for each cultivar over all test environments).

This simple type of graphical analysis has also given insight into a problem that was not well understood at that time. Most experiments where Gatcher performed particularly poorly were from one geographic area. Further examination of this trend revealed that soils in this area tended to have large populations of a root lesion nematode (*Pratylenchus thornei*) that causes significant yield reductions, and Gatcher was far more susceptible than Cook. This is an example of an unknown pathogen or disease contributing to repeatable G×E interactions for yield. A breeding strategy based on improving the resistance and tolerance of wheat cultivars to the nematode was possible (by understanding the nature of this interaction). The strategy uses a specific nematode screening nursery and does not rely on multienvironment yield trials.

G×E Interaction for Yield: An Audit for Queensland

The initial step in all our G×E work was, within the limits of the constraints listed above, to analyse the data available to determine the extent and nature of the G×E interactions within the then target region for the QWRI wheat breeding program.

Pre-release varietal evaluation in Queensland was initiated in 1972 and there had been a reasonable sampling of years and environments when this audit was commenced in the late 1970s. The material evaluated included the current industry standards, the products of local breeding programs and, occasionally, parents used in the breeding program. Consequently, the lines tested were relevant to the material that would be evaluated for release in the near future. The major concern was that only a small number of sites and lines were common in consecutive pairs of years and very few were common to three or more years. Consequently, the data were, to some extent, compromised in that there was a relatively limited sampling of years, sites and genotypes. However, by analysing consecutive pairs of years (e.g. 1972–73), a relatively large number of years was examined (Table 1). Data from 100 lines grown at the same three sites over three years (1968–70) were also available. These data were also less than ideal for an audit of G×E interaction for this region as the number of sites is far too limited and the lines far too diverse relative to the germplasm used within the breeding program. Nevertheless, three consecutive years were sampled that were not common to the years sampled in the first data set (Table 1).

Table 1. Variance component estimates for wheat multi-environment trials conducted in Queensland, 1968–73.

Variance components	1968–70	1972–73
Genotypes (σ^2_g)	1.88	0.024
Genotype × year (σ^2_{gy})	1.33	0.010
Genotype × site (σ^2_{gs})	9.67	0.023
Genotype × year × site (σ^2_{gsy})	8.66	0.031
Number		
genotypes	100	9
sites	3	14
years	3	2

Statistical analysis procedures have progressed greatly since this foundation analysis was undertaken and it is now no longer necessary to obtain balanced data sets (Patterson and Thompson 1975; DeLacy et al. 1990). Cooper and Somrith (these proceedings) give an example of strategies for dealing with unbalanced data sets in multienvironment trials.

The genotypic variation and the three interaction components were all significant in the data sets presented, and variance components were computed by equating observed and expected mean squares and solving for the components of variance, so that the actual magnitude of the confounding effect of the G×E interaction on genetic variation could be determined (Table 1; Yates and Cochran 1938).

In both data sets the variance components for genotype-by-year interaction were less than those for genotypes but were not insignificant, suggesting that testing across years was necessary to adequately sample G×E interaction effects (Table 1). The genotype-by-site interactions ranged from equal in size to the genetic component variance to five times greater, suggesting that there were predictable regional differences in G×E interaction for yield within the target region.

The genotype–year–site variance components were of approximately the same magnitude as the genotype–site interaction components. This suggested that there is a large nonpredictable element in the G×E interaction within the target region that cannot be measured through systematic sampling and cannot be emulated by testing across sites within a single year.

The first conclusion from these data is that it will not be possible to develop cultivars that would be specifically adapted to a particular region, as the genotype–year–site interactions are at least as large as the genotype–site interactions, and genotype–year interactions are also important. Consequently, the objective must be to develop cultivars that perform well across a wide range of production environments encountered within the target region. However, knowledge of regional effects in varietal evaluation may lead to an enhanced sampling of G×E interactions in a particular year due to the importance of the genotype–site interaction component. The challenge was to devise a selection strategy that would identify widely adapted cultivars. This strategy must employ testing across years as well as sites.

Systematic Responses

Linear

Finlay and Wilkinson (1963) determined that a large portion of the G×E interaction for yield of a set of barley lines evaluated in South Australia was a linear function of the mean yield of the trials. This has been examined by many authors and was considered to be an attractive option in the development of a yield evaluation strategy for wheat in Queensland. For wheat in Queensland, the portion of the total G×E interaction that could be attributed to a linear response to variation in environment mean yield varied from quite insignificant to a level where it may have some utility (Table 2). The data set with the largest linear G×E interaction included a high proportion of lines that have little relevance to the material emanating from the local wheat breeding programs and sampled a very limited number of sites. The data sets that included a high proportion of actual or potential cultivars for the target region and sampled the region more effectively exhibited limited linear G×E interactions for yield. Therefore, it was concluded that the joint linear regression approach of Finlay and Wilkinson (1963) was an inappropriate statistical method for yield evaluation in Queensland.

Table 2. Proportion of the G×E interaction that was attributable to the linear component of the response of cultivars to variation in environment mean yield in several data sets for wheat in Queensland.

Data set	Year	Number			% linear G×E
		Cultivar	Sites	Years	
QWRT[1]	1973	11	27	1	1.81
QWRT	1974	11	23	1	6.95
QWRT	1975	10	20	1	5.33
QWRT	1976	10	15	1	4.25
Adaptation trials		100	3	3	29.1

[1] Queensland wheat regional trials

Pattern analysis

The second approach used to analyse the systematic component of G×E interactions was to identify geographic areas that gave similar genotype response patterns. The first step in this approach was to apply pattern analysis methods to a data set sampling four consecutive years. In this analysis, yields of the lines were considered to be an attribute of environment. The patterns obtained were then compared to acknowledged geographic regions to determine whether there was any correspondence.

Pattern analysis was used to partition the test environments into a discrete number of groups. The actual number of groups was determined by the proportion of the total G×E interaction retained among the groups. The rule applied here was that the G×E interaction variation partitioned among the groups should be relatively high if the grouping of test environments would be informative concerning the similarity of genotype responses within the environment groups.

After some investigation of the influence of data transformation on mean yield of environments, the effect of scale was removed by expressing the yield of each line as a percentage of site mean yield. The patterns obtained using the transformed data tended to have a relationship that acknowledged geographic regions (Table 3) and achieved a partition with high G×E interaction variation retained among groups (Table 4).

The grouping analysis for the 1974 Queensland trials illustrates the type of interpretations that were obtained (Table 3). Environmental groups 37 and 38 contain most of the central Queensland sites, with 38 being predominantly from the Central Highlands and 37 from the Dawson-Callide.

Two of the three single-member groups come from areas where the root lesion nematode (*P. thornei*) is now known to occur (6 and 8) and are sites where varietal variation for resistance and tolerance is clearly expressed. Groups 33, 35 and 36 predominantly contain environments from a single geographic region.

The conclusions drawn after a consideration of the patterns for each of the four years examined were as follows.

- There was a clear and consistent distinction between central and southern Queensland.
- There was a consistent difference between the Dawson-Callide and the Central Highlands subregions within central Queensland.

Table 3. Pattern analysis for grouping test environments in the 1974 Queensland wheat trials.

Group no.	Test site	Geographic location (region/subregion)	Geographic assignment for group
38	Clermont	CQ/Central Highlands	Central Queensland (predominantly Central Highlands)
	Orion	CQ/Central Highlands	
	Theodore	CQ/Dawson-Callide	
	Goondiwindi	SQ/southwest	
37	Baralaba	CQ/Dawson-Callide	Central Queensland/Dawson-Callide (same fusion as 38)
	Biloela	CQ/Dawson-Callide	
	Capella	CQ/Central Highlands	
	Jondaryan	SQ/Darling Downs	
8	Norwin	SQ/Darling Downs	SQ/Darling Downs[1]
15	Yelarbon	SQ/southwest	SQ/southwest
35	Brigalow	CQ/Dawson-Callide	SQ/west
	Wandoan	SQ/west	
	Tara	SQ/west	
33	Fernlees	CQ/Central Highlands	SQ/Maranoa
	Hodgson	SQ/Maranoa	
	Wallumbilla	SQ/Maranoa	
36	Clifton	SQ/Darling Downs	SQ/Darling Downs
	Allora	SQ/Darling Downs	
	Chinchilla	SQ/Darling Downs	
	Jimbour	SQ/Darling Downs	
6	Pirrinuan	SQ/Darling Downs	SQ/Darling Downs[1]

[1] Nematodes suspected in this area
CQ = central Queensland; SQ = southern Queensland

Table 4. Percentage of the G×E interaction sum of squares (%G×E SS) retained among environmental groups identified by classification on yield data from multienvironment trials conducted in Queensland, 1973–76.

No. of groups	% G×E SS retained among groups			
	1973	1974	1975	1976
5	65.6	57.7	61.8	60.2
6	70.1	64.5	67.3	67.8
7	74.1	69.5	72.0	74.1
8	77.4	73.5	76.3	79.0
9	80.0	77.1	80.4	83.0
10	82.4	80.6	83.3	86.3

- There was a less consistent difference between the Darling Downs and the southwest subregions in southern Queensland.
- The sampling of the Maranoa was too limited to come to any firm conclusion. However, in the only year where there were two sites (1974), they did group together.
- The western subregion was not a homogeneous region. Sites from this area tended to be grouped with the Darling Downs or the southwest subregions depending on the year.

From this analysis of groupings of environments based on the yields of genotypes, it was hypothesised that, for yield-testing purposes, the Queensland wheat-growing region could be considered as two major regions, central and southern Queensland, with the former having two subregions. In southern Queensland there were three subregions, with the western subregion often amalgamating with other regions depending on the year.

Testing the regional adaptation hypothesis

Clearly the above zones for the Queensland wheat target region were not established beyond doubt and further verification of the regional adaptation concept was needed before applying the findings to the development of an effective multienvironment yield evaluation strategy.

This was done by comparing the ratio of the G×E interaction variance components to that for genotypes for each region and subregion to the same ratio estimated for the whole of Queensland. This step was based on data (1977–78) that were not included in the original grouping analysis. The ratio was used because it is a measure of the extent to which genetic differences are confounded by G×E interaction effects. The larger the ratio the greater the confounding effects. The hypothesis that Queensland can be partitioned into regions and subregions will be supported if the extent of confounding appears to be less in individual regions or subregions than is observed for the whole Queensland region.

The ratio, σ^2_{ge}/σ^2_g, was estimated from the Queensland wheat variety trials for two years (1977 and 1978) (Table 5). The division of Queensland into regions resulted in a lower ratio for the individual regions. The division into subregions also resulted in a reduced ratio except for the western subregion in both years and the Dawson-Callide in 1977. The finding for the west was consistent with the previous observation that this was not a relatively homogeneous region. The low ratio, and thus high level of homogeneity, for both the southwest and Central Highlands subregions suggests that these are particularly homogeneous.

Table 5. The ratio of σ^2_{ge}/σ^2_g for grain yield data from the 1977 and 1978 Queensland wheat variety trials based on the regions and subregions identified by pattern analysis of yield data from the Queensland wheat variety trials of 1973–76.

	1977	1978
Southern Queensland	0.88	0.97
Darling Downs	0.56	0.87
southwest	0.18	0.16
west	1.60	1.14
Maranoa	–	0.68
Central Queensland	0.54	1.25
Dawson-Callide	0.83	0.76
Central Highlands	0.23	0.37
Queensland	1.30	2.08

Neither of the approaches proves conclusively that the Queensland wheat-growing area comprises geographic regions that elicit relatively homogeneous response patterns from released cultivars or varieties approaching release. However, the evidence was considered strong enough for the development of a yield evaluation system based on this premise, providing that the devised system was re-evaluated in the future.

Yield evaluation strategy

The yield evaluation strategy adopted (see Brennan et al. 1981) was based on the following considerations:

- testing across years should be extended as much as possible because of the importance of genotype–year σ^2_{gy} and genotype–site–year σ^2_{gly} interactions;
- it is highly probable that the Queensland wheat-growing region is composed of geographic areas that elicit relatively homogeneous genotype responses within these regions but require different forms of adaptation;
- very large numbers of lines have to be evaluated in early generations across the major regions; and
- a relatively small number of genotypes have to be evaluated in the immediate pre-release period both across and within the regions.

The yield evaluation strategy that was implemented had three phases, which are described below.

Early generations (F_4/F_5)

The objective was to shift the population mean in the direction of high yield and wide adaptation. Few sites could be used to evaluate early generation material because of the large numbers of lines to be evaluated and availability of seed. The sites should be chosen for consistently eliciting different genotype response patterns. Consequently, above-average performance at these sites would suggest wide adaptation. Three sites were used. One site was chosen to represent central Queensland and the other two to represent the two subregions in southern Queensland that were most consistently not grouped together, the Darling Downs and the southwest. This phase was to continue for two years to sample additional years, with only those lines performing well in the first year being tested in the second year. All trials had a single replication.

Mid-generations (F_6/F_7)

The objective of this phase was to clearly identify lines that had a high probability of exhibiting good yield and wide adaptation. It was decided to evaluate this material in replicated trials located in each of the subregions. This phase was to continue for two years, with only those performing well in the first year entering the second year of testing.

Pre-release testing

The objective of this stage of testing was to confirm the high yield and wide adaptation of the lines promoted from mid-generation testing. However, it was also considered necessary to identify any lines exhibiting specific adaptation to a particular subregion. This involves multisite testing in each region and subregion for more than one year. The number of years and sites for each region was determined using the method proposed by Rasmusson and Lambert (1961) on the basis that we wanted to detect a 5% difference in yield as significant 80% of the time.

Re-Evaluation of Yield Evaluation Strategy

The yield evaluation strategy described above was put in place in the late 1970s and was re-evaluated in 1993 (Brennan et al. 1993) using yield data from the Queensland wheat variety trials conducted from 1987 to 1992.

The following were found to be consistent with previous findings:

- there was a large σ^2_{ge} relative to σ^2_g;
- a low proportion of the G×E interaction sums of squares was a linear function of the environment mean yield; and
- there was a consistent difference in the genotype response patterns between the central and southern Queensland regions.

However, the pattern analysis did not reflect the previously identified subregion groupings. If it is assumed that the sampling of test environments was adequate in both studies, and this would appear to be a sound assumption when the similarities between the two sets of conclusions are considered, then the differences in the findings of the two studies could reflect differences in the adaptation of the genotypes evaluated in the trials. The lack of groupings on the basis of subregions suggests that the lines included in the re-evaluation study do not express specific adaptation to particular subregions and are thus equally well adapted to all subregions within southern and central Queensland. Consequently, it could be concluded that the lines that have been tested more recently are exhibiting wider adaptation than those evaluated in the initial study over the period 1972–78. While this hypothesis has to be tested further, it does suggest that the yield evaluation system currently employed for wheat in Queensland has been effective in identifying cultivars with improved adaptation to a wide range of environments. Equally, there are no indications from this re-evaluation that changes to the yield evaluation system are required, as it is demonstrably achieving its objectives.

Non-Systematic Response

The non-systematic responses for yield of wheat in Queensland were found to be large, particularly the genotype–site–year interaction effects (Brennan and Byth 1979; Brennan et al. 1981). Limited testing across years may result in the identification of a population exhibiting adaptation to the particular set of years sampled, and this may not reflect the adaptation required for a successful cultivar. Consequently, there was a need to devise selection strategies that emphasised excellence in performance across years rather than in a particular year. A number of selection strategies were examined, and the following appeared to contribute to effective selection of widely adapted lines:

- selection for average relative yield across all test environments;
- inclusion of a high-input site in the trial system;
- weighting trials by the inverse of the Euclidean distance from the most frequently encountered 'environment'.

Relative Yield

Relative yield is defined here as the yield of a particular line, expressed as the percentage of the trial mean yield. This transformation removes the effects of scale from line yield variation in a particular environment. Consequently, the mean yield of a line across a range of environments has an equal contribution from all the test environments rather than a proportionally higher contribution from environments where greater magnitudes of variance are expressed. Selection for high relative yield was found to produce the highest overall yield advance and the yield advance was more consistent across the test environments (Brennan and Byth 1979). The latter suggests that lines selected were adapted to a wide range of environmental conditions. The original study was undertaken on one set of 100 lines that were not all representative of the material in breeding programs and at a limited set of sites. Consequently, there is a need to confirm these conclusions on a different, more relevant data set.

High-Input Test Location

The highest mean correlation for one environment with all others tended to be with the higher-input environments (Brennan and Byth 1979). This suggested that genotype responses for high-input environments may be more indicative of responses in different years and locations than would responses in lower-input environments. This finding was re-examined by Cooper et al. (1995) and they found that high-input environments were important for identifying lines with broad adaptation in the Queensland target production region.

Weighting by Euclidean Distance

When the relative yields of two cultivars are plotted against each other, a fairly random distribution is generally obtained. The centre point of this joint distribution is determined by the mean for each cultivar over all of the test environments. This represents the best estimate of the relative performance of these two cultivars (Fig. 1). For the Queensland wheat variety trials conducted from 1975 to 1978, distinct distributions of the environments were obtained for each year. This reflects the large genotype-by-year interactions experienced in this region (Fig. 2). However, in each year there were environments where the relative yields for the two cultivars were similar to the yield for the mean of the two cultivars over all trials. This suggests that these environments may be better predictors of the long-term relative performance of these two cultivars. Consequently, a system that recognises and emphasises test environments that better predict relative yield of wheat lines and de-emphasises those environments that do not would be expected to enhance the effectiveness and efficiency of a multienvironment yield-testing strategy.

The first step in implementing this selection strategy was to determine a procedure for categorising environments. This was achieved by identifying genotypes that tended not be grouped together during pattern analysis, when yield measured in environments was used as the attributes of the genotypes. The assumption made here is that, by not grouping together, these genotypes tend to measure different features of the wheat-growing environment. Four such genotypes were identified and used to locate the test environments in a four-dimensional space. Genotypes selected on this basis have been referred to as probe or indicator genotypes (Cooper et al. 1990; Eisemann et al. 1990). We are working on developing

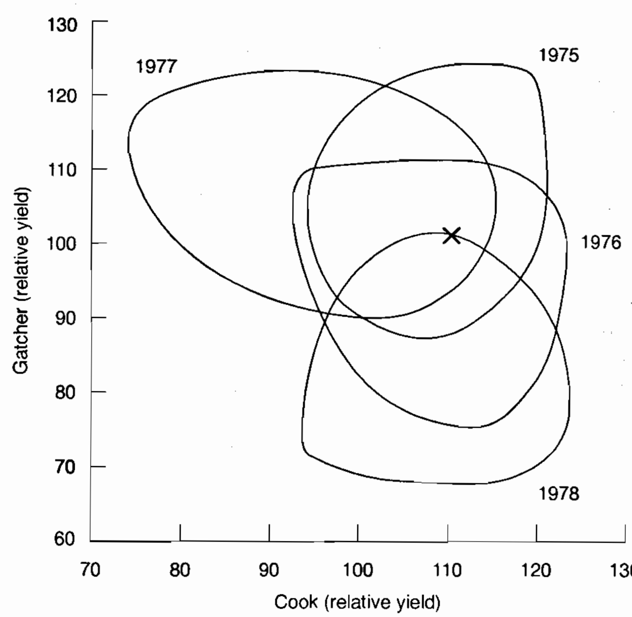

Figure 2. Distribution of relative performance of Cook and Gatcher for each year, 1975–78 (× marks the centre point of the joint distributions; see Figure 1).

an appropriate set of probe genotypes for the types of environments encountered in Queensland.

By definition, the point specified by plotting the means over all test environments for each probe is the best prediction of the relative performance of the probe genotypes. The distance from this point to each environment, which can be estimated as a Euclidean distance, is a measure of predictive value of each environment. The smaller the Euclidean distance the better the environment will be as a predictor of expected relative cultivar performance in the target population of environments.

This hypothesis was tested by deriving weighted means for each genotype after weighting by the inverse of the square of the Euclidean distance of each environment from the point specified by the overall mean of the probe genotypes. The weighted means were then compared by correlating across years (Table 6). In two of the three pairs of years there was a substantial increase in the correlations of relative genotype performance with weighting. This suggests that the value of one year's data as a predictor of the performance in a second year was enhanced by the weighting procedure. This did not occur for the 1979–81 comparison, where there was already a good agreement between the years before weighting, indicating a low genotype-by-year interaction for this combination of years (Brennan and Sheppard 1985). These findings were based on a limited set of probe genotypes and this hypothesis requires testing with different data sets. Testing of this hypothesis is currently under way.

Table 6. Genotypic correlations with and without weighting cultivar yield by the inverse of squared Euclidean distance (1/SED) for four cultivars common to the four years of the Queensland wheat variety trials, 1977–81.

Weighting	Coefficient of determination		
	1977–78	1978–79	1979–81
None	0.002	0.116	0.524
1/SED	0.375	0.381*	0.555*

* = $P < 0.05$

Conclusions

There is a range of strategies that can enhance the predictive value of the data generated in a yield evaluation program. However, none will compensate for actually testing across years and locations in a manner that effectively samples the target production environments. The multienvironment testing program described here has been implemented in the Queensland wheat breeding program, and a line may have been evaluated in up to 90 environments spanning seven years using a structured evaluation strategy before it is released for commercial production.

The undeniable measure of the success of this breeding program is that, although the Queensland wheat-growing environment is very different from that in most other parts of Australia (Brennan and Shepherd 1985; Brennan et al. 1986), cultivars emanating from this program are grown in significant areas in all Australian states. Also, in Australia the market share of Queensland-bred cultivars is second only to that of South Australia, which has a very similar growing environment to that of southern New South Wales, Victoria and Western Australia.

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Seedling Screening in Dry Seasons for Drought Resistance in Rice

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Abstract

A method for screening seedlings for drought resistance was examined in 10 dry-season experiments in Thailand. It was based on visual estimation of leaf death (drought score) during the seedling stage after irrigation was withheld. In only two experiments was significant genotypic variation observed before plants were 70 days old. There was however no association between drought score observed during the dry season and grain yield of the genotype obtained in the wet-season experiments where late-season drought developed. Several problems associated with the seedling screening in the dry season were identified: lack of consistent stress development during the dry season, site variability and associated variability in drought score, and difficulty in accurately estimating drought score. These problems would need to be minimised before consistent genotypic variation in drought score could be observed.

DROUGHT is a major constraint for large areas of rainfed lowland rice in Thailand. Its occurrence is, however, erratic because of yearly variation in rainfall; hence, screening genotypes during a wet season is not reliable. A screening technique used commonly for rice lines is visual drought score (standard evaluation system: IRRI 1980), in which genotypes are subjected to water stress at seedling stages in the dry season and plant response is scored on the amount of leaf death (De Datta et al. 1988). Ingram et al. (1990) compared canopy temperature based stress indices, grain yield, uprooting force and visual scoring of stressed plants, and noted that visual scoring was the best method of screening for drought resistance where a controlled water deficit could be imposed. However, drought score determined at the seedling stage is not always a good indicator of grain yield under drought. For example, Puckridge and O'Toole (1981) found no relationship between the two, and suggested that in the field, visual scoring was screening mainly for root development, which does not necessarily result in better grain production. This paper reports the results of 10 experiments in Thailand which examined the reliability of the dry-season seedling screening technique for drought resistance in rainfed lowland rice.

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Experimental Procedure

Ten experiments were conducted in the 1993–1995 dry seasons (December–April) at Khon Kaen, Phitsanulok, Sanpatong, Surin and Ubon Ratchathani, Thailand. In most experiments 35 common lines/cultivars were grown in plots of 1.5×2.5 m with four replications. In some experiments seedlings were transplanted when they were around four weeks old, while in others direct seeding was used. Hill spacing was 25×25 cm. The field was flood irrigated for 2–4 weeks before water was drained. Adequate fertiliser was applied. When water stress developed, the amount of leaf death was scored about once a week, using a scale of 0–9 (drought score) according to the standard evaluation system developed by IRRI (1980). Score 0 is no death of leaf part, whereas score 9 indicates apparent plant death.

Problems with the Technique

Expected genotypic variation in drought score of seedlings was not obtained in most experiments. Several problems were recognised during the experiments at different locations.

Large plot-to-plot variation in drought score

In several experiments no significant genotypic variation in drought score was obtained due to heterogeneity of the site. This may be caused by non-uniformity of the soil within a paddy, for example, the soil surface not being levelled, resulting in unevenness in establishment under direct seeding with flood irrigation. The problem was aggravated by poor growth in the dry season, caused by low temperature. It is essential to choose a uniform site for this type of experiment. An experiment occupying a large area should be avoided if this increases site variability. Plot size may be reduced to a minimum of about 2 m × 2 m.

Lack of stress development at early growth stages

In many experiments stress did not develop during seedling stages. When seedlings were transplanted, they were already about six weeks old by the time water was drained from the main paddy. When experiments were commenced in the early part of the dry season in December or January, low temperature slowed down the growth, and this appeared to have contributed to the lack of stress development during the seedling stage. In some experiments there was rain in March and April, and this further delayed stress development. Once the panicle starts to develop, this may affect the development of drought symptoms. Genotypes differ greatly at the time of panicle initiation in the dry season, and the experiment should be completed in 60 days or so after seeding.

It is important to choose a site which has a high temperature and low probability of rainfall during the seedling growth in the dry season. Early commencement of the experiment is likely to encounter low temperatures (for example, at Khon Kaen the mean temperature is about 22°C in December and 24°C in January) whereas late seeding will result in a higher likelihood of seedlings being exposed to rainfall. Thus there may be only a short period suitable for conducting the dry-season screening. Direct seeding should be used with necessary caution for good establishment and weed control. Sprinkler irrigation is preferable to flood irrigation for good establishment with direct seeding. While glasshouse screening will ensure drought development at the seedling stage, experimental errors appear to be too large for routine screening exercises (Henderson et al. 1995).

Difficulty in estimating drought score

Drought score is based on visual estimation of leaf death. When different observers were given the same samples, they differed often in their score by 1 or 2. Estimation of drought score was more difficult in older plants where natural leaf death took place. Diseases may also cause similar leaf death symptoms (e.g. leaf blast). It is important to standardise the scoring system through training and use of photographs of different drought damage of leaves so that different observers give the same scores as often as possible, particularly when more than one site is involved in screening exercises. Usefulness of such training sessions for improvement of visual estimation of leaf damage by insects was documented by Fielding (1992).

Genotypic Differences in Drought Score

In most of the 10 dry-season experiments conducted in Thailand, drought did not develop during early stages of growth. In the experiment at Sanpatong in 1994, however, moderate drought developed by 60 days after seeding (26 January). Change in mean drought score of 35 genotypes is shown in Figure 1. Before 145 mm of rainfall on 27–29 March, mean drought score exceeded 4. Significant genotypic variation was observed just prior to the rainfall and results obtained on 25 March are shown in Table 1. It is noted that popular cultivars in rainfed lowland rice in Thailand (KDML105, RD6 and NSG19) did not have low drought scores. Significant genotypic variation occurred later in April, but there was no correlation in drought score between the two dates (25 March and 18 April) when mean drought scores were similar.

In two other experiments (Khon Kaen 1993 and 1994) moderate drought also developed before 70 days after seeding (data not shown). In Khon Kaen 1994, however, there was no significant genotypic variation in drought score on any measurement occasion. In the Khon Kaen 1993 experiment, on the other hand, there was significant genotypic variation throughout the period, with a mean drought score of 4.1 at about 70 days after seeding. Genotypic variation at the time of measurement was compared with that at 25 March in the Sanpatong 1994 experiment where the mean drought score was similar. Of the 35 cultivars used in each experiment, only 12 were common to both experiments. The analysis indicates a strong genotypic effect ($P < 0.01$), but no significant interaction effect of genotype and experiment.

Table 1. Drought score of rice lines/cultivars determined on 25 March 1994, Sanpatong, Northern Thailand. Note that five cultivars (NSG19, KDML105, Chiangsaen, RD23, RD6) were repeated and appear twice in this table.

Drought score	Lines/cultivars
2.7 a	IR43506-UBN-520-2-1-1
3.3 ab	E-Pad
3.7 abc	KPM148, Khao Strok
4.0 bcd	RD6, NSG19, LPT123, IR20, Lemont, KDML105, RD23, Chiangsaen, Leum Dern, Leuang Dawk Koon, Daeng Noi, Lum Narai, Taw Chaw Daw, Leuang Bun-ma, IR43450-SKN-506-2-2-1-1, IR52532-SKN-23-B-1-2, IR57546-PMI-1-B-2-2, IR57514-PMI-5-B-1-2, BKNBR82027-NSR-8-1, IR43049-CPA-510-3-3-1-1, IR49766-KKN-54-B-B-6-1, RD6
4.3 bcde	Tah Tae, Chabah Sarahn, Puang Sawan
4.7 cde	KDML105, RD10, RD23, NSG19, Khao Luang, Jumpah Tawng
5.0 de	Khao Yai, Leuang Samer
5.3 e	Chiangsaen, E-Nawn, IR43062-PMI-B-15-1-2-2

Note: Lines/cultivars with the same letters are not significantly different ($P < 0.05$).

Genotypic differences in drought score obtained at Sanpatong in 1994 were examined in relation to those in grain yield of wet-season experiments where drought developed, and grain yields of the same 35 lines/cultivars were recorded. Drought developed in a number of wet-season experiments conducted in 1992–1995 in Thailand and Lao People's Democratic Republic, but genotypic variation was mostly related to phenological differences among the genotypes (Satit Rajatasereekul et al., this volume). In two experiments (Sakon Nakhon 1992, Vientiane 1993) where late-season drought developed, there was significant variation in grain yield among cultivars that flowered about the same time. There was however no association between drought score obtained at Sanpatong and grain yield obtained in these experiments. One possible reason for the lack of association between the two is change in genotype ranking of drought score during growth (Henderson et al. 1993), and those cultivars with low drought score during the vegetative stage may not show similar resistance when drought develops late in the season, as occurred in the Sakon Nakhon and Vientiane experiments. Other experiments of ours show that development of drought score during the vegetative stage is affected by plant size, and cultivars with large plant size tend to show a large drought score during seedling stage drought, but the cultivar differences in drought score may be small at later stages when all cultivars would have covered the ground completely.

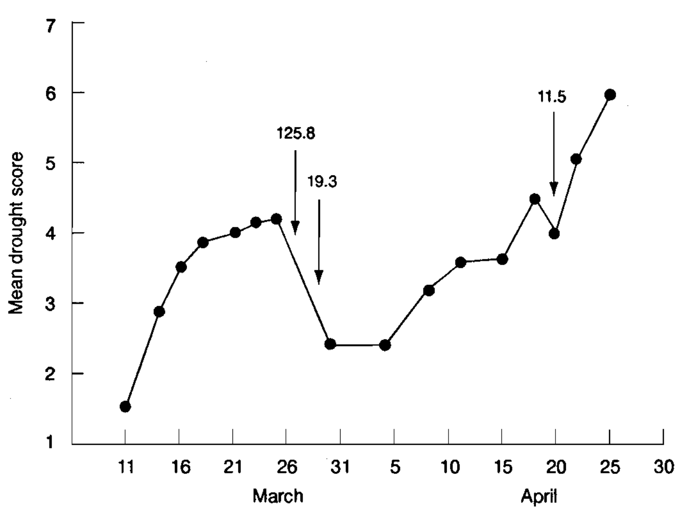

Figure 1. Mean drought score determined at various times at Sanpatong, 1994. Rice was sown on 26 January. Arrow and number indicate time and amount (mm) of rainfall.

Conclusion

While this study could not conclude whether or not selection of lines using seedling drought score in the dry season is useful for development of drought-resistant cultivars, it demonstrated a difficulty with reliability of the technique, and hence the importance of developing a sound protocol for dry-season screening. The choice of site, time of planting and cultural practice for direct seeding needs to be established before the validity of the screening method can be judged.

Acknowledgment

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Root Traits to Increase Drought Resistance in Rainfed Lowland Rice

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Abstract

Drought may cause a large reduction in the yield of rainfed lowland rice. A well-developed root system in the subsoil is a drought-resistant trait in upland conditions, and is also expected to confer advantages under rainfed lowland conditions. The root system of rice was studied in several rainfed lowland experiments at the Ubon Rice Research Centre. Roots of rainfed lowland rice were shallow, and this was associated with a hardpan in the soil that was developed as a result of puddling. Examination of rice root systems was difficult due to large spatial variability. This was, however, partially overcome by the use of steel tubes for soil-root sampling of a large number of samples in a short time period. Genotypes showed differences in root-mass density and root-length density at 10–30 cm depths. While those differences were rather small, they were associated with genotypic differences in water extraction from the subsoil, and also with visual estimation of retention of green leaves during a dry period.

DROUGHT is common in rainfed lowland rice-growing areas and is a major constraint for rice production in Northeastern Thailand. The rice crop may experience intermittent or prolonged drought during early growth stages, which often reduces crop growth and subsequent grain yield. If rainfed lowland rice starts to flower after the disappearance of standing water, towards the end of the wet season, the stored soil water in the root zone is often not sufficient to complete grain filling, causing yield reduction (Jearakongman et al. 1995). Rapid loss of standing water due to the high percolation rates in the coarse-textured soils of Northeastern Thailand increases the probability of such yield-reducing droughts occurring.

A number of physiological and morphological characteristics that could minimise the effect of drought in rice have been studied. A good root system, i.e. dense, thick and deep roots, is one of the major drought-resistant characteristics for the upland rice ecosystem (O'Toole 1982). A deep root system would be advantageous in extracting more water from deeper soil layers. Under upland conditions, Lilley and Fukai (1994), and other researchers, have shown that there are genotypic differences in root depth and resultant water extraction from the soil. It is, however, not clear whether or not rice genotypes can express root traits that are related to drought resistance in the rainfed lowland ecosystem (Fukai and Cooper 1995). Root systems in the lowland ecosystem are shallow because soil environments are unfavourable for root growth. The soil environment changes from aerobic in unflooded conditions to anaerobic in conditions with standing water, which may limit oxygen availability to roots in deeper soil layers. The hardpan that develops with puddling of paddies may also limit root growth. Furthermore, low soil fertility and acidity, which are common in Northeastern Thailand (Table 1), could reduce root growth. The restriction of root growth at depth would act to reduce the expression of genotypic variation in root length unless the genotypes also possessed adaptations to the unfavourable subsoil environment.

This paper reports the results of a root study under rainfed lowland conditions at the Ubon Rice Research Centre, Northeastern Thailand.

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Table 1. Properties of loamy sand soil (with low fertility and low pH) from a farmer's field near the Ubon Rice Research Centre, Northeastern Thailand.

Properties	Soil depth (cm)	
	0–10	10–30
pH	4.8	5.1
Organic matter (%)	0.27	0.30
Total N	0.01	0.02
Available P (ppm)	9	7
Exchangeable K (ppm)	10	10
Soil texture	Loamy sand	Loamy sand
- Sand (%)	84	84
- Silt (%)	11	12
- Clay (%)	5	4

Horizontal Variation of Root Systems

Rainfed lowland rice is commonly transplanted with a hill spacing of 15–30 cm, and this practice contributes to horizontal variation in root-length density (RLD cm/cm^3) and makes root studies rather difficult. A common practice in recovering roots is to use a metal monolith sampler with a dimension of 20 × 20 × 50 cm (depth) to cover the whole space between adjacent hills. Using this sampler, RLD near the soil surface (0–20 cm soil depth) often has a small coefficient of variation and genotypic differences can be easily detected. However, in the deeper soil layers, the experimental error variations become larger relative to the genotypic differences and treatment differences are often not detected, as shown in Table 2.

A wet-season experiment was conducted to determine the best sampling method to detect significant genotypic treatment effects on root growth. Two cultivars, Mahsuri and IR62266-42-6-2, were grown with 20 × 20 cm hill spacing in a randomised block design with three replications. Soil samples were taken at around flowering time by the metal monolith sampler described above, and also by a 38-mm diameter steel tube. In the latter, soil cores were taken at two positions, immediately adjacent to hills and 10 cm away from hills (midway). Results indicated that spatial variation is important only in the top 5 cm soil depth, where soil cores taken adjacent to hills had four times the RLD of those taken at the midway position (Fig. 1). The metal monolith sampler results were closer to those obtained from sampling the midway position than those from the adjacent position. There was no significant position effect below 10 cm,

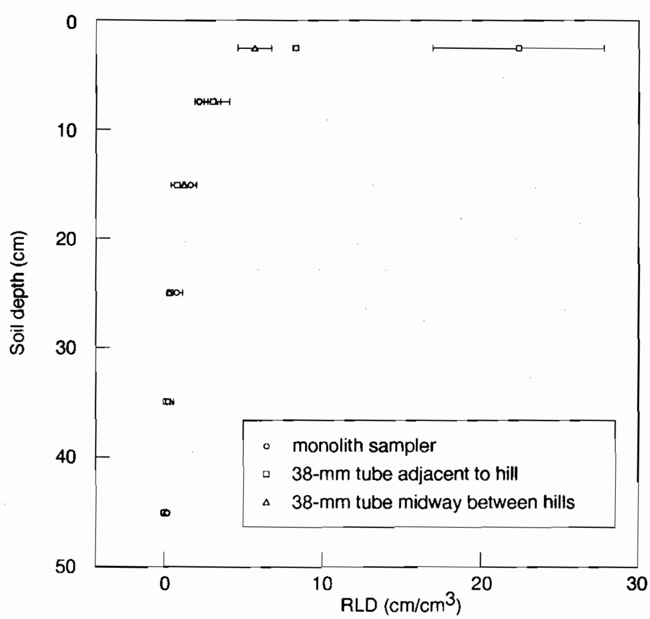

Figure 1. Mean root-length density (RLD) of two rice cultivars grown in loamy sand soil under rainfed lowland conditions; root samples were taken using a 20 × 20 × 50 cm metal monolith sampler (circle symbol) centred over a hill, and a 38-mm metal tube sampled immediately adjacent to a hill (square symbol) and midway between hills (triangular symbol).

and samples could be taken with the steel tube method at any position across hills. The steel tube method was more than 10-times faster than the monolith method in root sample collection and was suitable for the sandy soil used in the experiment. The tube method may not work as effectively in soils with a higher clay content.

Table 2. Analysis of variance[1] for root-length density at 0–50 cm soil depth of a typical rainfed lowland rice experiment at Ubon Rice Research Centre.

Soil sample[2]	DF	Sum of squares	Mean square	F-value	Probability
0–10 cm soil depth					
Blocks	4	2.0	0.512		
Cultivar	5	20.6	4.129	7.6	0.000
Error mean square	20	10.8	0.543		
Total	29	33.5			
CV (%)	13.7				
10–20 cm soil depth					
Blocks	4	1.32	0.331		
Cultivar	5	2.06	0.413	2.78	0.046
Error mean square	20	2.97	0.148		
Total	29	6.36			
CV (%)	27.0				
20–30 cm soil depth					
Blocks	4	0.172	4.31E-02		
Cultivar	5	0.314	6.29E-02	3.44	0.021
Error mean square	20	0.365	1.83E-02		
Total	29	0.852			
CV (%)	52.8				
30–40 cm soil depth					
Blocks	4	1.49E-01	1.37E-02		
Cultivar	5	2.03E-01	1.41E-02	1.04	0.422
Error mean square	20	7.80E-01	1.39E-02		
Total	29	0.113			
CV (%)	75.7				
40–50 cm soil depth					
Blocks	4	3.78E-01	3.95E-04		
Cultivar	5	9.01E-01	3.18E-03	1.4	0.267
Error mean square	20	2.58E-01	2.13E-03		
Total	29	3.86E-01			
CV (%)	38.5				

[1] Based on 6 cultivars, 5 replications and 4 samples per plot
[2] Soil samples were taken using a metal monolith sampler (20 × 20 × 50 cm)
DF = degrees of freedom; CV = coefficient of variation

Table 3. Profiles of root-length density (cm/cm^3) of rice grown under lowland conditions.

Authors	Plant age	Soil type	Soil depth (cm)				
			0–10	10–20	20–30	30–40	40–50
Hasegawa et al. (1985) (calculated from Table 2)	Averages of 30, 42, 65 and 92 days old	–	11.9 (79)	1.3 (8)	0.9 (6)	0.9 (6)	0.2 (1.3)
Sharma et al. (1987)	Flowering	Clay loam	4.8 (74)	1.0 (16)	0.5 (8)	0.15 (2)	–
Mambani et al. (1989)	Flowering	Maahas clay	10.7 (92)	0.7 (6)	0.1 (1)	0.1 (1)	–
Nabheerong (1993) (calculated from Fig. 5)	Flowering	Clay	5.4 (69)	1.5 (19)	0.5 (6)	0.4 (5)	–
Pantuwan et al. (1996) (mean of 6 cultivars)	Flowering	Loamy sand	5.4 (75)	1.4 (20)	0.26 (4)	0.08 (1.2)	0.03 (0.4)
Pantuwan (unpublished) (mean of 6 cultivars)	Flowering	Clay	5.5 (81)	0.84 (12)	0.32 (5)	0.11 (1.6)	0.01 (0.2)
		Loamy sand	8.6 (72)	2.26 (19)	0.86 (7)	0.14 (1.2)	0.02 (0.2)
Samson et al. (1995) (mean of 8 cultivars)	Panicle initiation	Loamy sand	4.1 (94)	0.18 (4)	0.07 (1.6)	0.02 (0.5)	–

Note: Values shown in parentheses are the root length in each layer, expressed as a percentage of total root length in the whole profile.

Root Profiles

It is well known that rice grown in lowland paddies has a shallow root system. Results of several lowland experiments conducted by different authors indicate that 69–94% of roots are located in the top 10 cm of the soil and hardly any roots are found below 30 cm (Table 3). The hardpan generally develops between 10 and 30 cm soil depth in rainfed paddies, and soil penetration resistance peaks at about 20–30 cm, as was the case for the soil used for the experiments at the Ubon Rice Research Centre (Fig. 2). The hardpan is considered to be a major constraint to root penetration into the subsoil (Hasegawa et al. 1985), though it would be useful for retention of standing water in rainfed lowland paddies.

We conducted a rainfed lowland experiment in the wet season of 1993 to investigate the effect of soil strength on root growth using three treatments with six rice cultivars — RD15, Nam Sagui 19, Khao Dawk Mali 105 (KDML105), RD9, IR46 and Mahsuri — with three replications. Soils were of loamy sand texture. In one treatment (control) the soil was ploughed to a depth of 15 cm, as commonly practiced in Northeastern Thailand. For the second treatment (low soil strength) the soil was mixed with rice-hull charcoal at the rate of $600\ m^3/ha$ and ploughed to a depth of 30 cm. In the other treatment (high soil strength) a 12-tonne road roller was passed over the soil 10 times to compact it and then the soil was ploughed only to a depth of 5 cm.

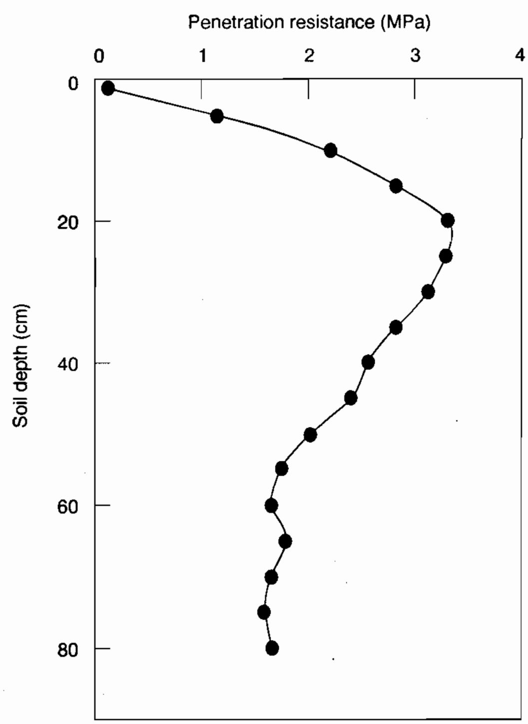

Figure 2. Penetration resistance of soil used for experiments at Ubon Rice Research Centre, Northeastern Thailand; data show development of hardpan in the subsoil.

Different plough depths in various treatments were achieved by using a pair of discs attached to a two-wheel tractor. Roots of all cultivars were sampled at flowering, using the monolith method. Results showed that the loosely packed soil in the low soil strength treatment had about 80% higher RLD at 40–50 cm soil depth than the control soil (Fig. 3). The high strength soil treatment reduced RLD at below 20 cm. In another experiment at Ubon Rice Research Centre, Wade et al. (1996) also found a large reduction in and variation of RLDs below 20 cm soil depth for some cultivars in a subsoil compaction treatment compared with an irrigation treatment. These results suggest that the shallow root system in the lowland system is associated with high soil strength in the subsoil, although other factors may be involved in the shallowness of the root system. Subsoil compaction to reduce percolation loss from the loamy sand soils would result in a reduced root length and possibly reduced soil water available to the plants once standing water disappears.

Genotypic Variation in Root Systems

Root system characteristics, e.g. root mass/length density, root thickness and root penetration resistance and depth, have been shown to be associated with drought avoidance of cultivars in upland conditions (O'Toole and Chang 1979; Yoshida and Hasegawa 1982; Ekanayake et al. 1985). Upland rice cultivars

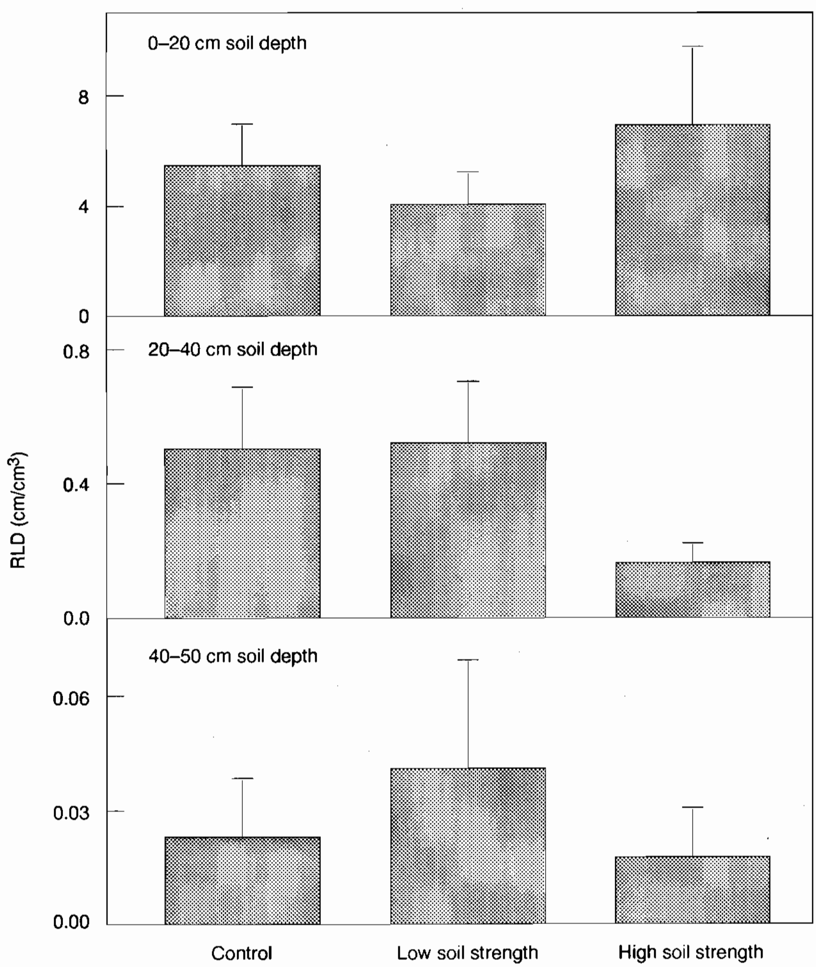

Figure 3. Root-length density (RLD) in response to soil strength: *control* — ploughed to 15 cm depth; *low soil strength* — rice-hull charcoal 600 m^3/ha and ploughed to 30 cm depth; *high soil strength* — 10 passes with 12-tonne road roller and ploughed to 5 cm depth (data were average of six cultivars).

generally have deeper root systems than lowland cultivars (Chang and Vergara 1975; Puckridge and O'Toole 1981). It is, however, difficult to demonstrate significant genotypic variation for these root characteristics in rainfed lowland conditions, which is at least partly due to the large sampling variation encountered (Wade et al. 1996). When drought occurs, a cultivar with a deep root system is expected to take up more water from the subsoil, and this should delay leaf drying.

Several rainfed lowland experiments have been conducted recently at the Ubon Centre to demonstrate genotypic variation in root mass density (RMD, mg/cm^3) and RLD and its effect on drought resistance. In all these experiments genotypes were compared in a randomised block design with four replications. In one experiment, RMD at flowering stage was found to be significantly different among six cultivars in both the top (0–20 cm) and bottom (20–50 cm) layers (Fig. 4). In a 1995 dry-season experiment where irrigation was applied until the booting stage, and then water was drained, there was significant genotypic variation in RLD at flowering in different layers down to 30 cm (Fig. 5). In the 20–30 cm layer, IR42 had the highest

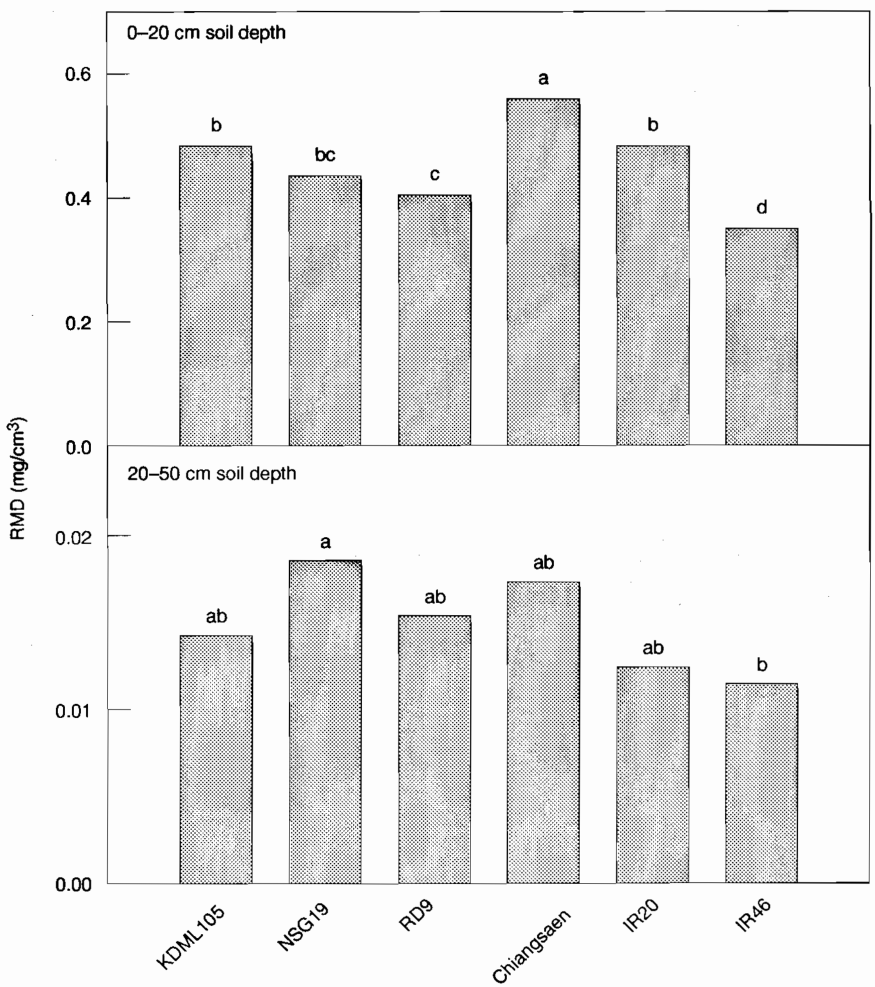

Figure 4. Root-mass density (RMD) in the topsoil (0–20 cm) and subsoil (20–50 cm) layers for six rice cultivars grown in a loamy sand soil under rainfed lowland conditions. RMD values shown with a common letter are not significantly different at $P < 0.05$.

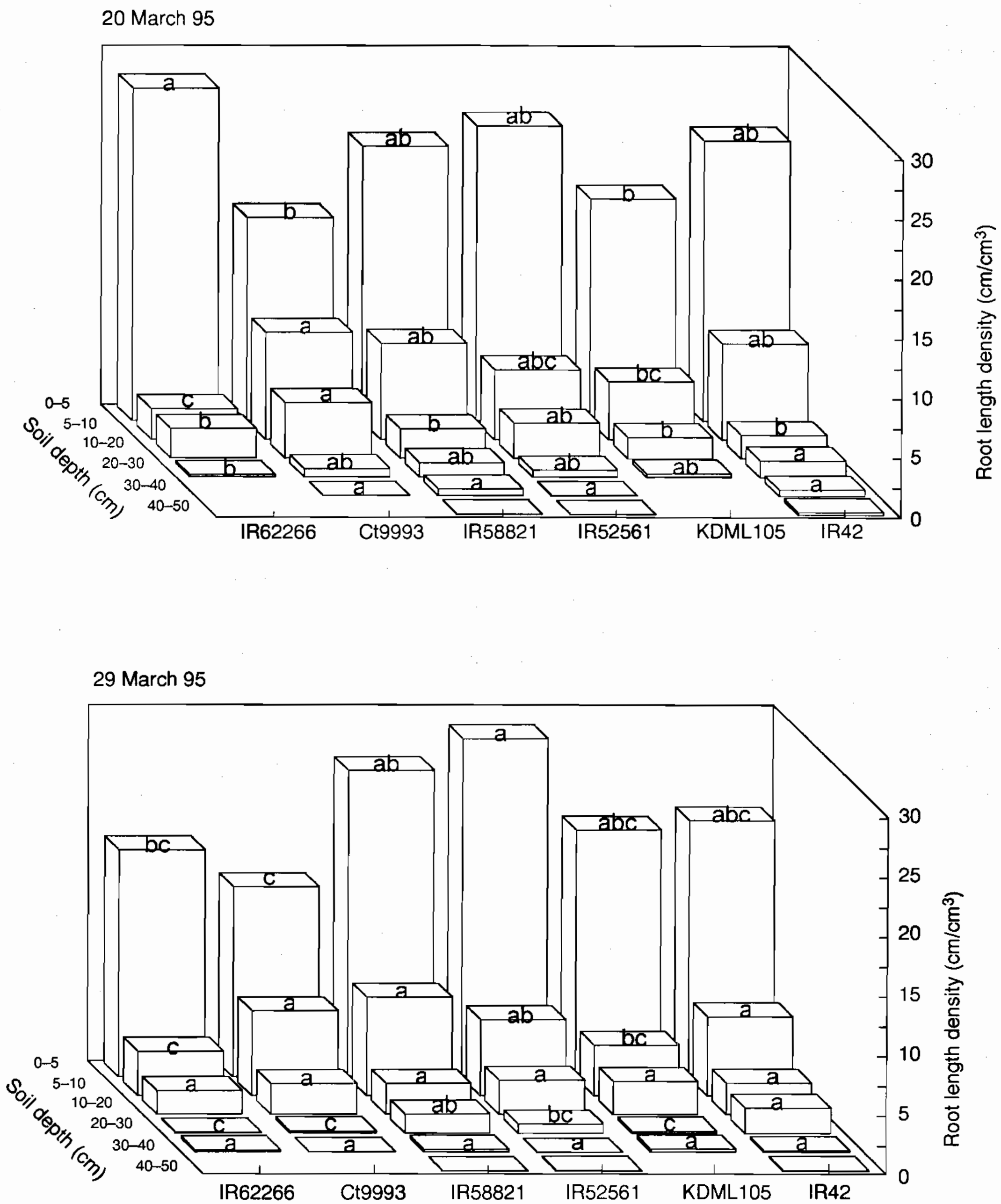

Figure 5. Root-length density (RLD) at flowering for six rice cultivars grown in a loamy sand soil under irrigated conditions until booting stage when water was drained (measurements at two dates shown). RLD values of different cultivars shown with a common letter are not significantly different at $P < 0.05$.

RLD on both measurement occasions. The results from these two experiments (Figs 4 and 5) indicate that the popular rainfed lowland cultivar KDML105 does not have a large root system at depth. It was also noted in these experiments that the cultivar with the highest root mass/length in the uppermost soil layer did not have the highest root mass/length in the lower layers — see Chiangsaen in the first experiment (Fig. 4), and IR62266 on 20 March 1995 in the second experiment (Fig. 5).

Water Extraction by Roots

Under upland conditions, water extraction has been shown to be associated with RLD (Lilley and Fukai 1994) and root depth (Puckridge and O'Toole 1981). Because the root system under lowland conditions is shallow, water extraction by roots in the subsoil is small. It is also difficult to estimate water extraction accurately in lowland conditions because of the complicating effects of deep drainage and lateral movement of water in the subsoil. In the 1995 dry season experiment where variation in RLD was found (Fig. 5), as mentioned above, water extraction below 10 cm during a 10-day drying period tended to be highest in IR42 and IR58821, although a significant effect was found only in the 40–50 cm soil depth (Table 4). These cultivars tended to have high RLD below 20 cm, and KDML105, which extracted the smallest amount of water, tended to have low RLD at depth. This result implies that a small genotypic difference in root system in the subsoil layers can cause differences in uptake of water, whereas variation in root density near the soil surface may not affect water uptake because the top layer of soil is often very dry and the root system is sufficiently large for all cultivars in this soil layer.

Roots and Drought Resistance

Drought scores that quantify leaf drying (standard evaluation system, IRRI 1980) have been used to screen for drought resistance under field conditions in recent years at the Ubon Centre. Doubled-haploid lines of a cross between CT9993-5-10-1-M and IR62266-42-6-2 were grown in the 1996 dry season to examine the relationship between root mass and drought resistance of eight contrasting rice lines. These lines showed significant differences for drought score. Four susceptible and four resistant lines were selected, and their root mass determined at about 60 days after sowing. Six levels of soil layers — 0–5, 5–10, 10–20, 20–30, 30–40 and 40–50 cm from the soil surface—were sampled using a 38-mm metal tube to determine RMD. The group of drought-resistant lines consistently produced greater RMD than the drought-susceptible lines in all soil layers, and this was detected as significant in three of the layers (Fig. 6). These results suggest that lines with more root weight per unit soil volume, particularly in the 10–30 cm soil layer, can extract more water and maintain green leaves for a longer period.

Table 4. Water extraction (mm) during a 10-day drying period at flowering for six rice cultivars grown in a loamy sand soil.

Cultivars	Soil depth (cm)						Total
	0–5	5–10	10–20	20–30	30–40	40–50	
IR62266	2.3	1.3	2.8	2.9	1.1	2.4ab	12.8ab
CT9993	2.7	2.0	1.9	2.5	3.3	1.8b	14.2ab
IR58821	1.7	1.7	4.0	3.5	3.3	5.0a	19.3a
IR52561	2.2	1.8	3.0	1.7	1.6	1.7b	12.0ab
KDML105	1.5	1.9	0.5	1.4	1.3	2.0ab	8.6b
IR42	1.4	1.7	3.4	3.7	3.4	5.1a	18.7a
CV (%)	58.8	35.7	87.4	70	71.5	64.1	40.7

CV = coefficient of variation
Note: Water extraction figures followed by a common letter are not significantly different ($P < 0.05$).

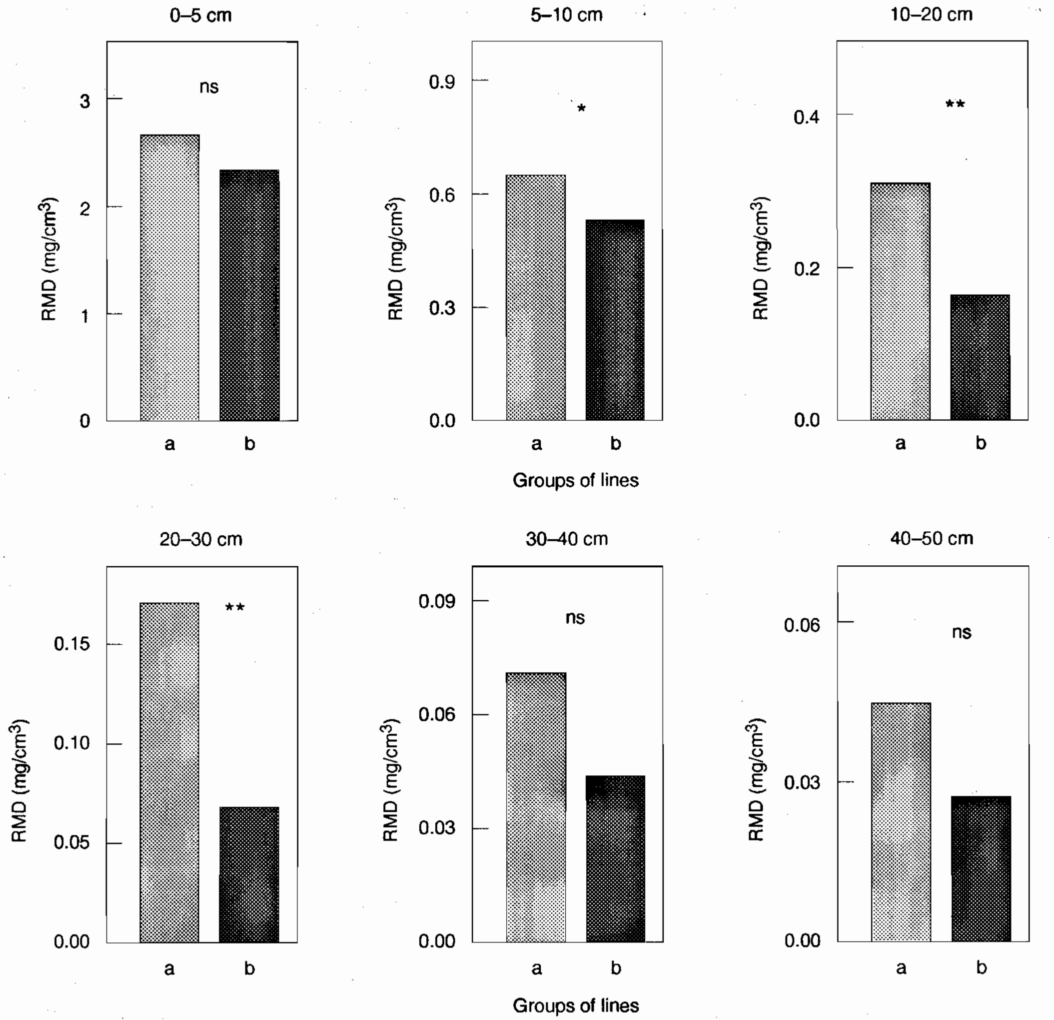

Figure 6. Mean root-mass density (RMD) at different soil layers, of two groups of doubled-haploid lines; drought-resistant group (a) and drought-susceptible group (b); data were average of four lines. (* = significant at $P < 0.05$; ** = significant at $P < 0.01$; ns = not significant at $P = 0.05$)

Conclusion

The root system of rice in the rainfed lowland ecosystem is shallow. Hardpans are common in the paddies and the high soil strength associated with the hardpan inhibits development of deep roots penetrating into the subsoil layers. Detecting significant genotypic variation for root growth parameters is difficult because of a high experimental error variability associated with root measurements, particularly in the deeper soil layers. Expression of genotypic variation in root systems was detected with experiments that collected a large number of soil samples in rainfed lowland conditions, although the differences observed were rather small. The differences in water extraction by roots among genotypes were also rather small but were found to be associated with root-mass density. Genotypes with large root systems in the subsoil showed drought-resistance characteristics in the drought environment examined at the Ubon Centre. A well-developed deep root system can be considered as one of the drought-resistant traits for rice grown under rainfed lowland conditions, but measuring root characteristics of many genotypes is difficult and time consuming. The implications of the genotypic variation in root systems for genetically improving drought resistance of rainfed lowland rice are, however, unclear at the moment and need to be evaluated.

Acknowledgments

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Genotypic Variation for Water Relations and Growth during the Vegetative Stage among Six Rice Lines Contrasting in Maintenance of High Leaf Water Potential

Boonrat Jongdee*, Shu Fukai* and M. Cooper*

Abstract

Genotypic variation for leaf water potential was examined among six rice lines in terms of its association with other water-relations attributes and total dry-matter growth during the vegetative stage of development. Plants were grown under upland field conditions with adequate water for 46 days from sowing, and then either with or without continuing irrigation for a further six weeks. Differences in leaf water potential among the lines were observed at midday under well-watered conditions, and were maintained throughout the stress period. The plants adjusted osmotically during the daytime even under well-watered conditions. Under stress conditions, osmotic adjustment reached a maximum by the third week for the predawn and the second week for the midday readings, when leaf water potential was about −1.6 MPa. Estimating osmotic adjustment was complicated by genotypic differences for predawn osmotic potential at the initiation of the stress period. Nevertheless, it was observed and contributed to variation in the leaf water potential at which the lines lost positive turgor.

The genotypic variation for leaf water potential was related to plant size but was not fully explained by either plant size (water demand), water use (supply) or the demand to supply ratio. While this characteristic was associated with variation for turgor, it did not appear to contribute to any variation in total dry-matter growth. The lack of influence of the observed variation for leaf water potential on variation for dry-matter production may be associated with the large genotypic differences in total dry matter under well-watered conditions. In addition, obtaining precise estimates of dry-matter growth was difficult and the error in its estimation was large compared with that for the water-relations attributes. These large experimental errors will complicate any studies investigating the role of variation of water-relations attributes on the variation for dry-matter production in rice.

DROUGHT is a serious problem, causing low productivity in rainfed rice. One strategy for reducing the effect of drought on rice production is the development of drought-resistant lines. While this strategy has been widely advocated for many crops, successful examples of its application are limited. O'Toole (1982) argued that improved drought resistance may be achieved by selecting for physio-morphological traits that contribute to drought resistance, and suggested several such traits for rice. However, limited work has been conducted to evaluate genotypic variation for the putative drought-resistance traits, particularly in relation to their impact on growth and grain yield (Fukai and Cooper 1995).

Leaf water potential (LWP) has been adopted as an index of the whole-plant water status (Turner 1981) and maintenance of high leaf water potential is considered to be associated with drought avoidance mechanisms (Levitt 1972). There is some expectation that high leaf water potential may be a useful selection criterion, as it has been found to be associated with a number of traits, for example: rooting depth, stomatal conductance, canopy temperature, leaf rolling and leaf death (O'Toole and

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Moya 1981; Tomar and O'Toole 1982; Mambani and Lal 1983; Yang et al. 1983; Hsiao et al. 1984; Garrity and O'Toole 1995). Bidinger and Witcombe (1989) suggested that using integrative traits such as leaf water potential might be more effective and easier than using individual traits for selection of drought-resistant genotypes. Individual traits may each have only a small direct effect on crop growth and crop yield may be little affected by such traits. Genotypic variation for maintenance of leaf water potential has been reported for rice and hence could be exploited by breeding programs (O'Toole and Moya 1978) if they have the capacity to screen for this variation.

The main objective of the present work was to evaluate how genotypic variation for leaf water potential is associated with variation in other water-relations characteristics and the influence of this on growth of six rice lines. From previous work the lines studied were known to differ for leaf water potential during drought in the vegetative stage.

Materials and Methods

The experiment was conducted at the University of Queensland Research Farm, Redland Bay, latitude 27°37'S, longitude 153°19'E, in the humid coastal region of southeast Queensland. The soil is an Oxisol which contains 50% clay in the surface 0.2 m layer and 80–90% clay from 0.2–1.5 m (Kirkegaard et al. 1992). The experiment consisted of two trials, water stress and irrigated, and was conducted under upland field conditions. The experimental design was a randomised complete block with four replications. Four to six seeds per hill were sown by hand at a depth of 3–4 cm on 3 February 1995. Hills were 10 cm apart, row spacing was 25 cm, and plot size was 1.5 × 3.5 m. Basal fertiliser was applied at 40 kg N/ha, and another 40 kg N/ha was applied at four weeks after planting. The stress trial utilised a rainout shelter to prevent rain falling on the plots during the stress period. Plants were irrigated twice a week in both trials until 46 days after sowing, beyond which there was no further water input for the stress trial. The experiment was terminated six weeks after water was withheld (week 6). Six lines known to differ in maintenance of leaf water potential were used: BK88-BR6, a lowland-adapted, tall line from Thailand; Lemont, a lowland semidwarf cultivar from the USA; Ceysvoni, a lowland-adapted cultivar from Surinam; RD1, a lowland semidwarf type from Thailand; DPI99295, a lowland-adapted line from Australia; and Rikuto Norin 12 (RN12), an upland-adapted cultivar from Japan.

Plant water status was measured weekly in both trials at both predawn (1–3 am) and midday (1–3 pm). LWP, relative leaf water content (RLWC) and osmotic potential (OP) were estimated from the second-youngest fully developed leaf. The leaf tip, about 5 cm long, was used for estimation of LWP by the pressure chamber technique (Turner 1981). The remainder of the leaf-blade sample was cut into three pieces, of which the first two pieces, each about 1 cm long, were placed in a plastic epindorf tube for estimation of RLWC by the method described by Barrs and Weatherley (1962). The third piece was wrapped in plastic sheet and aluminium foil, and then placed in liquid nitrogen for later estimation of OP with a Wescor 5100c vapour pressure osmometer. Stomatal conductance was measured at the same time as midday LWP from the beginning of the stress period (week 0) until three weeks after stress had commenced (week 3). Turgor pressure was estimated as the difference between LWP and OP. Osmotic adjustment (OA) was calculated as the difference in OP at full turgor, after adjusting for RLWC, between the stress and non-stress measurements, using the value at predawn week 1 as the non-stress reference point.

Radiation interception was measured one day before each dry-matter harvest using a 1 m linear sensor probe. Plant samples were harvested (0.5 m^2) at weeks 0, 2, 4 and 6. Above ground, dry weight, green leaf area index (LAI) and tiller number per plant were determined in both control and stress trials. Root samples for determination of root-length density were taken for BK88-BR6 and Lemont at week 2 and week 6. The diameter of the soil core was 48 mm for the first sampling and 98 mm for the second sampling. The samples were taken between the two central rows of the plot to a depth of 100 cm. Root length was measured using the grid system described by Tennant (1975).

Just before each plant dry-matter sampling, volumetric soil water content was measured using a neutron moisture meter at 0.2 m intervals from 0.3 to 1.1 m below the soil surface. At the same time, gravimetric soil samples were taken from the 0.2 m surface soil layer.

Results

Development of water deficit

Figure 1 shows the mean temporal trends for LWP, RLWC, OP, turgor pressure (P), OA and stomatal conductance (g_S) in both the irrigated and stress trials for predawn and midday measurements. In the irrigated trial, the water-relations attributes were maintained at the same level throughout the experimental period. In the stress trial, the initial values of LWP and RLWC were maintained at the predawn level of the irrigated trial for 2–3 weeks and then they started to decline (Figs 1a and 1b). This decline, however, was detected by the midday measurements immediately after withholding water. Osmotic potential declined in response to water stress in a similar pattern to LWP, but the decrease in OP was of a smaller magnitude and ceased earlier in the stress period, at week 2 for the midday measurements and week 3 for the predawn measurements (Fig. 1c). Osmotic potential fluctuated slightly from week to week even under irrigated conditions, and this was reflected in the OA measurements (Fig. 1d). With the diurnal decrease in OP under irrigation, OA of about 0.3 megapascals (MPa) was recorded at midday, when water was fully available to the plants. Predawn OA developed later and was detected in week 2. Maximum OA was similar for both the predawn and midday measurements, with a value about 0.5 MPa, and occurred when LWP was about −1.6 MPa. OA contributed to the maintenance of turgor (P) when water stress had developed (Fig. 1e). Loss of midday turgor after week 3 of stress was due to the decrease in LWP being greater than in OP. It was clear that stomatal conductance decreased immediately after stress was imposed (Fig. 1f). Stomatal conductance was reduced by half after one week of stress. This indicates that the stomata of these rice lines are very sensitive to water deficit, with a slight decrease in LWP resulting in a substantial decrease in stomatal conductance.

Genotypic variation in leaf water potential

There was no genotypic variation in predawn LWP in the irrigated trial (data not shown). There was, however, significant variation at midday for one measurement time with BK88-BR6, RD1 and RN12 having lower LWP (Fig. 2a). In the stress trial, the differences among the lines in predawn LWP ($P < 0.05$) were detected from week 3 of the stress period, and these were maintained for the remainder of the stress period (Fig. 2b). In contrast, midday LWP was detected as significantly different between the lines from the beginning of the stress period (Fig. 2c). The variation in LWP was small at the early stages of water-stress period, but became much greater as the severity increased. The ranking of the lines for LWP was consistent in later stages from week 3 for both predawn and midday measurements. At the end of the stress period, Lemont and Ceysvoni had higher LWP than the other lines at predawn and midday. The four remaining lines were similar for predawn LWP but BK88-BR6 was lower than others for midday LWP.

Genotypic variation in other water-relations characters

The OP, P, OA and g_S values for predawn and midday measurements at week 0 and week 3 for the six lines in the stress trial are shown in Table 1. There were significant differences in OP at predawn at week 0, despite there being no significant variation in LWP. BK88-BR6 and RD1 had low OP of −1.92 and −1.81 MPa, respectively, whereas the other lines were between −1.43 and −1.52 MPa. The lower OP for these two lines was consistently observed throughout the stress period. Turgor at predawn week 0 was greater in BK88-BR6 and RD1 than in the other lines, but the difference was not observed at midday. The differences in turgor among the lines became greater as the severity of the stress increased. The turgor of BK88-BR6 reduced rapidly with stress, and at week 3 it was the lowest and estimated to be negative. Loss of turgor at week 3 predawn was small to nil for RD1, Lemont and Ceysvoni, and the turgor for these lines was greater than for other lines at week 3. These three lines also had higher LWP than the others at week 3. At this point in the stress cycle, turgor still remained positive for all lines at predawn, but some, such as BK88-BR6, had lost positive turgor at midday. Most of the lines, however, lost positive turgor by week 4 (data not shown).

Variation in stomatal conductance was observed from week 1 to week 3 in the stress trial, but there were no differences under well-watered conditions. Lemont had the greatest stomatal conductance at all times of measurement, but the other lines had similar levels of stomatal conductance.

Figure 3 shows the relationship between OP and LWP for the six lines. The decrease in OP was associated with a decrease in LWP in all lines, but the relationship differed among them. When LWP was zero, differences in initial value of OP among the lines were observed, with BK88-BR6 and RD1 significantly lower than the other lines. However, a more rapid decline in OP with decreasing LWP was found in Lemont, Ceysvoni and RD1. From the relationships shown in Figure 3, the LWP at which turgor would be lost was estimated; these values, together with maximum OA, are shown in Table 2. The observed value for maximum OA obtained from week 2 revealed that RDI had the greatest adjustment (0.73 MPa), which differed ($P < 0.05$) from that of DPI99295 and RN12. There was a tendency for the lines with the higher maximum OA to maintain positive turgor to a lower LWP. Turgor was lost at a LWP of –2.60, –2.35 and –2.20 MPa, for RD1, BK88-BR6 and Lemont respectively, compared with about –2.00 MPa for the other lines.

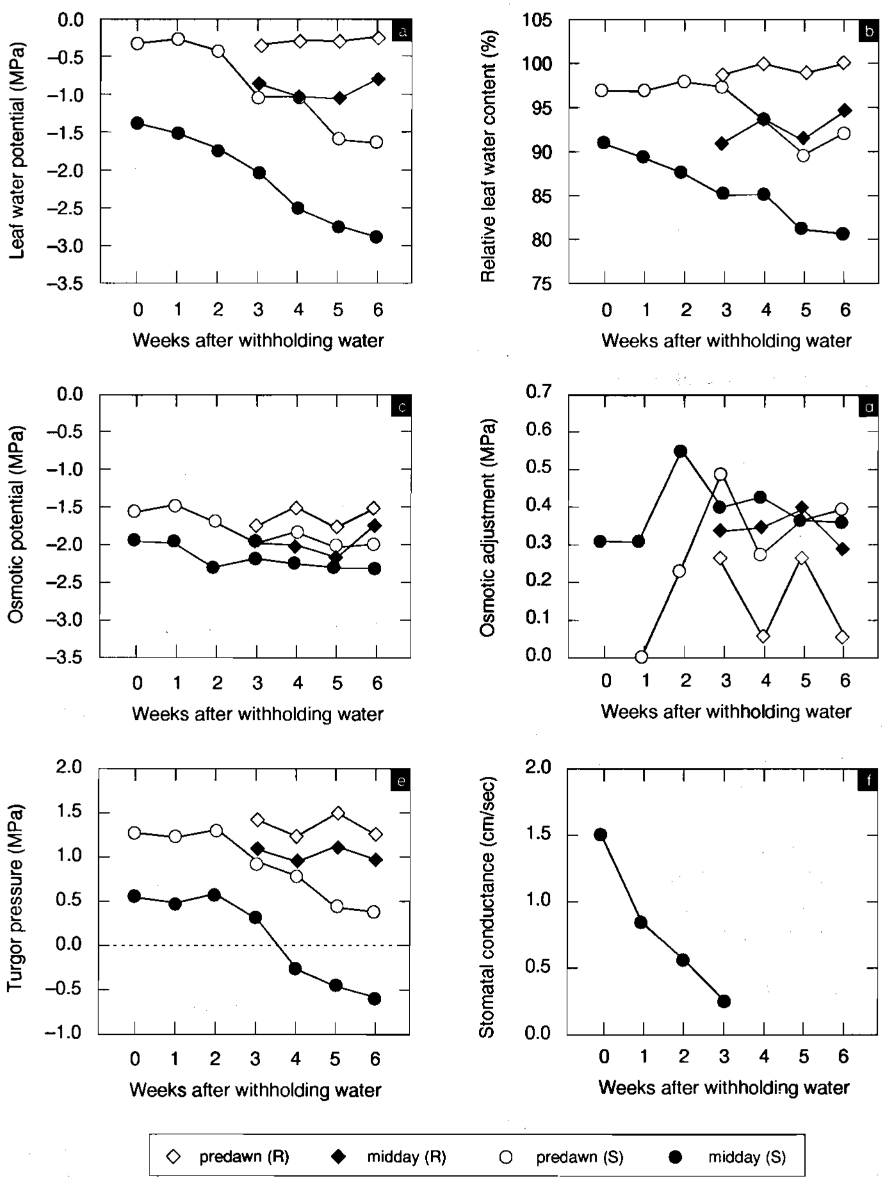

Figure 1. Change with time in (a) leaf water potential, (b) relative leaf water content, (c) osmotic potential, (d) osmotic adjustment, (e) turgor pressure, and (f) stomatal conductance for predawn and midday irrigated (R) and stress (S) trials.

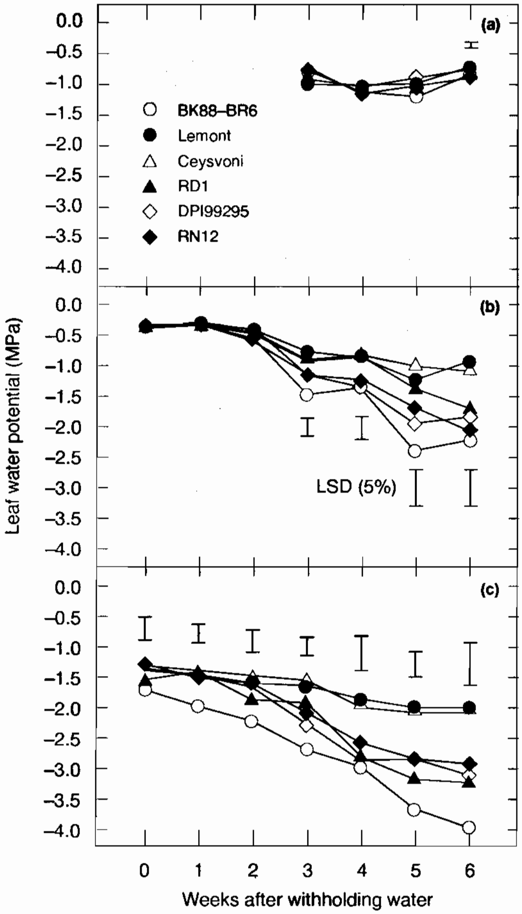

Figure 2. Change in leaf water potential with time for (a) midday irrigated, (b) predawn stress, and (c) midday stress; measured on six rice lines. (LSD = least significant difference)

Plant growth

In the irrigated trial, LAI was similar for the lines at week 0, but was higher in BK88-BR6 than in the others in subsequent weeks (Fig. 4). In the stress trial, LAI increased in a similar manner to the control for the first two weeks, but decreased for all lines thereafter. Under stress conditions, there were no significant differences among lines at any harvest time although LAI for RN12 tended to decrease sharply compared with the other lines.

Light interception was not significantly different among the six lines at the commencement of the stress period in either the control or stress trial (Figs 5a and 5b). In the control trial, differences ($P < 0.05$) were observed only at the second harvest, when BK88-BR6 intercepted more light than the others. All lines reached the maximum interception of 80–90% by the last harvest. In the stress trial, there were differences ($P < 0.05$) among lines from the second to last harvest. As in the control trial, BK88-BR6 had greater interception than did the other lines, though it was not significantly different from RN12 at any harvest.

The pattern of tiller development for each line was similar in control and stress conditions. All lines reached the maximum tillering stage at two weeks after the commencement of water stress (data not shown). Tiller number per plant differed ($P < 0.05$) among lines at all harvest times in both the control and the stress trials, and there was no interaction with time of measurement. The tiller number per plant for a line was the same in the stress and the control trials. Lines BK88-BR6 and RD1 had the largest number of tillers per plant (about 18–19) and DPI99295 (5) the lowest, while the others were intermediate (7–14).

Total dry matter (TDM) was significantly different ($P < 0.05$) among lines at all harvest times in both the stress and control trials, except at the beginning of the stress period in the control trial (Fig. 6). Total dry matter was greatest for BK88-BR6 in most harvests in both trials. In the control trial, Lemont and RD1 were similar to Ceysvoni and RN12 but significantly lower than DPI99295. In the stress trial, RD1 and RN12 were significantly greater than DPI99295 but similar to Lemont and Ceysvoni. Dry-matter increase for any of the 2-week periods between harvests was not significantly different among lines. It is shown for the whole period of stress in Table 3. The total dry-matter increase of lines in the stress trial was less than 50% of that of the control trial. It varied from 580 to 394 g/m^2 in the control trial and 135 to 205 g/m^2 for the stress trial, but these differences were not significant ($P < 0.05$). It was, however, observed that BK88-BR6 and RN12 tended to produce a greater amount of dry matter than did the other lines in both the control and the stress trials.

There was no difference in water use (WU) for any of the 2-week periods between measurements. Total water use for the whole period of water stress was, however, significantly different among the lines (Table 3). The total water use for Lemont and BK88-BR6 was greater than for the others. The difference in water use in each soil layer was not significant, but these two lines tended to extract more water at 60–80 cm soil depth. The variation in water-use efficiency (WUE) (TDM/WU) was 2.87–3.83 g/m^2/mm. There was, however, no significant difference among the lines for WUE.

Table 1. Predawn, midday and overall mean for osmotic potential (OP), turgor pressure (P) and stomatal conductance (g) of six rice lines during water-stress.

Measurement		BK88-BR6	Lemont	Ceysvoni	RD1	DPI99295	RN12	LSD (5%)	Interaction
OP	Week 0								
	Predawn	−1.92	−1.43	−1.46	−1.81	−1.49	−1.52	0.12	
	Midday	−2.20	−1.80	−1.88	−2.13	−1.87	−1.92	0.13	
	Week 3								
	Predawn	−2.15	−1.81	−1.82	−2.40	−1.97	−1.93	0.16	
	Midday	−2.50	−1.96	−2.05	−2.51	−2.18	−2.16	0.12	
	Mean[1]	−2.28	−1.87	−1.85	−2.29	−1.90	−1.91	0.44	**
P	Week 0								
	Predawn	1.57	1.10	1.12	1.44	1.16	1.19	0.11	
	Midday	0.50	0.52	0.60	0.59	0.60	0.60	ns	
	Week 3								
	Predawn	0.68	1.02	0.92	1.45	0.81	0.79	0.32	
	Midday	−0.17	0.40	0.52	0.71	0.11	0.11	0.32	
	Mean[1]	0.29	0.69	0.67	0.74	0.30	0.33	0.10	**
g	Week 0	1.47	1.52	1.66	1.57	1.54	1.32	ns	
	Week 3	0.35	0.64	0.30	0.27	0.37	0.24	0.25	
	Mean[1]	0.69	1.02	0.84	0.77	0.83	0.68	0.12	**

[1] Mean of 14 measurements, including predawn and midday, for 6-week period of stress
LSD (5%) = least significant difference ($P < 0.05$); ns = not significant
** = significant interaction for line and time of measurement ($P < 0.01$)
Week 0 = time of stress commencement; Week 3 = 3 weeks after stress commencement

Table 2. Maximum osmotic adjustment (OA_{max}) and leaf water potential at zero turgor (LWP_{PO}) which was obtained from the regression for six rice lines during the water-stress period given in Figure 3 (MPa).

Lines	BK88–BR6	Lemont	Ceysvoni	RD1	DPI99295	RN12
OA_{max}	0.64	0.63	0.57	0.73	0.52	0.48
LWP_{PO}	−2.35	−2.20	−1.95	−2.60	−2.00	−2.00

Table 3. Total dry-matter production (ΔTDM), water used (WU) and water-use efficiency (WUE) during the water-stress period for six rice lines.

Lines	Irrigated ΔTDM (g/m^2)	Stress ΔTDM (g/m^2)	Stress WU (mm)	Stress WUE ($g/m^2/mm$)
BK88–BR6	580.44	193.73	57.27	3.49
Lemont	411.28	175.93	60.57	2.87
Ceysvoni	467.58	165.59	52.73	3.11
RD1	394.55	187.21	53.78	3.43
DPI99295	507.51	135.19	54.57	2.53
RN12	520.62	205.80	53.29	3.83
LSD 5%	ns	ns	4.04	ns

LSD (5%) = least significant difference ($P < 0.05$)
ns = not significant

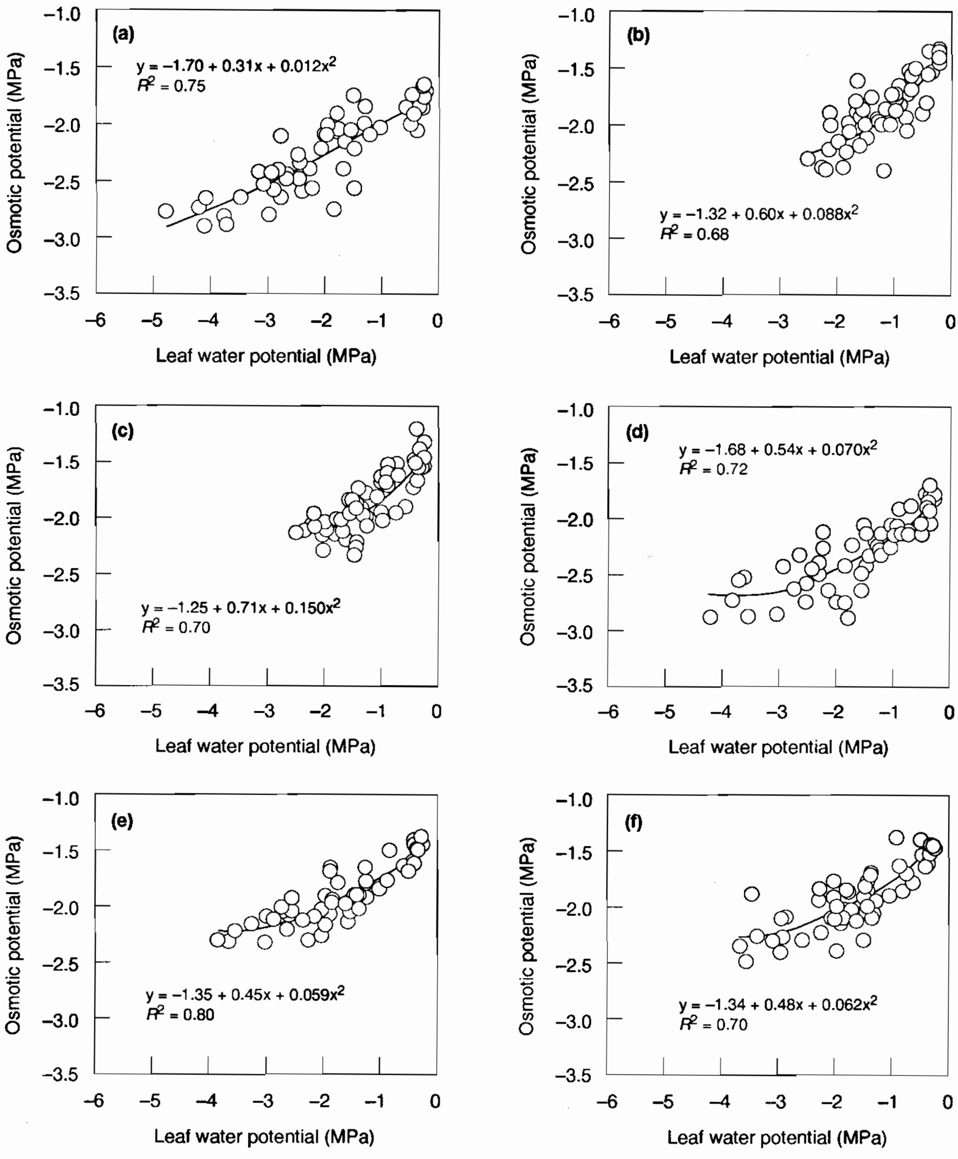

Figure 3. Relationship between leaf water potential and osmotic potential for six rice lines during the water-stress period: (a) BK88-BR6, (b) Lemont, (c) Ceysvoni, (d) RD1, (e) DPI99295, and (f) RN12.

The total root length was not significantly different between Lemont and BK88-BR6 in either control or stress conditions and at any time of measurement (Table 4). Between the two sampling times in the stress trial, total root length increased from 6.14 to 9.32 km/m^2 for BK88-BR6, and 5.38 to 8.95 km/m^2 for Lemont. An increase in root length at week 6 was observed in the shallow soil profile from the surface to about 60 cm depth (data not shown). The ratio of total root length to shoot weight was calculated and found to be consistent between the two sampling times, with values of 0.026 and 0.028 km/g for BK88-BR6 at week 2 and week 6, respectively. These were slightly lower than for Lemont, for which the ratios were 0.032 and 0.035 km/g at week 2 and week 6, respectively.

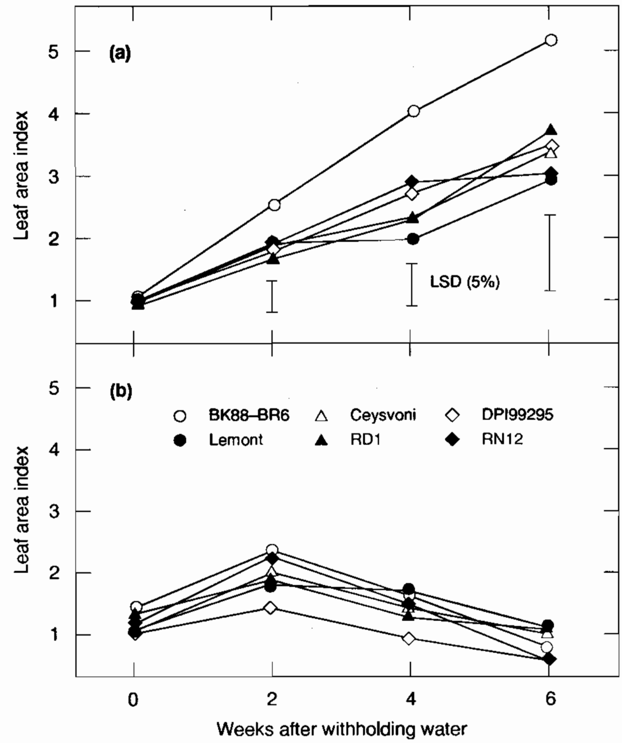

Figure 4. Change in leaf area index with time for six rice lines during the period of the water-stress cycle for (a) irrigated, and (b) stress trials.

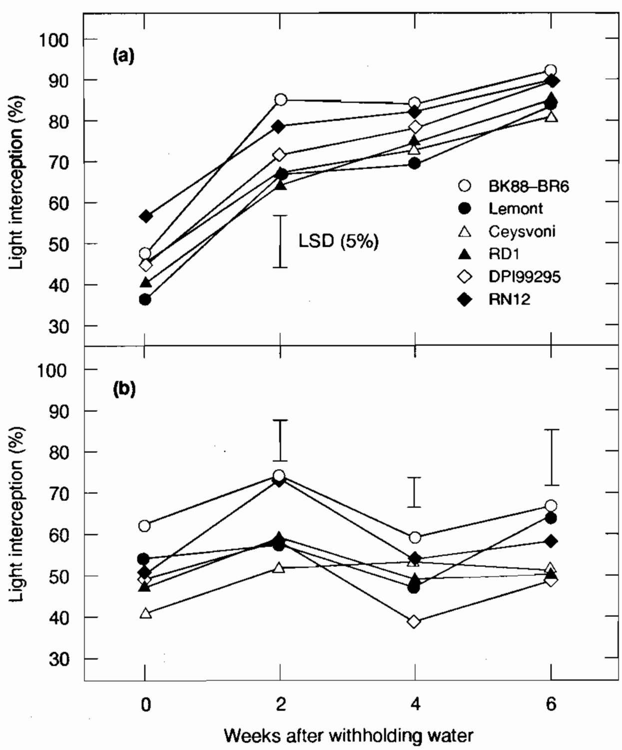

Figure 5. Change in percentage light interception for six rice lines during the period of the water-stress cycle for (a) irrigated, and (b) stress trials.

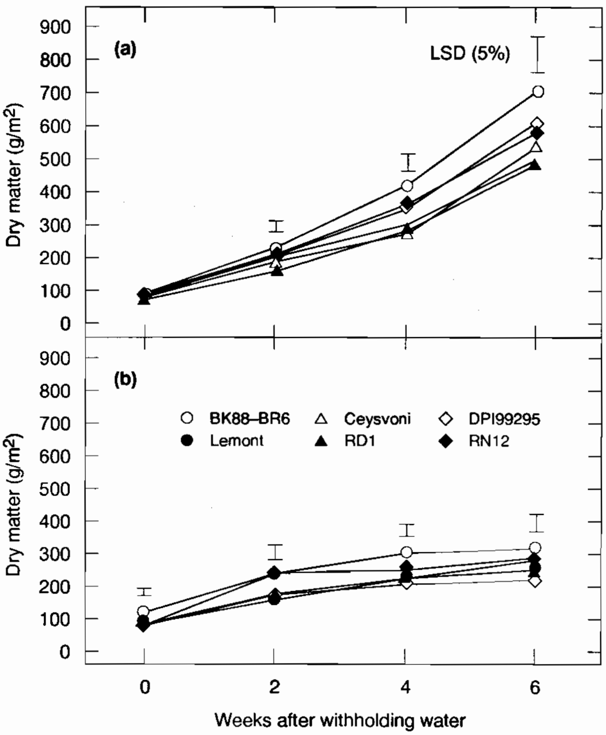

Figure 6. Change in total dry matter with time during the water-stress period for six rice lines: (a) irrigated, and (b) stress trials.

Table 4. Total root length for BK88-BR6 and Lemont at two and six weeks after the commencement of stress in stress and irrigated trials.

	Total root length (km/m^2)		
	Irrigated	Stress	
	6 weeks	2 weeks	6 weeks
BK88-BR6	8.06	6.14	9.32
Lemont	8.80	5.38	8.95
LSD (5%)	ns	ns	ns

LSD = least significant difference; ns = not significant

Association between leaf water potential and growth characteristics

The genotypic variation in the maintenance of leaf water potential was examined for its relationship with plant growth characters. Several plant characters, such as LAI, WU per area of leaf, and tiller number, were examined but there were no relationships with LWP. It was found that the genotypic variation for LWP was associated with light interception: BK88-BR6, with the highest interception, had the lowest LWP; and Ceysvoni, with low light interception, had high LWP. The linear association, however, was not strong, with an R^2 of 0.34.

The demand-supply ratio was measured by the mean light interception (%) per water use (mm) in a 2-week period. It provides an index of water shortage to the plants. This index was plotted against mean midday LWP for the corresponding 2-week period for each line (Fig. 7). Data for lines that were not significantly different for their regression coefficients and intercept were combined. For all lines the decrease in LWP was associated with an increase in demand-supply ratio during the stress period, but this relationship differed among the lines. For example, at the well-watered starting condition for the stress period, with demand-supply ratio of 2, LWP for BK88-BR6 was about –2.2 MPa compared with –1.5 MPa for the others. At the demand-supply ratio of 8, towards the end of the stress period, LWP for BK88-BR6 was –3.5 MPa, which was much less than the values of –2.2 MPa for Lemont and Ceysvoni and –2.8 MPa for RD1, DPI99295 and RN12. The results thus indicate that the genotypic variation in LWP cannot be explained solely by the differences in ability to extract water or the size of the plant canopy, and that an enhanced interpretation is obtained when both factors are considered together.

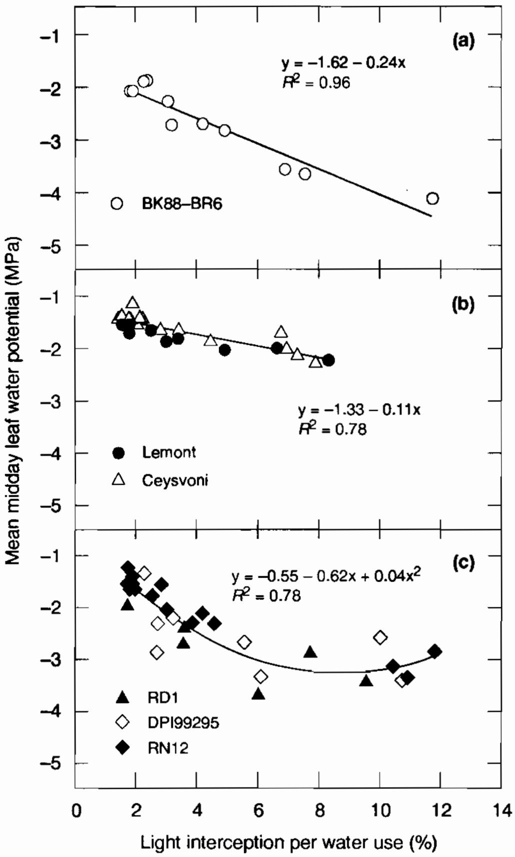

Figure 7. Relationships between mean midday leaf water potential and demand-supply ratio [light interception (%) per water use (mm) in two weeks] for six rice lines during a pre-flowering water-stress period.

The genotypic variation in dry-matter production during the stress period was not related to LWP and P. Total dry matter at 2-week periods was plotted against cumulative water use, and linear regression was computed for each line (Fig. 8). Total dry matter for all lines increased with cumulative water use but the relationship was different among lines. Line BK88-BR6 had a significantly higher intercept value than the other lines, which were all similar. Differences in regression slope were observed among the lines, DPI99295 having the smallest slope, which was significantly different from that of BK88-BR6 and RD1. Based on the WUE estimated from the actual value (TDM/WU), DPI99295 was also the smallest but there was no significant difference among the lines. The difference in TDM was due to the difference in initial growth.

Discussion

This experiment provided evidence that there was consistent genotypic variation for LWP among six rice lines during the preflowering water-stress period. The results confirmed that Lemont and Ceysvoni were able to maintain high leaf water potential, as reported by Henderson et al. (1993) and Lilley and Fukai (1994a). While no differences were found at predawn under well-watered conditions, midday LWP was lower for BK88-BR6 and RD1. Discrimination among the lines for LWP was much clearer during the period of development of water stress. Water use was shown to differ among the lines but this did not appear to explain the genotypic variation for LWP. For example, BK88-BR6 and Lemont extracted similar amounts of water but differed greatly in LWP. Plant size is a morphological character influencing water loss which contributes to the variation of maintenance of LWP (Lilley and Fukai 1994b). In particular, the large number of tillers possessed by BK88-BR6 may be a factor contributing to this line's large demand for water. The lower midday LWP in BK88-BR6 and RN12 was associated with larger plant size. However, the different relationships between LWP and the demand-supply ratio for lines indicates that other factors are also likely to be involved in determination of genotypic variation for LWP. The fact that LWP differed at midday under well-watered conditions suggests the internal water conductance may differ among the lines.

Maximum osmotic adjustment found in this experiment varied from 0.48 to 0.73 MPa, which is similar to other reports for rice (Steponkus et al. 1982; Hsiao et al. 1984). Variation in maximum OA was observed among the lines, with RD1 having significantly higher OA than DPI99295 and RN12, while LWP was not significantly different among these lines. This result contrasts with the report by Turner et al. (1986b) that genotypic variation in OA is due to the differences in stress severity among lines. The difficulty in estimating OA should be emphasised, as the initial OP differed among lines even at predawn under well-watered conditions; for example, BK88-BR6 and RD1 had a lower OP than the other lines under what were considered to be low-stress control conditions. These differences might be due to differences in the degree of stress, as BK88-BR6 and RD1 were more stressed at midday even at week 0 or under irrigated conditions. Examination of the expression of the water-relations attributes during the diurnal cycle indicated that OA was induced in rice even under well-watered con-

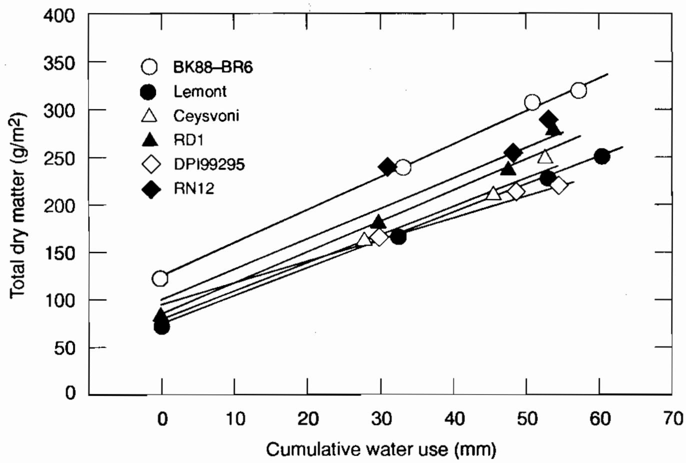

Figure 8. Relationships between cumulative water use and total dry matter for six rice lines during a preflowering water-stress period.

ditions. Munns and Weir (1981) reported that OA was induced during the daytime in wheat, and a similar result was also found in sorghum (Girma and Krieg 1992). While the degree of adjustment may not be clear, the result showed that loss of turgor in RD1 occurred at a lower LWP than in the other lines, indicating that OA played a significant role in maintenance of positive turgor in these lines.

Although there was a large genotypic variation in LWP, dry-matter increase during the stress period was not significantly different among the six lines. This result was similar to that obtained by Turner et al. (1986a) and Lilley and Fukai (1994b). One reason for the non-association may be the large genotypic variation in dry-matter production under well-watered conditions. The line BK88-BR6 had the highest growth under irrigated conditions, and it also appeared to grow better in the early part of the stress period, when stress was less severe. Another problem was the large experimental error variation involved in estimating dry-matter production. The coefficient of variation (CV) for total dry matter was about 12–14% at any harvest but the CV for increase of dry matter during the stress period for each harvest increased from 31 to 57% as stress was more severe and dry-matter production decreased. In comparison, the other characters, such as LWP, OP and turgor, had a CV of about 7–10%, and WU was about 10% during week 0 to week 4 but increased to 26% during week 4 to week 6 of the stress period. Clearly, it is necessary to estimate dry-matter production more accurately than can be achieved by current methods in order to evaluate the relationships between growth parameters of plant and water-relations attributes.

Acknowledgments

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Soil Limitations for Rainfed Lowland Rice in Lao PDR

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Abstract

Rainfed lowland rice accounts for 62% of the cultivated rice area and 76% of production in the Lao PDR. Approximately 86% of the rainfed lowland rice area is in the central and southern agricultural regions, adjacent to the Mekong River. Much of the remaining area occupies rather narrow valleys in the north of the country.

Soils through much of the rice-producing area of the Mekong River valley are derived mainly from old alluvial deposits and, in some provinces, sandstone materials. They are usually highly weathered, moderately acid, loams, sandy loams, and loamy sands — Alisols, Acrisols, Leptosols, Cambisols and Gleysols. They typically have a topsoil sand content exceeding 65% (sometimes more than 80%) and a clay content occasionally as little as 5%. Their poor water-holding capacity makes them very drought prone. Low organic matter, cation exchange capacities and base saturation percentage are usual. Extractable acidity is generally high in the Acrisols and Alisols. Many areas are acutely phosphorus (P) deficient, but the P requirement for rice can be met with as little as 6.5 kg P/ha in some soils. In other soils the initial requirement is between 13 and 19 kg P/ha. Soils in rainfed lowland areas of northern Laos are often more fertile and large responses to nitrogen (N) application alone can be expected. Early wet-season cropping of *Sesbania rostrata* can provide part of the rice crop's N requirement, but supplementary fertiliser N is usually required at about 45 days after transplanting. In soils of the Mekong River valley, good growth of *S. rostrata* is usually dependent on P fertilisation. Preliminary results indicate that a single P application of 9–13 kg P/ha to the *S. rostrata* is sufficient to meet the P requirements of a *S. rostrata* rice-cropping system. There are indications of a potassium requirement in parts of the southern region.

RICE is the most important crop in the Lao People's Democratic Republic (Lao PDR). The planted area of about 642 000 ha in 1995 represented more than 80% of the cropped area. Rainfed lowland rice cultivation accounts for approximately 62% of the area under rice cultivation and 76% of production.

Approximately 86% of the rainfed lowland rice area is in the central and southern agricultural regions. Six major rice-producing plains are recognised — Vientiane plain (Vientiane Province and Vientiane Municipality), Borikhamxay, Sebang-Faay (Khammouane and Savannakhet Provinces), Sebang-Hiang (Savannakhet Province), Sedone (Saravane Province) and Champassak plain. These plains are the focus of the Lao government's current efforts to raise the level of national rice self-sufficiency. The topography of much of this area comprises a system of low-level ancient terraces with an elevation of about 200 m above sea-level.

The remaining area of rainfed lowland rice cultivation mostly occupies rather narrow river valleys in the north of the country, with occasional large continuous areas of between 500 and 2000 ha. Some of these areas are at an altitude of up to 1000 m above sea-level.

Soils and Soil Classification

The Lao government is concentrating its soil survey resources on the central and southern agricultural regions. Maps for about 80% of this area are already available, and preliminary soils information is availa-

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ble for a much wider area. Completed soils maps on a scale of 1:50 000 for the whole area are expected to be available in 1997–98.

The soils through much of the Mekong floodplain are mainly derived from old alluvial deposits and, in some provinces (Savannakhet and Saravane), sandstone materials. They are usually highly weathered, moderately acid loams, sandy loams and loamy sands–Alisols, Acrisols, Leptosols, Cambisols and Gleysols. They typically have a topsoil sand content exceeding 65%, and as high as 85%, with a clay content sometimes as little as 5%. Low organic matter content, cation exchange capacities (CEC) and percent base saturation are also usual. Extractable acidity is generally high in the Acrisols and Alisols.

Soils in areas of rainfed lowland cultivation in the north of the country are generally sandy loams, loams and clay loams — Cambisols, Fluvisols and Luvisols. Apart from the larger plains, the soils in most of the northern area have yet to be classified and mapped. However, they are generally recognised as being more fertile than those in much of the central and southern regions.

The Drought Problem

The sandy nature of soils in much of the Mekong floodplain, and their resulting poor moisture retention capacity, makes them very drought prone. Even after periods of heavy rain, there may be standing water in the lowland fields for only a few days. Farmers rate drought as the most serious production constraint in almost all provinces in the central and southern agricultural regions (Khotsimuang et al. 1995). In a 1993 survey of farm households in nine districts of seven provinces, respondents in eight districts ranked drought as the most important constraint among a list of 11 potential production constraints that included drought, insects, weeds, diseases, soil fertility, labour, cultivars, crabs or snails, rodents, credit and flooding. In the ninth district, drought was regarded as the second most important constraint after insects. In many districts, the significance of drought was greater than the simple ranking suggested. This was particularly evident in the survey results for the provinces of Champassak, Saravane and Sayabouly (Fig. 1).

All phases of the growth cycle of the rice crop have the potential for drought stress. However, drought problems are generally more frequently encountered in three phases of growth, any of which can have a significant impact on final grain yield. These phases are similar to those described by Fukai et al. (1995) for Northeastern Thailand. Transplanting can often be delayed because of inadequate rainfall during June and July. As a result, seedlings may often be more than 40 days old at the time of transplanting. Sometimes the delay may result in areas not being cropped at all. Drought conditions are sometimes encountered soon after transplanting, which, in some years, can result in almost complete crop failure. Years in which there is an unseasonal early end to the wet season can cause severe drought stress to later-maturing and normally high-yielding varieties during the grain-filling stage, with a resulting marked yield reduction.

Soil Fertility Limitations to Rice Production

The soils through much of the rainfed lowland area of Lao PDR are inherently infertile. Systematic studies on their limitations for rice production commenced in 1991 with the establishment of the National Rice Research Program, supported through the Lao-IRRI Project. These studies have slowly spread throughout the country as the rice research network has expanded. Initial research has been aimed at characterising responses to nitrogen (N), phosphorus (P) and potassium (K) on the major soil groups, followed by quantifying the minimum input levels required to sustain yield improvements, for those nutrients shown to be deficient.

Studies between 1991 and 1995 have established P deficiency in most areas of rainfed lowland rice cultivation in the central and southern agricultural regions. Response to P fertilisers is common, rice yield often increasing more than twofold (Fig. 2). In Vientiane Municipality (Luvisols and Leptosols), and the provinces of Vientiane (Alisols and Cambisols), Saravane (Alisols and Luvisols), and Champassak (Acrisols, Alisols and Luvisols), the P deficiency is acute and must be alleviated before responses can be obtained to the application of N. In Champassak Province, the yield improvement in on-farm studies from the combined application of 60 kg N/ha and 13 kg P/ha, relative to N alone, ranged from 65% (1.19–2.44 t/ha) in Soukhouma district, to 240% (1.06–3.60 t/ha) in Phonethong district. In Soukhouma district, a suggestion from 1995 data of a potential further significant yield response when K is combined with N and P (Fig. 2), is being clarified in 1996. In Saravane Province the magnitude of the responses to the joint application of N and P was

41–114% over three districts. In Vientiane Province, parts of which have had a history of some fertiliser application, the responses to the joint application of N and P have generally been less marked. In the provinces of Khammouane (Cambisols) and Savannakhet (Alisols, Cambisols and Solonetz), a response to N can usually be obtained independent of P, but the joint application of N and P is required to maximise yield potential. Borikhamxay Province (Paksan district) has shown relatively little P response and has given yield responses mainly to N (Table 1).

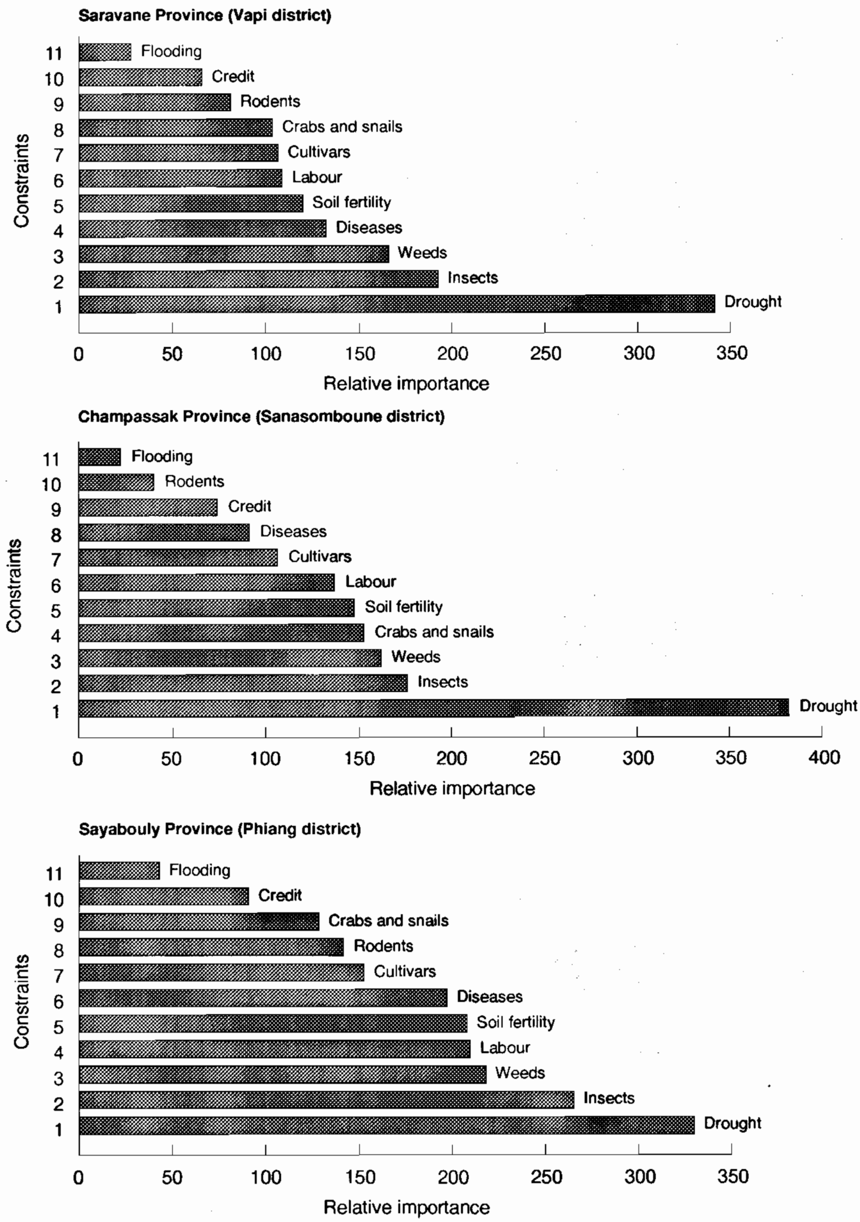

Figure 1. Relative rating of drought and other production constraints in the rainfed lowland environment of Champassak, Saravane and Sayabouly Provinces.

In areas without a history of fertiliser use, initial P application levels required to meet crop requirements are relatively low (Fig. 3; Table 1). In much of Savannakhet Province, an application of as little as 6.5 kg P/ha appears to be sufficient. In most other areas, a basal application of about 13 kg P/ha is required. Exceptions apply in Vientiane Municipality and the Gnommalath district of Khammouane Province, where a slightly higher requirement of between 13 and 19 kg/ha has been demonstrated; this reflects the higher clay content and resulting higher P fixation capability of the soils (mainly Cambisols) in these areas.

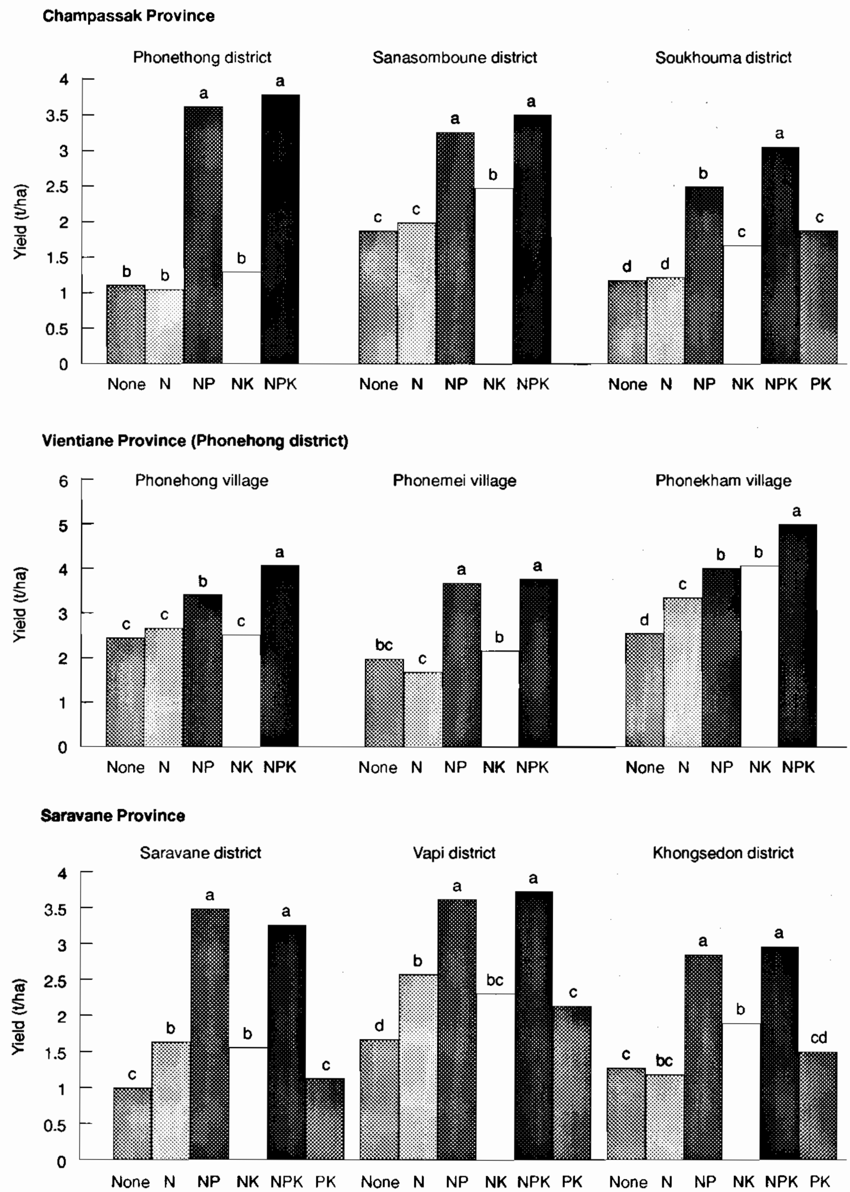

Figure 2. Rice yield responses in on-farm NPK application studies conducted in Champassak, Vientiane and Saravane Provinces 1992–95. Yields shown with a common letter on the histogram are not significantly different ($P < 0.05$ by DMR; applies within each data set only).

Table 1. Nutrient deficiencies and recommended nutrient application levels for areas of rainfed lowland rice cultivation in Lao PDR.

Province/district	Soil classification or texture[1]	Nutrient deficiencies	Recommendation (kg/ha)		
			N	P	K
Central and southern agricultural regions					
1. Vientiane Municipality					
-Naxaythong	Alisols	N, P	60–90	13-19	0
-Saythany	Leptosols	N, P[2]	60–90	13-19	0
-Sikhottabong	Luvisols	N, P[2]	60–90	13-19	0
2. Vientiane Province					
-Phonehong	Alisols, Cambisols	N, P[2]	60–90	6-13	0
-Thourakhom	Alisols	N, P[2]	60–90	6-13	0
3. Borikhamxay Province					
-Paksan	Acrisols	N	90	?	0
4. Khammouane Province					
-Thakhek	Alisols	N, P	60	13	0
-Nongbok	Cambisols	N, P	90	13?	0
-Gnommalath	Cambisols	N, P	90	13–19	0
5. Savannakhet Province					
-Khanthabouly	Alisols	N, P	60	6	0
-Champhone	Solonetz	N, P	60–90	6	0
-Saybouly	Cambisols	N, P	60	6	0
6. Saravane Province					
-Saravane	Alisols, Luvisols	N, P[2]	60–90	13	0
-Vapi	Luvisols	N, P[2]	60–90	13	0
-Khongsedon	Luvisols	N, P[2]	60–90	13	0
7. Champassak Province					
-Champassak	Cambisols	N, P	60–90	13	0
-Pakse	Cambisols, Acrisols	N, P	90	13	0
-Phonethong	Acrisols, Alisols	N, P[2]	90	13	0
-Sanasomboune	Luvisols	N, P[2]	90	13	0
-Soukhouma	Luvisols	N, P[2], K?	60?	6–13(?)	?
8. Xieng Khouang Province					
-Phasay	Clay loam	N, P[2]	60?	19–26	0
Northern agricultural region					
9. Luang Prabang Province					
-Chompetch	Clay loam	N?	60–90?	0?	0?
10. Luang Namtha Province					
-Namtha	Clay loam	N	<60	0	0
-Sing	Clay loam	N, P?	30–60	?	0
11. Sayabouly Province					
-Phiang	Alisols, Acrisols	N	60?	?	0

Table 1. (Continued) Nutrient deficiencies and recommended nutrient application levels for areas of rainfed lowland rice cultivation in Lao PDR.

Province/district	Soil classification or texture[1]	Nutrient deficiencies	Recommendation (kg/ha)		
			N	P	K
12. Oudomxay Province					
-Xay	Loamy sand	N, P	60	6	0
13. Phongsaly Province					
-Bounneua	Sandy loam	N, P? K?	?	?	?
14. Houaphanh Province					
-Samneua	Clay loam	N, P[2]	<60	13–19	0
-Xiengkho	na	N	90	0	0
15. Bokeo Province					
-Houayxay	Clay loam	N, P? K?	?	?	?
-Thonepheung	Clay loam	N, P[2]	?	?	0

[1] For soils yet to be classified
[2] Acute deficiency
? Yet to be defined or verified
na = not available

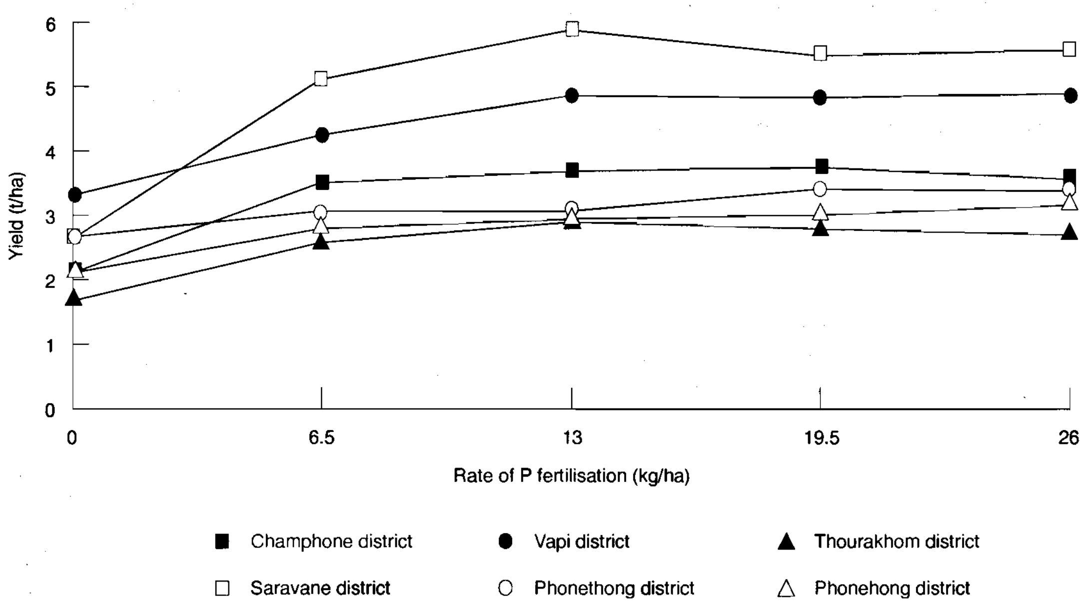

Figure 3. Grain yield response to the application of P fertiliser in six districts, 1994 wet season.

Once the P deficiency has been alleviated, rice in all areas in the central and southern regions shows marked responses to N. This N response has generally been greatest on the sandy Cambisol and Solonetz soils of Savannakhet Province, where yield improvements of more than 100% have been recorded, in response to split applications of about 60 kg N/ha (Lao-IRRI Project 1993, 1994, 1995).

In the northern agricultural region, where the growing environment is more varied, greater differences in nutrient responses exist between and within provinces. Acute P deficiency, similar to that of much of the central and southern regions, has been demonstrated in parts of the provinces of Xieng Khouang (Phasay district), Houaphanh (Samneua district) and Bokeaw (Thonepheung district) (Lao-IRRI 1993, 1995). Most other areas have shown marked responses to N alone, although in Namtha district of Luang Namtha Province, where the soils are exceptionally fertile, high yields are recorded without any fertiliser inputs. However, the nutrient response studies in the northern region are incomplete. In some parts of the provinces of Luang Namtha (Sing district) and Sayabouly (Phiang district), rather complex nutrient interactions and requirements have yet to be clarified.

Soil Limitations to Green Manure (GM) Crop Cultivation

In line with Lao government policy to minimise the use of chemical fertilisers in agriculture, studies commenced in 1991 to evaluate the potential use of green manure (GM) crops as a source of organic N in a rainfed lowland, rice-based cropping system. During the period 1991–95, the potential was assessed of *Sesbania rostrata*, *S. cannabina*, *Crotalaria juncea*, *Aeschynomene afraspera*, and the grain legumes blackbean, mungbean and cowpea. The crops were sown with the opening wet-season rains, and incorporated after 55–65 days of growth, before transplanting the rice crop. The performance of the individual GM crops has varied from year to year due to variability in early wet season rainfall pattern (Lao-IRRI Project 1992, 1993, 1994, 1995). The most consistent performance has come from *S. rostrata*, which, under favourable conditions, has provided an input into the system of up to 130 kg N/ha. However, the N contribution usually does not exceed 70–80 kg/ha.

The performance of potential GM crops, as with rice, is largely determined by the P status of the soil and the associated need for P fertilisation. A sevenfold yield response of *S. rostrata* was measured to the application of 13 kg P/ha in an unreplicated on-farm study in Champassak Province in 1993 (Lao-IRRI Project 1993). In the 1994 wet season, experiments were conducted in the provinces of Champassak (Acrisol) and Savannakhet (Cambisol) in the southern and lower central regions, respectively, to further study the response of *S. rostrata* to P fertiliser.

Applying about 13 kg P/ha, there was a fourfold increase (from 2.75 to 11.19 t/ha) in the fresh weight biomass of *S. rostrata* in the Champassak study, and a 12-fold increase (from 0.34 to 4.22 t/ha) in Savannakhet Province (Fig. 4). A similar response was obtained in another study in Savannakhet Province in the 1995 wet season (Fig. 4). These results clearly indicate that, for much of the rainfed lowland area of central and southern Laos where P deficiencies have been demonstrated, the potential use of GM crops such as *S. rostrata* is very much dependent on P fertiliser application. There is probably a similar requirement for grain legume cultivation in these areas.

Phosphate Nutrition in a GM-Rice Cropping Sequence

Following the demonstrations of the dependence of the yield performance of both rice and potential GM crops on P fertilisation, studies were initiated in 1994 and 1995 to examine whether it is possible to make a single P application to the GM crop (*S. rostrata*), and then rely on the release of P after incorporation of the GM crop, to meet the P needs of the rice crop that is planted immediately after the GM crop.

The 1994 studies were undertaken under on-farm conditions in Champassak Province (Phonethong district) on an Alisol soil, and in Savannakhet Province (Champhone district) in a Dystric Cambisol. Although the benefits of improved P nutrition were clearly demonstrated in the 1994 studies (Lathvilayvong et al. 1995), the potential response of the following rice crop to the release of P following decomposition of the GM crop was masked by an N deficiency late in the growth of the rice crop. The N input from the *S. rostrata* was insufficient to meet the requirements of the rice crop. In 1995, the study was repeated in the same general area in Savannakhet Province, but with the treatments being amended to ensure that there would be at least one where, following incorporation of the GM crop, the N requirement of the rice crop would be met and the potential P contribution from the GM crop could be assessed.

As in the 1994 studies, in 1995 there was also a clear response, to P fertilisation, in the growth of *S. rostrata* (Table 2). The average fresh weight biomass yield from the P treatments (T4–T7) was 4.3 times that from the zero P treatments (4.94 and 1.14 t/ha respectively).

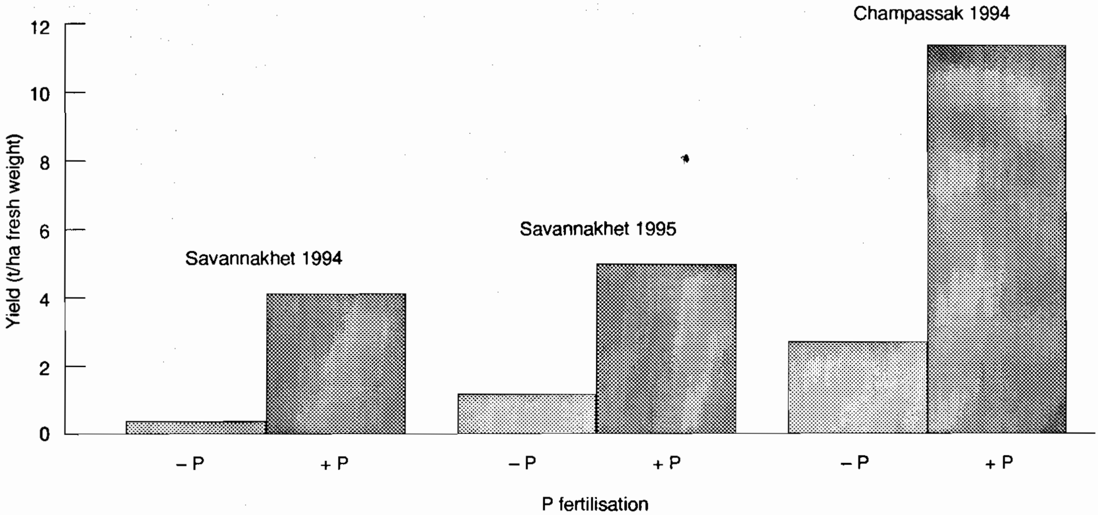

Figure 4. *Sesbania rostrata* yield response to P fertilisation, Savannakhet and Champassak Provinces.

Table 2. *Sesbania rostrata* and rice production in green manure (GM)–rice-cropping sequence, as affected by P application to the GM and various fertiliser treatments to the rice crop, Champhone district, Savannakhet Province, 1995 wet season.

Treatments				GM crop[1] biomass yield (t/ha)[2]	Rice crop[1]			
GM crop	Rice crop (kg/ha)				Yield (t/ha)	Tiller (no./hill)	Panicle (no./hill)	Height cm
	N	P	K					
T1. No GM crop	00	13	16	–	1.97d	4.2d	3.7d	86b
T2. No GM crop	60	13	16	–	3.52a	7.9a	8.0a	88ab
T3. *S. rostrata* (–P)	00	13	16	1.14b	2.15cd	4.7d	4.0d	88ab
T4. *S. rostrata* (+P)[3]	00	13	16	5.35a	2.49c	5.7c	4.5c	89ab
T5. *S. rostrata* (+P)[3]	00	00	16	5.50a	2.30cd	5.7c	4.5c	89ab
T6. *S. rostrata* (+P)[3]	30[4]	13	16	4.09a	3.18ab	6.5b	6.2b	90a
T7. *S. rostrata* (+P)[3]	30[4]	00	16	4.81a	3.10b	7.0b	6.0b	91a
Average				4.18	2.67	5.9	5.3	89
F–test				**	**	**	**	ns
CV (%)				32.5	8.5	8.4	5.6	2.6

[1] Means followed by a common letter are not significantly different ($P < 0.05$ by DMR)
[2] Fresh weight
[3] P treatments applied by broadcasting 8.6 kg P/ha as triple superphosphate at sowing
[4] Applied as urea 45 days after transplanting
** = $P < 0.01$; ns = not significant
CV = coefficient of variation

The highest grain yield recorded in the succeeding rice crop was 3.52 t/ha from the application of 60 kg N/ha (without a preceding GM crop). This was 79% higher than for the zero N treatment, thereby clearly demonstrating the potential for a response to either inorganic or organic sources of N. Where *S. rostrata* was grown before the rice crop, the highest yield (about 3.14 t/ha) was achieved from treatments (T6 and T7) where P was applied to the GM crop at sowing, and 30 kg/ha supplementary N was applied to the rice crop about 45 days after transplanting. Significantly, there was no grain yield difference between treatments with (T6) and without (T7) the addition of P to the rice crop, following P application to the *S. rostrata* at sowing. The results suggest that the P requirement of the rice crop was met from the P released from the *S. rostrata*, as a result of decomposition. The higher absolute yield from the rice plots receiving the inorganic fertiliser N, relative to the combination of organic and inorganic N sources, suggests that the latter system was unable to meet the total N requirements of the rice crop. The average fresh weight biomass of about 4.9 t/ha (with P) at the time of incorporation was low. This reflected the combined effects of dry conditions experienced immediately after sowing, which affected germination and subsequent growth, and the limited growing period; the GM crop was incorporated 55 days after broadcast seeding. The rice crop was transplanted 12 days after incorporation. This result again highlights the fact that the use of GM crops alone are unlikely to be able to provide the total N requirement of rice grown in the rainfed lowland environment. This is consistent with the findings of George et al. (1992).

Improving Rice Production in the Rainfed Lowland Environment

Although research on the management of the soils in the rainfed lowland rice environment of Lao PDR is relatively recent, the results of this research clearly indicate inherent problems of fertility and texture that are major constraints to improving rice yields. Approaches to reducing the significance of the drought problem are already being reflected in the cultivar improvement strategies being adopted. End-of-season drought is being 'managed' through drought avoidance, by the conscious selection for earlier-maturing cultivars, which have the same yield potential as some late-maturing cultivars, currently preferred by farmers, but which can often become drought stressed in years when the wet season ends early. One cultivar (Phone Ngam 1) has been released, and a number of promising lines have been identified. For early- and mid-season drought effects, current selection and breeding programs are aimed at seeking improved drought tolerance. Much of this work is being done in the context of joint research within the Rainfed Lowland Rice Research Consortium, and in collaboration with the University of Queensland research program supported by the Australian Centre for International Agricultural Research (ACIAR). The Lao preference for glutinous cultivars limits the genetic base available for cultivar improvement under these programs. Studies on early wet-season direct seeding are also based on attempts to minimise the potential impact of periodic early wet-season drought.

The rice nutrition studies have highlighted the limit currently placed on yield levels by the P status of soils in much of the rainfed lowland area of Lao PDR. At the same time, the potential for significant improvements in productivity through nutrient inputs, often at relatively low levels, has been clearly demonstrated. The critical role of improved P nutrition has been defined. Unfortunately, the P fertiliser needs of Lao PDR will have to be met through the use of imported P-based commercial fertilisers, the most appropriate forms of which have yet to be defined. Although no geological surveys have yet been undertaken to identify possible reserves of rock phosphate in the country, geological surveys for other purposes have not reported possible rock phosphate sources (Doungsila et al. 1995). Ongoing research is being aimed at better defining P budgets in the rice production system, minimising the cost of P application through possible seedbed P application, and the longer term P input requirements of the system.

The results of studies undertaken between 1991 and 1994 have also demonstrated both the potential and limitations of organic sources of N for meeting the N input needs of higher-yielding rice crops. Green manure crops such as *S. rostrata* have the potential for providing an organic source for part of the N requirements of the rice crop. The use of some inorganic fertiliser N will be unavoidable. However, to access the potential contribution to the system of GM crops, problems of seed availability to farmers have yet to be addressed. The potential role of *S. rostrata* as a host to the root knot nematode of rice, *Meloidogyne graminicola*, has yet to be clarified.

However, other potential GM crops with reported greater potential resistance to *M. graminicola*, including *A. afraspera*, are currently being evaluated.

Although the nutritional studies in the rainfed lowland rice environment have initially centered on the major nutrients N, P and K, it is recognised that other nutritional problems may also occur.

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Response of Rainfed Lowland Rice to Phosphorus Fertiliser Application in Cambodia

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Abstract

A large proportion of the soils used for rice production in Cambodia are deficient in phosphorus (P) but responses to P fertiliser application have been inconsistent. Marked differences in the chemical properties of the soils affect the release of P to the soil solution following flooding, and the retention of nitrogen (N), potassium (K) and water in the soil. The low cation exchange capacity (CEC) and organic carbon (C) contents of the acid sandy soils cause difficulties in maintaining N and K supplies for adequate plant growth, and responses to P fertiliser applications have been low. On soils with higher CEC and organic C content and low levels of available P, responses to P fertiliser application have been higher. Agronomists and plant breeders need to recognise these differences in the field in order to apply appropriate breeding and management strategies.

THE soils supporting much of Cambodia's rice crop are acutely deficient in phosphorus (P). Nevertheless, responses of crops to P fertiliser application have often been erratic and unpredictable. The use of phosphate fertiliser by farmers in the country is rising rapidly. Less than 5000 tonnes of diammonium phosphate (DAP) was imported in 1992 compared to more than an estimated 40 000 tonnes in 1996 (Ministry of Agriculture, unpublished). In order to manage this fertiliser efficiently, it is important to obtain a better understanding of the factors affecting the crop response to phosphate application on Cambodian soils.

There is a very large body of information on P fertiliser management and the factors affecting crop response in general. Recent reviews provide a good understanding of factors controlling P availability in soils (Barrow 1990; Kirk et al. 1990; Willett 1991), the processes of P uptake by lowland rice (Kirk et al. 1997) and P fertiliser management (Diamond 1985; De Datta et al. 1990). Applying this knowledge to the rice-growing soils of Cambodia requires an empirical understanding of crop responses to P fertiliser application and some data on soil chemical properties. Some of this information is available and some can be gained from studies on similar soils of neighbouring countries.

This paper briefly describes the response of rice to applications of P fertiliser to the main rice-growing soils in Cambodia and provides some speculation on the factors controlling these responses.

The Rice-Growing Environment of Cambodia

Eleven major soils have been identified in Cambodia based on their significance for rice production (White et al. 1997). Nearly all soils have a slightly acid pH, and significant areas have a low to moderate cation exchange capacity (CEC), organic carbon (C), total nitrogen (N), and available P levels (CIAP 1993). In a study of 103 soil samples collected throughout Cambodia, Saeki et al. (1959) concluded that the soils have a favourably weak acidity, but are extremely poor in available plant nutrients. Kawaguchi and Kyuma (1974) compared the fertil-

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ity characteristics of soils from tropical Asia and concluded that soils from Cambodia and Thailand had many characteristics in common: silica content was very high, while iron (Fe), aluminium (Al), manganese, alkaline earths, and total P were amongst the lowest of any country sampled. Cambodian soils have also been compared with 25 lowland soils from northeast Thailand by regressing CEC against clay content, total C and pH for each set of samples (Willett 1994). The analysis indicated that, in general terms, the fertility of the soils from both regions was similar. Cambodian soils, however, had a greater CEC per unit clay than those from northeast Thailand, possibly indicating less strongly weathered clay in Cambodia (Willett 1994).

Ninety percent of Cambodia's rice is grown during the wet season. Most is grown as rainfed lowland rice, with a small proportion receiving supplementary irrigation (< 15%) or grown in flood-prone areas (< 7%) (Nesbitt 1991). Rainfall is extremely variable both between and within seasons. Crops frequently suffer from drought and flood stress within the same year.

Almost all of the wet-season rice harvest is from traditional cultivars. About half of the cropped area does not receive fertiliser (CIAP 1993) and on most areas receiving fertiliser, only low rates of N and P are applied. Small areas may receive high doses of fertiliser if a crop is grown in the dry season.

At just over 1.3 t/ha, the national average rainfed lowland rice yields are the lowest in Asia.

Responses to Phosphorus Fertiliser Application

The only published data on the response of rice to fertiliser application in Cambodia are those of Lip et al. (1960) who conducted a series of trials from 1956 to 1958. After 30 years of turmoil, integrated nutrient management research resumed in 1990 with the formation of the Cambodia-IRRI-Australia Project (CIAP). Only in the last two years (1994 and 1995), however, have comprehensive fertiliser response trials been conducted. Figure 1 shows typical responses of modern lowland rice cultivars (Santapheap III or IR66) on four different soils in 1995, a year of very consistent rainfall in which water availability was not a serious constraint to yield. The trials involved the application of N, P and potassium (K) as follows: N, P (for the Krakor and Kbal Po soil types), N, P, K (Koktrap soil type) and N, P, K, sulfur (S) (Prey Khmer, Prateah Lang and Bakan soil types). The different types of soil are described in more detail below. The trials used fractional factorial designs following the procedures of Colwell (1994). A square-root quadratic model has been fitted to the trial data from each site. The graphs in Figure 1 represent the modelled response to N or P alone or applied with 100 kg N/ha (for the P curve), 100 kg P_2O_5/ha (for the N curve), 80 kg K_2O/ha (Koktrap, Prey Khmer, Prateah Lang and Bakan soils only) and 60 kg S/ha (Pursat, Prateah Lang and Bakan soils only). Data are for rainfed rice grown during the wet season except for Takeo, where they are for irrigated rice grown during the dry season.

Prey Khmer soils

About 10% of the rice area in Cambodia contains soils with a sandy profile extending 50 cm or deeper. This soil type has been named Prey Khmer (includes Entisols and Ultisols; White et al. 1997). Farmers have generally reported poor responses to fertiliser application on this soil type. Published data show no response to N and P fertiliser unless K is also applied (Lip et al. 1960). A rate of 30:30:30 ($N:P_2O_5:K_2O$) increased yield by 200–300 kg/ha (20–30%). Higher rates of fertiliser had no effect. The application of green manure (*Chromolaena odorata*), cut and carried from the forest, increased yield by between 200% and 400%. Results of CIAP's trials on this soil type similarly showed a very low response to fertiliser (Fig. 1). Phosphate application, in particular, had no effect on yield even when applied together with N, K, and S.

Chemical analysis of Prey Khmer soil shows that it is similar to some of the soils of northeast Thailand described by Ragland and Boonpuckdee (1987) and Willett and Intrawech (1988), in which the response to inorganic fertiliser application was poor or sometimes absent but good responses to green manure occurred. Because the soils have low total Fe and organic C contents and high concentrations of acidity relative to CEC, chemical reduction following flooding is slow, and hence the redox potential and pH changes are correspondingly slow (Ragland and Boonpuckdee 1987). Under these conditions, P available to the plant remains very low unless P fertiliser is applied. On some sandy soils in northeast Thailand, soil solution P increased rapidly during initial flooding, but it also decreased rapidly (Willett and Intrawech 1988). In addition, the extremely low CEC of this soil made it difficult to

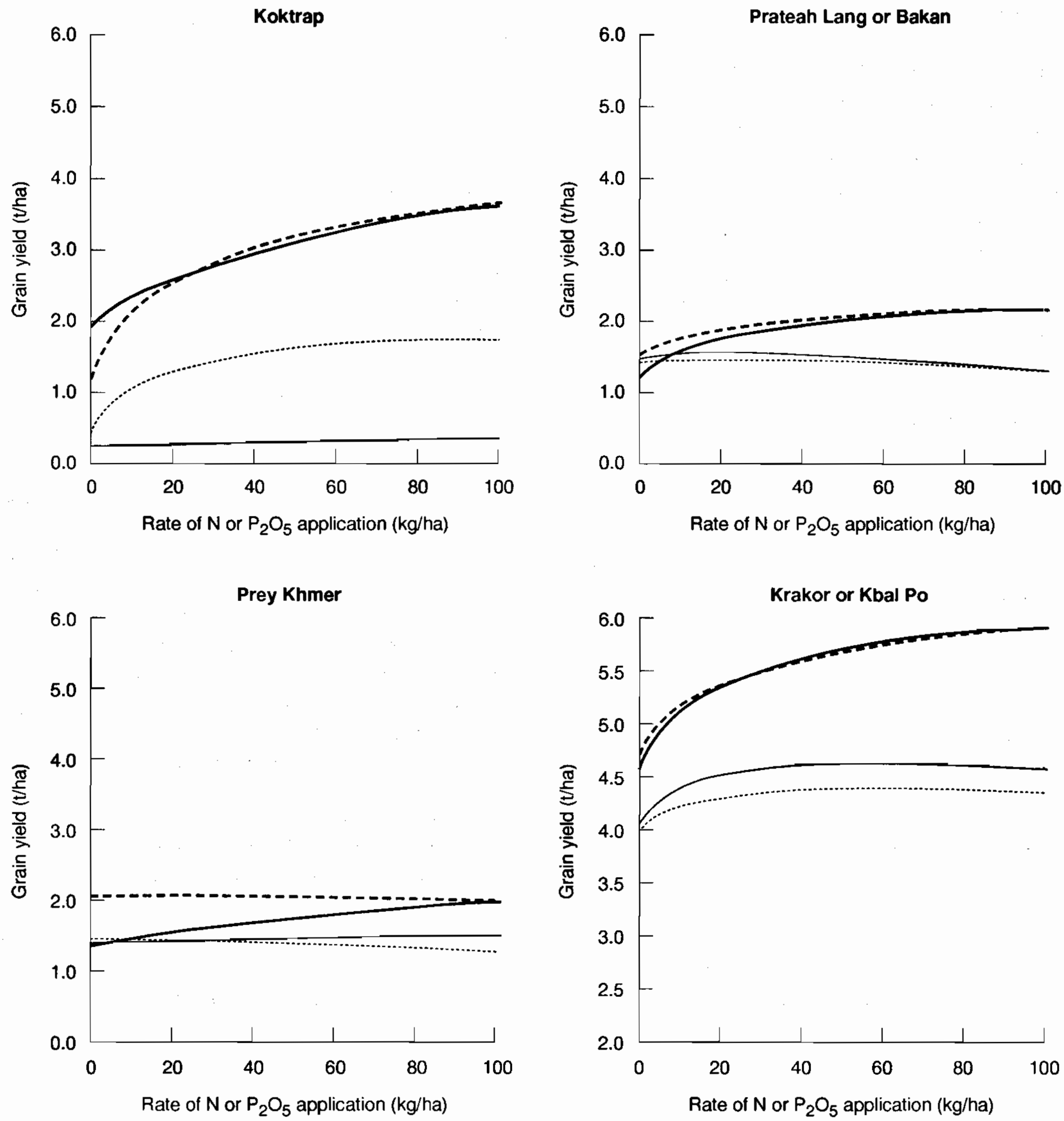

Figure 1. The predicted grain yield of rice in response to N or P application. N applied alone (—); N applied with P, K or S (▬); P applied alone (····); P applied with N, K or S (‒ ‒).

retain an adequate supply of N and K to the plant from added fertiliser (Ragland and Boonpuckdee 1987).

Prateah Lang and Bakan soils

Prateah Lang or Bakan soil types (include Ultisols or Alfisols) have a shallow sandy or loamy horizon over a heavier textured subsoil; White et al 1997) and occupy about 45% of the rice-growing area of Cambodia. Chemical analysis of the surface soil shows that it is similar to Prey Khmer soil (Table 1), although farmers generally report more consistent responses to fertiliser on this soil type. Phosphate applied alone (30 kg P_2O_5/ha) or with N (30 or 60 kg N/ha) increased yields by 0.5 or 1.5 t/ha respectively (50–160%) on the Prateah Lang soil occurring on the old terraces near Kandal; applying N (60 kg N/ha) without P decreased yields (Lip et al. 1960).

The modelled response to fertiliser application showed that phosphate application had only a small effect on yields on this soil type (Fig. 1). When P was applied at the highest rate together with N, K and S, yields were increased from 1.5 t/ha to just over 2.0 t/ha. Phosphate or N applied alone had no effect or tended to decrease yields at high application rates. Larger responses to fertiliser were obtained in another study on this soil type that examined the effect of applying triple superphosphate (TSP) or rock phosphate to rice in the dry season with adequate basal levels of N and K (Seng et al. 1995). Nitrogen and K were reapplied to the same plots the following wet season, but P was not applied, in order to examine the residual effect of P. In both seasons, grain yields were increased by more than 1.0 t/ha by phosphate application (Fig. 2). There was no significant difference in the response of rice between years or between phosphate sources, although phosphate uptake was lower in the second year than in the first year and with TSP than with rock phosphate.

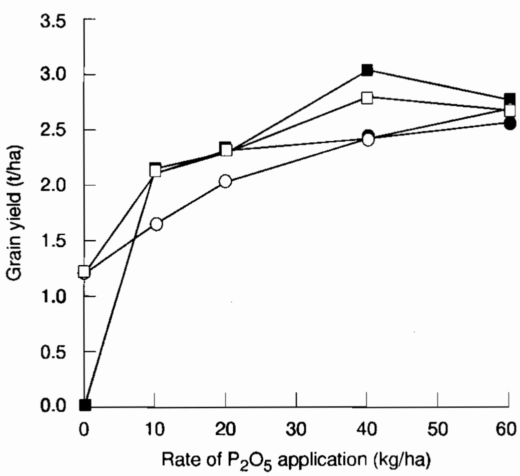

Figure 2. The effect of triple superphosphate (TSP) (●,○) and rock phosphate (■,□) on the grain yield of rice grown in the dry (●,■) and wet seasons (○,□) on the Prateah Lang soil type. The phosphate was applied in the first (dry) season only. N and K were applied in both the wet and the dry seasons.

The pH and Eh (redox potential) of Prateah Lang soil were also studied in a separate pot experiment and were changed rapidly by flooding. Nevertheless, without straw application the Eh remained above 200 mV and the pH mostly at or below 5.5, despite the soil being flooded for nine weeks (Fig. 3; Seng Vang et al. unpublished). Adding straw substantially increased the pH and stimulated reduction. These effects were also similar to changes observed by Ragland and Boonpuckdee (1987) for the sandy soils of the northeast of Thailand. The fixation capacity of this soil was also low (Table 1; Seng et al., unpublished).

As with the Prey Khmer soil, P availability is likely to remain low on this soil despite flooding. Increases in P availability at relatively low application rates of P fertiliser would, nevertheless, be expected because of the low P fixation capacity. The long-term availability of P applied to the soil is difficult to predict but may be high, as indicated in Figure 2, given that the total levels of Fe and Al are low. The low CEC would be expected to limit the response to high rates of P fertiliser because of the inherent problems of maintaining an adequate supply of N and K to high-yielding crops. This problem, however, may be less severe than on the Prey Khmer soils because the clay subsoil reduces water infiltration and leaching of N, and its higher CEC may act as a reservoir for some nutrients.

Koktrap soils

Koktrap soils (include Ultisols or Alfisols), which have a loamy or clayey profile with moderate organic C content and low to moderate CEC, produce very low yields of rice without fertiliser application and occupy about 5% of the rice area (White et al. 1997). Farmers report this soil type to be amongst the poorest in Cambodia and say that application of urea alone will severely reduce growth or kill plants.

Data from CIAP's fertiliser response curves show that without fertiliser yields were less than 0.5 t/ha (Fig. 1). Response to P application, however, was great. Phosphate applied alone increased yields by about 1.0 t/ha, and P applied with N increased yields from less than 1.5 t/ha to more than 3.0 t/ha. Nitrogen applied alone did not increase yields, and applying P and K without N produced almost 2.0 t/ha.

Changes in pH or Eh on flooding of the soil were less than the changes that occurred with the Prateah Lang soil (Seng Vang et al., unpublished). Even after several weeks of flooding, without straw application, the Eh remained above 250 mV and the pH did not increase above 5 until after seven weeks of flooding (Fig. 3). P fixation of this soil is also greater than that which occurred on the sandy soil (Table 1; Seng Vang et al., unpublished).

Table 1. Chemical properties of the soils used for rice production in Cambodia.

	Prey Khmer		Prateah Lang and Bakan		Koktrap		Krakor and Kbal Po	
pH 1:1 (H_20)	5.7	(15)	5.7	(37)	5	(8)	5.7	(28)
Organic C (%)[1]	0.31	(15)	0.31	(37)	1.24	(8)	0.97	(28)
Total N (%)[2]	0.03	(15)	0.03	(37)	0.12	(8)	0.1	(28)
CEC (meq/100g)[3]	1.09	(13)	1.28	(31)	7.23	(8)	14.25	(26)
Total P_2O_5 (%)	0.11	(4)	0.06	(6)	0.19	(1)	0.34	(9)
Available P (ppm)[4]	0.65	(4)	0.23	(24)	2.6	(3)	4.41	(16)
P-sorbed (meq/100)[5]	na		46	(15)	210	(2)	329	(10)
Particle size analysis[6]								
clay	4.4	(15)	8.1	(36)	28.9	(8)	36.8	(25)
silt	14.4	(15)	49.6	(36)	40.1	(8)	34.9	(25)
sand	81.1	(15)	42.5	(36)	31	(8)	27.6	(25)
Extractable Fe (%) (active)[7]	0.2	(8)	0.1	(23)	0.3	(6)	0.8	(18)
Exchangeable Al (meq/100g)[8]	0.03	(9)	0.3	(9)	2.6	(5)	3.5	(5)

[1] Walkley and Black (1934)
[2] Varley (1966)
[3] Cation exchange capacity; ADAS (1981)
[4] Olsen et al. (1954)
[5] Peaslee and Fox (1978)
[6] Pipette method: sand 0.05–2 mm; silt 0.002–0.05 mm; clay <0.002 mm
[7] Asami and Kumada (1959)
[8] Page et al. (1984)
na = not available
Note: Figures are means of the number of samples shown in brackets.

These chemical properties suggest that available P levels in Koktrap soil would also be low, despite flooding. The higher P fixation may cause P levels to remain lower than in the sandy soils and high rates of P fertiliser would be required to increase P availability to the plant. Better responses to high rates of P fertiliser, however, would be expected because the moderate CEC and organic C values allow higher potential yields due to a more consistent supply of N and K.

Krakor and Kbal Po soils

Krakor and Kbal Po soils (include Inceptisols) have a clayey profile with moderate organic C content and moderate CEC. They receive regular addition of sediment from rivers or lakes and occupy about 30% of the rice area (White et al. 1997). About 4.0 t/ha was produced when no fertiliser was applied at Takeo, which was the highest unfertilised yield of all sites. Applying P alone increased yields slightly. Applying P together with N increased yields by about 2.0 t/ha. In a long-term experiment on the same soil type on a nearby site in Vietnam, applying N without P caused rice yields to decline by 376 kg/ha/year from an initial level of 3.9 t/ha (Pham Sy Tan et al. 1995). Application of both N and P were required to halt the yield decline. Little chemical data are available for this soil apart from those shown in Table 1. The relatively higher levels of Fe and organic C in these soils would be expected to cause a greater increase in P availability with flooding than seen on the other soils.

Differences between Traditional and Modern Cultivars

Chaudhary and Nesbitt (1993) claimed that modern cultivars gave higher yields than traditional cultivars when grown with or without fertiliser in Cambodia, but their study was skewed towards higher-yielding sites. Grain yields ranged from 2.5 to 5.4 t/ha, which is well above the average rice yield obtained by Cambodian rainfed lowland rice farmers. Other data from nutrient management trials conducted on farmers' fields suggest that modern cultivars performed worse than traditional cultivars on soils where yields were 1.5 t/ha or less (CIAP 1992). Comparisons between cultivars, however, were complicated by the difficulty of matching sowing and maturity dates. In another study examining up to 10 cultivars grown in 17–30 environments in Cambodia between 1992 and 1995, fertiliser practice did not contribute to the genotype-by-environment interaction (Ledesma et al. 1997). Weather-related factors, such as rainfall and temperature, contributed most to the interaction between genotype and environment.

Conclusion

Soil P levels are likely to be low and P fertiliser is likely to be needed for adequate growth of rice on the acid sandy soils supporting much of Cambodia's rice crop. The supply of water, N and other nutrients to the plant, however, will have a large influence on responses to P fertiliser. The success of selecting plants tolerant to low P levels on these soils is similarly likely to depend on the plant's ability to obtain adequate quantities of these other nutrients. On soils where the N and water supply are more consistent, but where P levels remain low, responses to P fertiliser application are similarly likely to be more consistent. Likewise, selecting plants tolerant to low P levels may produce more consistent benefits on these soils. Plant breeders and agronomists need a simple system to recognise these soils in the field so that they can apply appropriate breeding and management strategies.

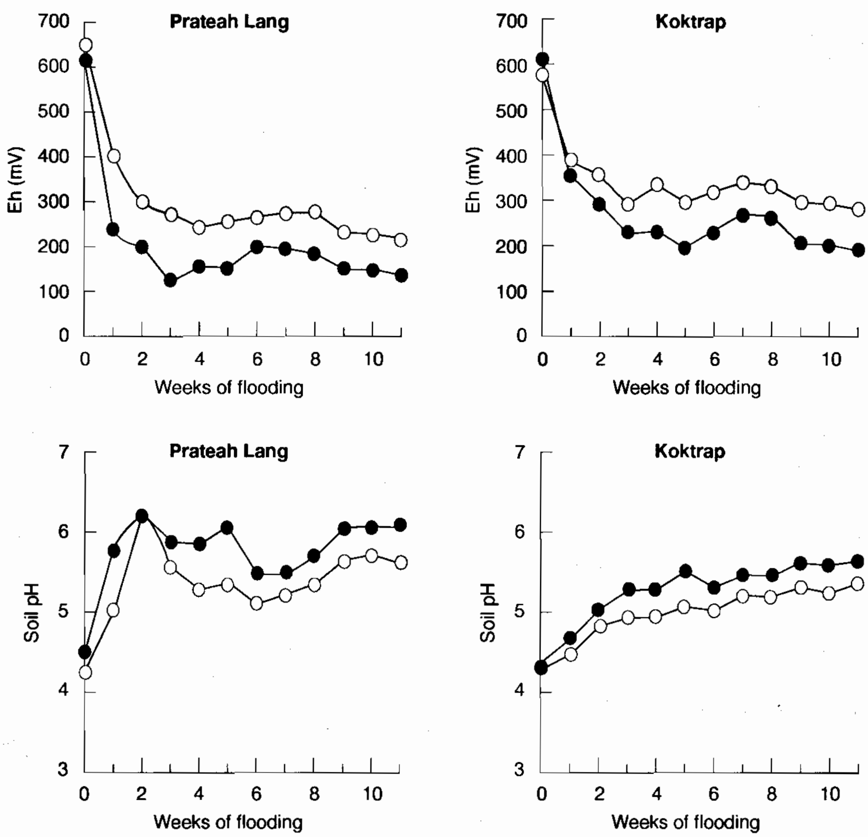

Figure 3. The change in pH and Eh on flooding of the Koktrap and Prateah Lang soils put into pots with (●) or without (○) 2 g straw/kg soil and incubated for 11 weeks (Seng at al.; unpublished).

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Soil Physical Limitations for Rainfed Lowland Rice

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Abstract

Rainfed lowland rice occupies about 25% of the world's rice-growing area and 40% of rice lands in South and Southeast Asia, where it is cultivated on soils varying from light to heavy in texture. The major risks and hazards associated with rainfed lowland rice are related to weather and associated soil problems. Soil physical limitations, such as soil moisture stress, especially associated with impeded drainage, traffic pan development, excessive permeability of coarse-textured soils, poor soil strength, disaggregation, thermal properties, and salinity and alkalinity, influence yield and stability. These poor physical conditions also influence the production of non-rice crops which may follow rice. This paper: (i) discusses the effect of soil physical constraints on growth and yield of rice and non-rice crops grown after rice; (ii) presents a case study to show how managed rainfed Vertisols in the erratic rainfall of central India can be used for increasing rice yields and cropping intensity; and (iii) identifies research gaps related to soil physical constraints for high and more stable levels of production in rainfed lowland rice. Research is needed on the management of land and water resources to reduce drought hazard and minimise the adverse effects of impeded drainage, evaluation of the potential of improved cultivars in a poor soil physical environment, and establishment of non-rice crops after rainfed lowland rice grown in sequence to utilise the residual soil moisture.

NEARLY 75% of the world's rice (*Oryza sativa* L.) depends entirely on rainfall for water. Rainfed lowland rice occupies about 25% of the world's rice area and 40% of the rice area of South and Southeast Asia. Khush (1984) grouped rainfed lowland rice areas into five subcategories based on variability in amount, timing and duration of rainfall, depth and duration of standing water, soil type, topography and other related variables. These subcategories are:

- rainfed shallow, with favourable moisture status throughout most of the growing period;
- rainfed shallow that is drought prone at any crop growth stage;
- rainfed shallow that is drought and submergence prone;
- rainfed shallow that is submergence prone; and
- rainfed medium–deep, on waterlogged low-lying areas that have impeded drainage and standing water depth from 0.25 to 0.50 m.

In general, the rainfed lowland rice system lacks control over the amount and timing of water, and hence both moisture insufficiency and moisture excess are encountered.

There are two systems of rainfed lowland rice cultivation. In one the fields are puddled and inundated (kept wet) during the entire crop growth period. The other one starts with the land being dry and ends up with a wet paddy. In this system the rice is dry-drilled in the early part of the monsoon, and it becomes wet when water is impounded when the heavy rains arrive. Both systems have limitations for achieving high, stable levels of rice production.

A number of soil physical properties are important for growing rice and for rice-based cropping systems. These properties are related to the pore spaces where retention and movement of water and air occur. Pore spaces depend on soil texture and structure. Coarse-

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textured (light) soils are excessively permeable and therefore have high downward losses of water and nutrients. Fine-textured (heavy) soils are slowly permeable and cause difficulties for tillage. For example, the lowland rice soils of Sri Lanka are predominantly sandy and contain little clay, whereas the soils of Bangladesh are generally silty. Sandy, loamy and heavy clay (with very little silt) soils are commonly cultivated for rainfed lowland rice in India and Thailand, whereas in Philippines the soils have a medium to heavy texture. The lowest yield and the highest instability of the paddy–wheat (*Triticum aestivum* L.) system are reported on the southwest Bihar plains because the region is characterised by rainfed cropping and red-yellow soils (Ramesh Kumar et al. 1996).

In order to manage various soils, the rice farmers puddle the fields. Puddling involves soaking of soil with water to saturation, ploughing, and thereafter harrowing and planking during which soil clods are broken and puddled with water. This process has several advantages to rice farmers, but requires a large amount of water for field preparation, destroys soil aggregates, results in formation of hardpan below the puddled layer, hinders regeneration of the soil structure and delays land preparation for an upland crop following the rainfed lowland rice crop.

This paper discusses the soil physical limitations for rainfed lowland rice, including soil moisture stress, impeded drainage, poor soil strength and fluffiness, excessive permeability of light-textured soils, salinity and alkalinity, traffic pan development, and disaggregation. It examines the adverse effect of these poor physical conditions on the growing of non-rice crops after lowland rice crops.

Soil Moisture Stress

Flooding and stagnant water are the main problems for rice production on the lowland plains and river floodplains, which account for 50–67% of the total rainfed lowland rice, whereas drought is the major problem on the terraced slopes. The plateaus may experience either drought or waterlogging. Yield is severely reduced when drought occurs at a critical growth stage. If the monsoon broke for more than 7–10 days, there would be moisture stress in the crop, which would be more severe on light-textured soils (Krishnamoorty 1979).

The soil physical environment of rainfed lowland rice is primarily influenced by the depth of submergence. The depth of ponding normally exceeds 5 cm in areas where rainfall is high and is concentrated in the early monsoon months (July–August), and where there are high-intensity storms (e.g. eastern India). The depth of ponding leads to a reduction in oxygen concentration, temperature and refracted light intensity, and restricts the development of nodal adventitious roots and leaves. Optimum generation of nodal roots and leaves that help in the development of viable tillers occurs in shallow (3 ± 1 cm) water (Kar et al. 1974).

The physical properties of the soil in rainfed lowland rice-growing areas play an important role in drought-prone areas. Drought-prone soils are typically shallow, coarse-textured loam or sandy loam overlying coarse sands or gravels or unconsolidated debris with limited available water capacity (Ghildyal and Tomar 1982). Such soils are also relatively deep, with a high mechanical impedance layer limiting the profile depth (Coimbatore, Tamil-Nadu). Drought-prone soils include hardening red, sandy loam soils with a high bulk density and low intake rate (Hyderabad, Andhra Pradesh) (Ghildyal and Tomar 1982) and heavy-textured, deep black (Jabalpur, Madhya Pradesh) and mixed red and black (Rewa, Madhya Pradesh) soils with a low intake rate, high runoff and short rainfall period (Tomar et al. 1995). The availability of soil water to growing plants is influenced by rooting characteristics (Hsiao et al. 1980). Therefore, rice cultivars such as Dular, which had higher root length density at deeper soil levels (Fig. 1), extracted more water from deeper layers in all three soils — silty clay loam, loam and loamy sand — than did IR36 (Table 1).

Puddling influences pore size distribution and thus water retention and transmission. From the physics of soil water retention and transmission for puddled and non-puddled rice soils, it appears that rainfed lowland rice may experience more drought stress during prolonged rainless periods in puddled than in non-puddled soil. Puddled soil retains more water at a given soil water potential and may have higher unsaturated hydraulic conductivity, but evaporation losses from puddled soils are low. In a black clay soil (Vertisol) at Jabalpur, India, the moisture content at harvest was similar in puddled and non-puddled soil, but the rate and extent of drying were greater in non-puddled soil (Gupta and Jaggi 1979). Rice grown on a puddled soil consequently may suffer less in mild drought than rice on non-puddled soil (De Datta and Kerim 1974). The boundaries between mild and severe moisture stress are not known, and more systematic research is needed on this.

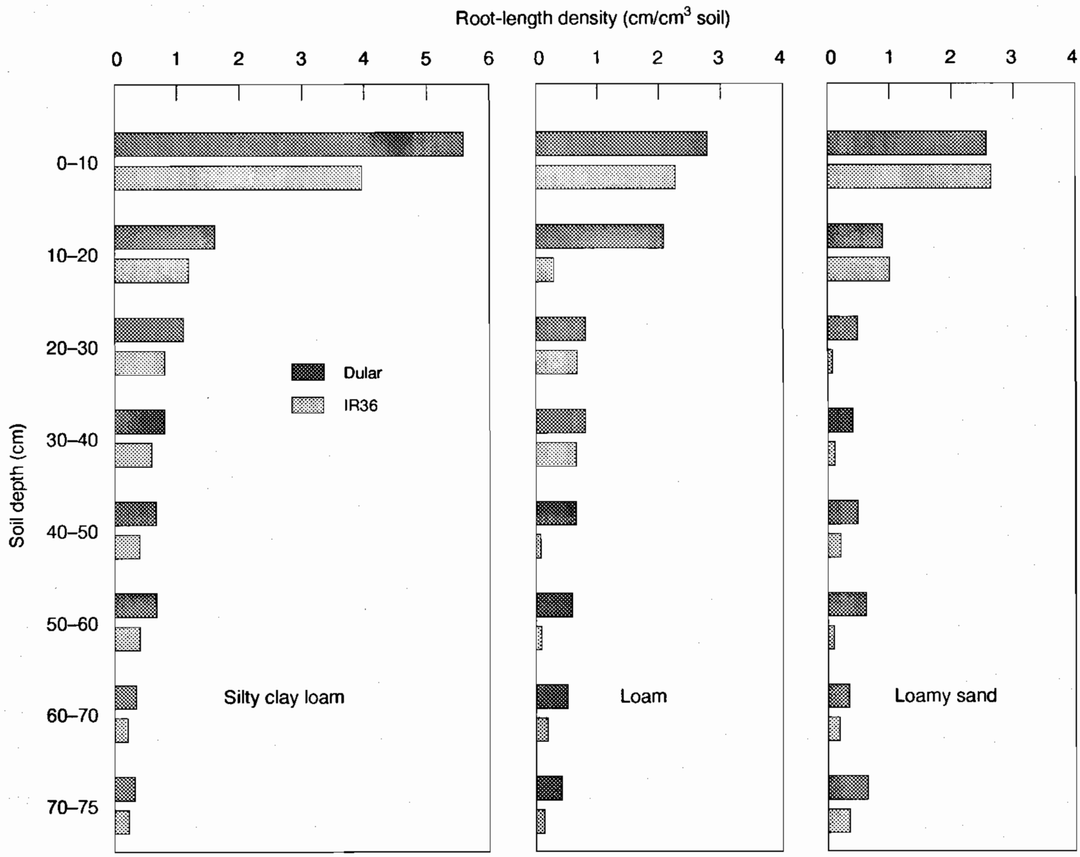

Figure 1. Root-length density patterns of IR36 and Dular in silty clay loam, loam and loamy sand, 0–75 cm depth (Tomar and O'Toole 1979).

Table 1. Soil water content and water use by rice in three soils during a drying period.

Period	Silty clay loam		Loam		Loamy sand	
	Moisture content (cm^3/cm^3)	Water use (cm)	Moisture content (cm^3/cm^3)	Water use (cm)	Moisture content (cm^3/cm^3)	Water use (cm)
IR 36						
3 days of withholding water	0.50		0.40		0.30	
At lower limit	0.27	14.93	0.21	14.60	0.17	9.66
Dular						
3 days of withholding water	0.52		0.41		0.31	
At lower limit	0.27	18.54	0.21	15.30	0.31	13.61

Source: Tomar and O' Toole (1979)

An integrated strategy for maximising crop production in drought-prone areas must consider agroclimatic conditions and a combination of soil and agronomic management practices. Bunding, puddling, soil amendments, and subsurface barriers help reduce water requirement for lowland rice (Hundal and Tomar 1985).

Soil Structure

Disaggregation

Puddling is traditional in lowland rice cultivation, bringing about destruction of the natural soil structure and dispersion of soil particles. The aggregates and peds are converted into soft mud by the thorough mixing of soil in standing water. Repeated ploughings and harrowings or the use of puddlers partially or completely destroys soil aggregates, depending on their stability (Yun-sheng 1983; Sharma and De Datta 1986; Pagliai and Painuli 1991).

Repeated disaggregation progressively makes it more difficult to work in paddy fields and move around them (Kisu 1978). These problems are more serious in clayey soil. In Vertic Tropaquept soil in the Philippines, repeated puddling at 4-week intervals, each performed at a fixed energy level of 7 kJ/m^2, decreased the surviving aggregates (> 2 mm) in easily removable soft soil from 19 $g/100\ cm^3$ at no puddling to 12 $g/100\ cm^3$ after the third puddling (Pagliai and Painuli 1991). Aggregates of greater than 8 mm decreased from 12 to 7 $g/100\ cm^3$ after the first puddling, with an associated increase in both the 2–4 and 4–8 mm ranges. The following two puddlings decreased aggregates in all size ranges. Deterioration in the physical condition of some fine soils is believed to be responsible for the decline in rice production after only a few years of intensive monocultivation of rice.

Puddling increases the water-holding capacity of rice soils. This is particularly important for keeping the surface soil wet and reduced during brief periods of water shortage. If clay soils dry for long enough, the soft mud cracks and dries to a stiff paste. When the soil floods again, the cracks do not completely close and may cause water and nutrient loss through percolation.

During puddling a well-aggregated porous soil is converted into a mud of massive structure. In the puddled layer, clay particles, or clusters thereof, occur in parallel rows and are surrounded by water-saturated capillary pores. Thus, the soil body is reduced to a two-phase system, solid and liquid; the gaseous phase is either eliminated or entrapped in storage or residual pores.

The destruction of aggregates triggers a series of changes in the physical properties of soils that affect plant growth and the use of farm machinery. Kisu (1978) reported that in continuously submerged clay soils, progressive deterioration of soil structure by puddling makes soils excessively soft, creating problems for tractors. The disaggregation and dispersion of soil materials result in increased bulk density and minimal aeration porosity. When the puddled soil dries, ploughing for a subsequent upland crop leads to a cloddy seedbed that adversely affects the crops planted after rainfed lowland rice.

Soil porosity

The soil porosity changes during puddling depend upon the initial soil structure. The total porosity is related to bulk density and may decrease or increase upon puddling, depending on whether puddling induces a more open or a more packed structure (Greenland 1981). The total pore volume usually increases during puddling, perhaps temporarily. Sharma and De Datta (1985) reported an increase in total porosity of 11% in a clay soil and 13% in a clay loam soil. However, Painuli et al. (1988) reported a marginal decrease in the 0–10 cm surface soil (Vertic Tropaquept) from 66% to 62–64%.

The effect of puddling and compaction in soils of varied texture is depicted in Figure 2. In a clay soil (Vertic Tropaquept), puddling decreased pores greater than 50 μm (transmission pores) by about 88% and increased pores between 0.5 and 50 μm (storage pores) and less than 0.5 μm (residual pores) by 167% and 26%, respectively, compared to non-puddled soil (Painuli et al. 1988). In a silty clay loam soil (Typic Hapludalf), puddling decreased transmission pores by 50%, increased storage pores by only 23% and decreased residual pores by 3% over non-puddled soil; compaction resulted in a drastic decrease in transmission pores (95%), an increase in storage pores (48%), and a further decrease in residual pores (8%) (Acharya and Sood 1992).

Particle size distribution influences the size and rigidity of soil pores and consequently affects the growth and depth distribution of roots in lowland rice. Rice roots grow best in silty clay loam soil (Tomar and O'Toole 1979; Kar et al. 1979; Ghildyal and Tomar 1982). Tomar and O'Toole (1979) observed that the roots of the IR36 and Dular cultivars grew best in silty clay loam, but Dular had a relatively higher density than IR36 at lower depths in loam and loamy sand (Fig. 1). The influence of pore size and rigidity on rice root growth is less evident with finer soil particles and increased porosity.

Changes in pore size distribution due to puddling strongly influence other soil physical processes, such as gaseous exchange, water retention and transmission, and evaporation losses from soil.

Traffic pan

The long-term physical effect of puddling is the formation of a traffic pan — a compacted 5–10 cm thick subsurface horizon between 10 and 40 cm in depth. Traffic pans are formed by compression as a result of ploughing in wet conditions. Compared to the surface soil, the soil of a traffic pan has a higher dry bulk density and fewer medium to large pores (Leung and Lai 1974). Traffic pans have high water-retaining capacity, with a bulk density of 1.5 t/m^3 or more. Some soils have lime concretions and a gleyed horizon (Zitong 1986).

Soil composition influences the degree of pan formation. Traffic pans do not occur, for instance, in very sandy soils, but they do appear if the silt and clay content are somewhat higher than in loamy fine sand. Optimal conditions for compaction are present in fine loamy soils. Repeated puddling of sandy loam soil for rice and subsequent tilling operations for the succeeding upland (wheat, *T. aestivum*) crop, as shown in Table 2, result in the development of high soil strength, high bulk density and low permeability traffic pan in the subsoil within 3–4 years (Sur and Prihar 1989). If the clay content is much higher (e.g. Vertisols), the pan formation again becomes less pronounced. The hardpan formation may take as long as 200 years to develop, as in Polder lands of the Shiroishi area, Kyushu, Japan (Motomura et al. 1970). Poor pan formation is also found in soils with a stable structure and high organic matter content. Table 3 shows the physical properties of a hardpan formed in a typical lowland clay loam soil (Yun-sheng 1983).

Traffic pans have a positive effect on water economy and crop performance in most lowland rice areas, and they help support traffic in soils which are soft, deep and muddy. But pans have disadvantages for rice if their permeability decreases to nearly zero, resulting in the accumulation of toxic substances. A well-developed traffic pan creates a shallow soil that may seriously interfere with root growth and moisture and nutrient availability for crops. There is not sufficient information on this. In addition, ponding due to unseasonal rains may adversely affect the dryland crops grown after rice.

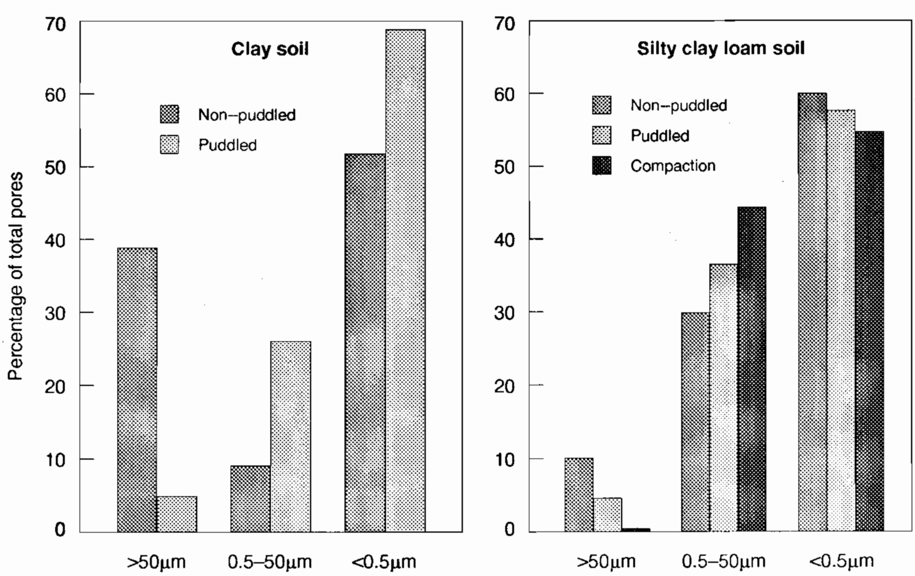

Figure 2. Effect of puddling on components of total porosity in clay and silty clay loam soils (Painuli et al. 1988, Acharya and Sood 1992).

Table 2. Bulk density, hydraulic conductivity and resistance to penetration under rice–wheat (RW) and corn–wheat (CW) cropping systems at harvest of wheat.

Depth (cm)	Bulk density (t/m^3)		Hydraulic conductivity (μm/second)		Resistance to penetration (MPa)	
	RW	CW	RW	CW	RW	CW
0–5	1.53	1.60	0.47	0.31	11.3	11.3
5–10	1.65	1.62	0.22	0.39	14.0	13.0
10–15	1.69	1.63	0.17	0.36	25.0	23.3
15–20	1.81	1.68	0.06	0.11	39.3	25.8
20–25	1.73	1.64	0.08	0.22	19.9	15.5
25–30	1.65	1.64	0.17	0.22	18.8	14.1

Source: Sur and Prihar (1989)

Table 3. Some physical properties of a puddled lowland clay loam soil for different horizons.

Soil properties	Plough layer	Plough pan	Below plough pan	Substratum
Bulk density (t/m^3)	1.20	1.35	–	1.56
Total porosity (% vol/vol)	53	44	–	42
Aeration porosity (% vol/vol)	15	2	3.7	negligible
Saturated hydraulic conductivity (μm/second)	120	0.19	0.36	0.12

Source: Yun-sheng (1983)

Excess Permeability

Rainfed lowland rice is also grown on coarse-textured Alfisols and Ultisols. These soils lose a considerable amount of water and nutrients by deep percolation. In addition, after the rains cease, they dry quickly because of low water-retention capacity and high permeability.

The productivity of these soils could be increased if water percolation and leaching of nitrogen were minimised. Surface compaction of lateritic sandy-loam increases bulk density and reduces saturated hydraulic conductivity (Table 4). Gupta et al. (1989) found that it also improved the water-retention capacity at 0–40 cm depth by 0.05 cm^3/cm^3 (two passes) or 0.10 cm^3/cm^3 (six passes).

Compaction technology involves deep ploughing of the soil followed by compaction at proctor moisture (the soil moisture content at which maximum compaction is obtained) by repeated (four to six) passes of a 90-cm long, 800-kg roller with a 45-cm diameter, and application of fertiliser to the soil surface followed by shallow ploughing to 5–10 cm depth.

Compared with the control (one pass), which yielded 3.2 t/ha, the grain yield of IR8 increased significantly with two passes without recultivation and with four passes with recultivation to a depth of 5 or 10 cm. The maximum yield (4.1 t/ha) was obtained with four passes and recultivation to 5 cm in depth. The maximum grain yield of the wheat cultivar Sonalika (4.1 t/ha) was obtained with four passes of the roller and recultivation up to 10 cm depth (Table 5).

Bulk Density

The bulk density of soil may increase or decrease as a result of puddling, depending upon the structure of the soil before puddling. In general, strong interparticle forces favour a well-oriented structure, whereas weak interparticle forces favour an open gel structure (Greenland 1981). Puddling of a well-aggregated soil results in a massive structure of increased bulk density. In swelling clays, however, even submergence without puddling substantially decreases bulk density (Virmani et al. 1982). Puddling of such a soil brings the soil particles back into suspension and lowers the bulk density. In a field experiment at the Interntional Rice Research Institute (IRRI), the bulk density immediately after puddling of a clay soil decreased from 0.83 to 0.53 t/m^3; that of a clay loam soil decreased from 1.16 to 0.81 t/m^3 (Sharma and De Datta 1985). However, the bulk density increased with time, due to the settling of particles (Table 6). Bulk density further increases on drying because of shrinkage. A dried puddled soil is very compact and hard and may develop broad and deep cracks, depending on the nature and amount of clay.

Root growth and grain yield in transplanted rice is negatively correlated with bulk density and soil

Table 4. Effect of compaction of lateritic sandy loam soil on bulk density and saturated hydraulic conductivity.

Soil depth (m)	Control		Compaction (6 passes)	
	Bulk density (t/m^3)	Ks (mm/day)	Bulk density (t/m^3)	Ks (mm/day)
0.0–0.15	1.59	860	1.85**	320
0.15–0.25	1.54	1300	1.68**	1155
0.25–0.35	1.51	2130	1.55^{ns}	2060

** = significant at 1% (in comparison of control and compaction)
Ks = saturated hydraulic conductivity
ns = not significant
Source: Gupta et al. (1989)

Table 5. Effect of compaction and depth of recultivation of a lateritic sandy loam on yield of rice IR8 and wheat Sonalika.

Passes of 800-kg roller (C)	Depth of recultivation (D) (m)				
	0.00	0.05	0.10	0.15	Average
			Grain yield of rice (IR8) (t/ha)		
1	3.20	2.97	2.79	2.70	2.91
2	3.74	3.26	3.17	2.82	3.24
4	3.03	4.06	3.68	3.26	3.50
6	2.79	3.74	3.80	3.12	3.36
Mean	3.19	3.50	3.36	2.97	
Standard error difference at 5%:					
	Compaction (C)	0.33			
	Depth of cultivation (D)	0.15			
	Interaction (C × D)	0.38			
			Grain yield of wheat (Sonalika) (t/ha)		
1	3.64	3.03	2.79	2.88	3.09
2	3.18	3.82	3.34	2.91	3.31
4	2.52	3.18	4.12	3.73	3.40
6	2.28	2.70	3.85	3.70	3.12
Mean	2.91	3.18	3.52	3.31	
Standard error difference at 5%:					
	Compaction (C)	0.27			
	Depth of cultivation (D)	0.21			
	Interaction (C × D)	0.42			

Source: Gupta et al. (1989)

Table 6. Effect of puddling on bulk density of clay and clay loam soils on 1 day and 60 days after transplanting (DAT).

Depth (m)	Bulk density (t/m^3)							
	Clay soil				Clay loam soil			
	1 DAT		60 DAT		1 DAT		60 DAT	
	P	NP	P	NP	P	NP	P	NP
0–0.1	0.53	0.83**	0.67	0.89**	0.81	1.16**	1.18	1.21^{ns}
0.1–0.2	0.68	0.91**	0.99	1.02^{ns}	1.09	1.23**	1.34	1.39^{ns}
0.2–0.3	1.02	1.00^{ns}	1.04	1.04^{ns}	1.27	1.29^{ns}	1.33	1.38^{ns}

P = pudddled; NP = non-puddled
ns= not significant
**= $P<0.01$
Source: Sharma and De Datta (1985)

strength (Gupta and Jaggi 1979). Sharma and De Datta (1986) showed that the root-length density and grain yield of rice in clay and clay loam soils declined with increasing bulk density from 0.6 to 1.2 t/m^3 and soil strength declined from nearly zero to 0.8 megapascals (MPa). However, an increase in the depth of mud beyond about 30 cm may again lower rice yields by increasing the susceptibility of rice to lodging (Briones and Raymundo 1962).

Thermal Properties of Soil

There has been little good systematic research on the thermal properties of lowland fields and their effect on rice. The available information indicates that throughout the crop season in temperate regions of India, the ponded water in a rice field maintains soil temperature at 7.5 cm depth at about 5°C higher than the continuously flowing water and significantly increases the grain yield of rice (Kanwar et al. 1978). In tropical areas, high percolation keeps the maximum temperature of the root zone lower (Patel et al. 1984; Hasegawa et al. 1985). It therefore appears that restricted percolation may or may not be beneficial to rainfed lowland rice, depending upon climatic conditions.

The depth of ponding and atmospheric temperature affect the soil–water temperature under submerged soil conditions. For rice, the optimum submerged soil temperature regime is 37–25°C for root growth (Kar et al. 1976) and 32–20°C for grain yield (Chaudhary and Ghildyal 1970). When the depth of ponding decreases to zero and the topsoil dries during drought periods, the viability of tillers decreases. Thus, shallow submergence is desirable.

Impeded Drainage

One of the major problems affecting rainfed lowland rice is the poor drainability of fine-textured, puddled or compacted soils. Saturated hydraulic conductivity and percolation losses are reduced in puddled fields due to close packing of soil particles in parallel orientation. A subsurface traffic pan further restricts the downward movement of water. This restricted percolation helps in maximising nutrient efficiency and economising on water use, but some percolation may be essential if phytotoxins accumulate in the root zone.

Gaseous diffusion of carbon dioxide and oxygen is 10 000 times lower in water than in air. In submerged puddled soil, the exchange of gases, especially carbon dioxide, between the outer atmosphere and the soil is severely restricted. However, the rice crop does not suffer from an oxygen deficiency because most of the oxygen requirement is met through oxygen transported from the aerial parts of the rice plant to the roots through intercellular gaseous spaces.

Impeded drainage brings about a moderately reduced to highly reduced condition (redox potential −100 to −300 mV), which leads to the development of toxic substances and non-availability of some essential plant nutrients. The fall of redox potential in iron-rich lateritic soil is intensified by low densities and high temperatures. A healthy reduced condition may be attained with a percolation rate of 10–20 mm/day (Mandal 1984).

In temperate areas, organic acids accumulate in the soil (Cho and Ponnamperuma 1971). Because rice is sensitive to organic acids, leaching is needed to maximise rice production (Cho and Ponnamperuma 1971; Patel et al. 1979). Higher percolation rates help to increase rice grain yields by keeping phytotoxins at low levels. In addition, higher percolation rates may benefit rice crops by regulating soil temperature and the oxygen content of the soil solution, and improving root growth and nutrient uptake (Patel et al. 1984; Hasegawa et al. 1985). Research in Japan, China and Korea suggests that a percolation rate of 0.05–0.25 μm/second is essential for rice yields above 6 t/ha (Sharma and De Datta 1986).

Salinity and Alkalinity

Saline soils

There are two main groups of salt-affected soils: saline and alkaline. Saline soils have excess neutral soluble salts such as chlorides and sulfates of sodium, magnesium, and calcium. Small quantities of boron and other toxic elements may also be present. The electrical conductivity of saturated extract of saline soil is at least 4 decisiemens per metre (dS/m) with pH less than 8.2. Many soils have pH less than 7.0, and some are acidic (e.g. acid sulfate soils). Saline soils are well aggregated and have hydraulic conductivity similar to that of nonsaline soils. Rice crops grown on these soils are adversely affected during drought due to the high osmotic pressure of the soil solution.

The salinity of coastal saline soils varies seasonally. It is highest in May (the dry season), decreases as the wet season progresses and generally is lowest in September (towards the end of the wet season). Surface and subsurface drainage are impeded. Therefore, deep submergence in the wet season adversely affects rice growth. Salinity is common in inland soils in semiarid regions of India.

Rice does not tolerate excess salinity: rice yield is halved at 6–7 dS/m salinity in saturated soil paste extract (Mass and Hoffman 1977). However, a satisfactory yield of rice can be achieved even with 20–25 dS/m in topsoil saturated extract, if submergence is maintained throughout the crop growing season (van Alphen 1975).

Alkaline soils

Soils with an exchangeable sodium percentage (ESP) of more than 15 are characterised as alkaline. Their electrical conductivity is generally less than 4 dS/m, and saturated soil paste pH is greater than or equal to 8.2; it may be as high as 10. As ESP increases, soils become more dispersed and less permeable to air and water. Infiltration rate decreases drastically.

Rice tolerates exchangeable sodium because it grows well in standing water, but the infiltration rate needs to be sufficient to leach out toxic substances. Also, as rice has a shallow root system, it can grow well if sodicity is reduced in only the top few centimetres of soil. Excessive uptake of elemental sodium can be toxic at high ESP. Drought may affect rice in alkaline soils.

The rice yield decreases with an increase in sodicity (Table 7), but longer submergence of the soil before transplanting is beneficial in soils of high ESP (Swarup 1983).

Physical Constraints Affecting Upland Crops after Rice

In many parts of Asia, an upland crop is grown after rainfed lowland rice, primarily using residual moisture in the soil profile. The shift from a lowland puddled soil to a dryland soil requires major alteration in the physics of the soil because the land preparation for rice decreases the number and size of soil aggregates, and the number and size of water-transmitting pores. The conversion of a soil from the wet to the dry condition is therefore characterised by an improvement in the soil structure destroyed during puddling. When a well-puddled clayey soil dries, it hardens and it is difficult to prepare the seedbed for upland crops. Montmorillonitic clay soils with low organic matter and iron oxide content are more difficult to convert from lowland to dryland use than Kaolinitic clay, which has more organic matter and a higher iron oxide content (Briones 1977).

After rice is harvested, it takes a long time for lowland fields to attain a soil moisture level suitable for optimum seedbed preparation, because cultivation in wet soil produces cloddy surface soil, resulting in poor seed–soil contact, rapid drying, and reduced germination and seedling establishment. In Vertisols, the optimum soil moisture condition lasts for only a very brief period, and primary tillage under both wet and dry conditions will produce massive, hard clods that require enormous energy and effort to break by secondary tillage. Tillage after the rice harvest in Hyderabad (India) did not restore aggregate size distribution in a fine soil to its pre-puddled state (Prihar et al. 1985).

Having to wait for a puddled soil to arrive at the optimum tillage moisture has another disadvantage. A longer 'turnaround' time results in low crop yield (Emerson et al. 1987) due to increased soil profile desiccation and probably a less congenial aerial climate.

Table 7. Effect of exchangeable sodium percentage (ESP) and submergence before transplanting (presubmergence) on the yield of rice.

Duration of presubmergence (days)	Rice yield (t/ha) at ESP of 35	65	72	82	Mean
0	5.41	3.59	3.26	1.46	3.42
15	5.61	4.01	4.00	2.01	3.92
30	5.71	4.68	4.50	2.58	4.36
Mean	5.57	4.11	3.92	2.01	
LSD (5%): ESP = 0.16, presubmergence = 0.15, ESP × presubmergence = 0.30					

Source: Swarup (1983)

Compact subsurface layers of low permeability favour rice cultivation by reduced percolation and traffic support; they adversely affect the upland crops grown after lowland rice by encouraging waterlogging and offering mechanical resistance to the growing roots. The exploitable depth of soil is also reduced. The influence of pans on root growth and rice yield is unclear.

In India, low yields of non-rice crops such as wheat, linseed (*Linum usitatissimum* L.), mustard (*Brassica* spp.) and groundnut (*Arachis hypogaea* L.) are encountered after rice has been grown. In fine-textured soils at IRRI in the Philippines, a reduced yield of mungbean (*Vigna radiata* L.) has been reported (Woodhead and Maghari 1984). Working with high-swelling and cracking clayey soils (Vertisols) at Jabalpur, India, Tomar et al. (1996a) reported that rainfed lowland rice yields were only marginally higher in puddled plots (4.4 t/ha) than in direct-seeded rice (4.1 t/ha). When the wheat crop was grown after puddled and direct-seeded rice, the yields were 3.7 and 4.0 t/ha, respectively. Thus, in these soils puddling had little deleterious effect on wheat grain yield.

Managing Physical Properties of Vertisols: A Case Study

Vertisols — black clayey soils — occupy 257 million ha worldwide and 72.9 million ha in India. They are sticky and plastic when wet and very hard when dry (Table 8). They therefore have a narrow moisture range for optimum tillage operations. In central India, the rainfall (mean annual 1130 mm) received in the wet season, during the period from mid-June until September to mid-October, is highly erratic (Fig. 3). Vertisols are either cultivated as rainfed for lowland rice (low yield) or kept fallow in the rainy season, with post-rainy season crops raised on profile stored moisture. A land and water management practice — 'raised and sunken bed' (RSB) system — has been developed at the experimental station at J.N. Agricultural University, Jabalpur, Madhya Pradesh, India to increase productivity and cropping intensity of these soils. The RSB system has been developed for deep Vertisols receiving less than 700 mm annual rainfall.

Raised and sunken bed system

In the RSB system the land is shaped into 6–9 m wide, 0.30–0.35 m high raised beds running in parallel, with intervening sunken beds of 6 m width and 0.30–0.35 m depth. A motor grader moves the surface 0.15 m of soil from 6 m wide strips referred to as sunken beds to 6–9 m wide strips designated as raised beds (Tomar et al. 1996b).

Rainfed lowland rice has been grown in sunken beds and soybean (*Glycine max* L. Merrill) in raised beds in rainy seasons from 1979 to 1991. In the period after the rainy season, chickpea (*Cicer arietinum* L.), linseed and safflower (*Carthamus tinctorius* L.) were grown in raised beds and wheat in sunken beds. Results of the RSB system (Table 9) clearly show that the technology will help to increase rainfed lowland rice yields, reduce wet-season fallowing, and increase cropping intensity as well as stabilise yield levels.

Table 8. Some physical properties of soil at Typic Haplustert Experiment Station, Jabalpur.

Depth (m)	Bulk density (t/m^3)	Particle size distribution (%)			Soil water retention (m^3/m^3) at suction (kPa)			Basic infiltration rate(μm/second)
		Sand	Silt	Clay	0	33	1500	
0.0–0.2	1.33	18	27	55	0.47	0.32	0.20	0.75
0.2–0.4	1.51	17	27	56	0.49	0.33	0.22	–
0.4–0.6	1.58	18	26	56	0.47	0.34	0.23	–
0.6–0.8	1.63	16	31	53	0.52	0.37	0.23	–
0.8–1.0	1.60	17	28	54	0.50	0.36	0.23	–

Source: Tomar et al. (1996a)

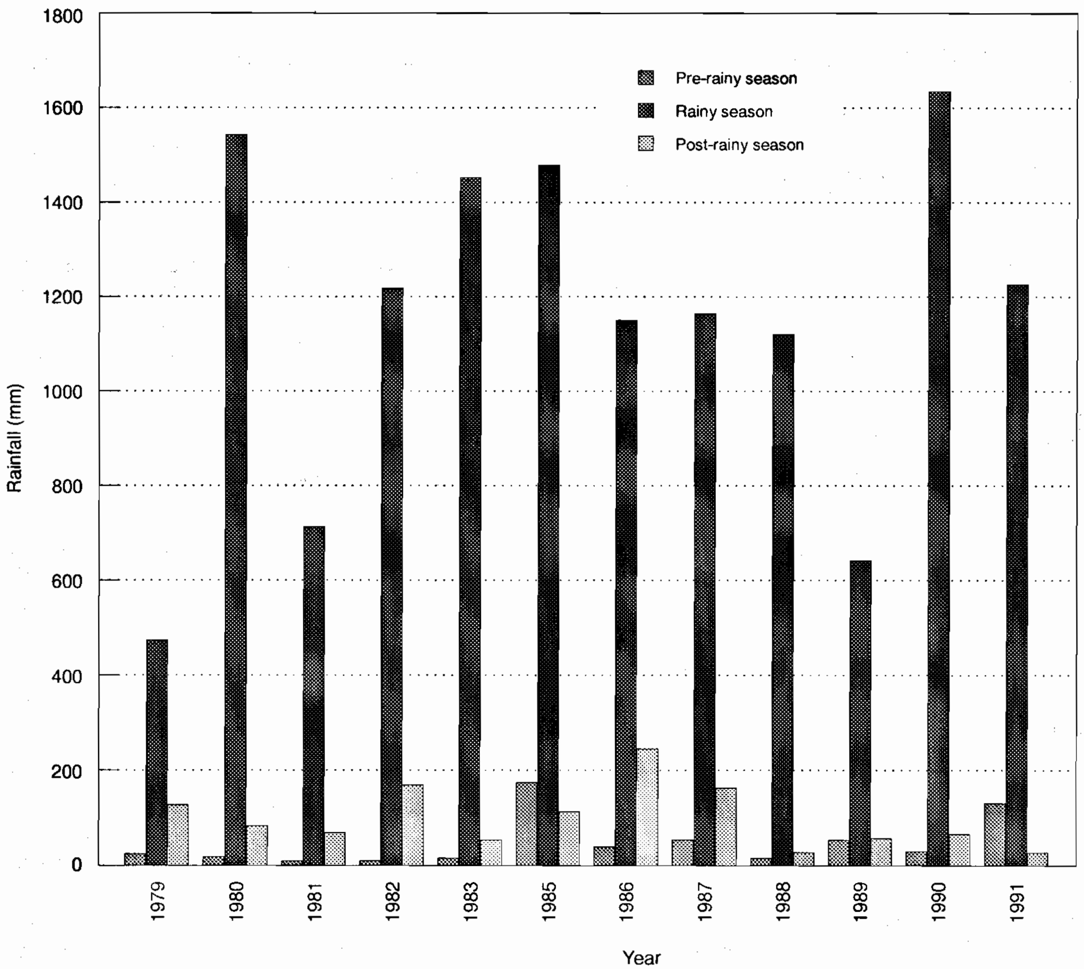

Figure 3. Rainfall distribution, central India, 1979–91.

Table 9. Yield of rainfed lowland rice and non-rice crops under raised- and sunken-bed systems, Jabalpur.

Crop	Yield (t/ha)			
	Sunken bed	Raised bed		Flat bed
		6 m wide	9 m wide	
Rainy season (1979–91)				
Paddy	2.58	–	–	1.20
Soybean	–	2.33	2.22	1.08
Post–rainy season (1986–87 to 1990–91)				
Chickpea	–	1.81	1.80	0.83
Linseed	–	1.10	0.90	0.64
Safflower	–	1.38	1.06	0.64
Wheat	1.30	–	–	–

Source: Tomar et al. (1996b)

Conclusions

The poor soil physical environment of rainfed lowland rice affects the production and stability levels of rice and those of subsequent non-rice crops in sequence. Improved rice cultivars and increased use of fertilisers and organic manures will contribute to increased production, but their full potential will be realised only if soil physical properties are properly understood and managed.

Water management is of primary importance in rainfed lowland rice. Proper understanding and management of soil physical properties will encourage better water use and its management. Watershed-based technology may help in this regard; it should therefore be evaluated for rainfed lowland systems.

Pertinent research is lacking on several aspects and should focus on reducing drought hazards and minimising the adverse effect of impeded drainage. Research is also needed on utilising the potential of improved rice cultivars in a poor soil physical environment. There is a need for research on the establishment of non-rice crops after rainfed lowland rice to utilise the residual soil moisture.

Very few soil physicists are working in close collaboration with rice breeders. However, such programs are definitely helpful for utilising the huge available potential for improved cultivars in poor soil physical environments, and in generating new rice cultivars adapted for specified constraints.

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Responses of Four Rice Cultivars to Lime and Irrigation in the Rainfed Lowlands of Northeastern Thailand

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Abstract

An experiment was conducted in the wet season of 1994 to examine the response of four contrasting rice cultivars to application of lime and irrigation at Ubon Ratchathani Rice Research Centre and Tapra near Khon Kaen city, Northeastern Thailand. The four rice cultivars were KDML105, NSG19, IR57514-PMI-5-B-1-2 and IR20. At Ubon, there was a large response of all cultivars to lime, though there was no drought during crop growth. When lime was applied, the average rice yield increased by 18%, and this increase was associated with increase in grain number per panicle. Among the four cultivars, IR57514-PMI-5-B-1-2 had the highest average grain yield, of 1.98 t/ha, whereas IR20 had the lowest yield, of 1.24 t/ha. At Tapra, only irrigated rice showed a response to lime. Under rainfed conditions, grain yield of KDML105, NSG19, IR57514-PMI-5-B-1-2 and IR20 was lower by 13, 20, 25 and 35%, respectively, compared to irrigated conditions. IR57514-PMI-5-B-1-2 had a high yield under both irrigated and rainfed conditions, whereas IR20 showed a high yield only under favourable conditions with lime application and irrigation.

RICE yield in Northeastern Thailand is very low, with an average of 1.64 t/ha, due to drought and adverse soil conditions. In this region, rainfed lowland rice occupies 4.16 million ha of the total rice area of 4.92 million ha (OAE 1994). Erratic rainfall distribution means there is inadequate water for optimum rice growth during the growing season. The typical rainfall distribution from May to October follows a bimodal pattern, with a minor peak in June and a major peak in September. Average annual rainfall in the northeast varies from less than 1000 mm in the rain-shadow area in the west to over 2300 mm along the Mekong River (Craig and Pison 1985). While the total amount of rainfall may be the same in different years or locations, rainfall distribution within a season varies greatly. At the beginning of a cropping season there might be heavy rainfalls, but they are often followed by long dry spells. The sandy soil that is common in Northeastern Thailand has low water-holding capacity, and water drains quickly from the paddy after rainfall. Hence, drought may occur at any time during a growing season.

The rainfed rice growing area in the northeast covers an extensive area of acidic sandy soil, stretching from Nakhon Ratchasima to the Mekong River. The soil is derived from highly weathered alluvium and has been further weathered by ferrolysis (Brinkman et al. 1977). The surface soils are generally acidic (pH < 5), with low cation exchange capacity and low fertility. Other factors affecting yield are the excessive levels of iron and aluminium released from these soils, and the fixation of phosphorus (P) that is not then available to the rice plant.

One recommended approach to improving crop yield on acid sandy soil is better water control to reduce oxidation and acid formation and to enhance leaching of the acid. However, under rainfed conditions where drought usually occurs, low soil pH is a major problem. Liming acid soil is one of the oldest methods of improving crop yield through improving

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problem soils. Lime increases soil pH as well as the availability of most plant nutrients. It also increases nitrogen (N) mineralisation (Kawaguchi and Kyuma 1969). Lime application and flooding conditions also increase soil pH (Sharma and Sinha 1989), and when lime was applied to upland rice, dry matter and grain yields increased by up to 32 and 19%, respectively (Fageria et al. 1991). Rice is the major crop suitable for these problem soils in Northeastern Thailand. The use of tolerant varieties and appropriate management are the keys to improving rice yields in the region. The objective of the study reported here was to find out if four rice cultivars differed in their ability to withstand low pH and drought.

Materials and Methods

Two field experiments were conducted at Ubon Rice Research Centre (Ubon) and at a previously uncropped area at Tapra about 12 km from Khon Kaen city in the wet season 1994. Split-plot design was used for both irrigated and rainfed conditions; there were four replications. Fertiliser with and without lime was assigned to main plots. Four rice cultivars, including three considered to be drought resistant (IR57514-PMI-5-B-1-2, KDML105 and NSG19) and one susceptible cultivar (IR20) were assigned to subplots.

At Ubon, basal fertiliser (40-40-20 kg/ha N-P_2O_5-K_2O) with and without lime was applied at the rate of 1500 kg/ha on 29 June 1994. Two days later, each variety was direct seeded with spacing of 25 × 25 cm in a plot that consisted of eight rows, each 5 m long. Fertiliser N was top-dressed at the rate of 20 kg N/ha on 2 September 1994. There was no irrigation, as the paddy was flooded three weeks after seeding rice, and flooded conditions continued throughout the crop growth. Therefore, we combined the two watering conditions and data were analysed with eight replications.

At Tapra, basal fertiliser at the rate of 30-30-30 kg/ha N-P_2O_5-K_2O with and without lime at the rate of 1000 kg/ha was applied before transplanting on 3 August 1994. Hill spacing was 25 × 25 cm, and each plot consisted of six rows, each 5 m long. Fertiliser N was top-dressed at the rate of 30 kg N/ha on 12 September 1994. In irrigated conditions, water was supplied to the paddies weekly from transplanting until 14 September, when all plots were flooded due to heavy rainfalls. The flooded conditions continued until harvest.

Data collection and analysis

Soil samples were taken before and after lime treatments were applied, then analysed for pH (1:1 H_2O), organic matter (Walkley), total N (microkjeldahl), available P (Bray II), and extractable potassium (K) (atomic absorption spectrophotometer). Water levels in the paddies were recorded weekly using 10-cm diameter PVC tubes. Number of days to flowering was recorded when 75% of panicles exserted above the flag leaf. Plant height from ground level to the tip of panicles was recorded for 10 plants. Grain yield (14% moisture content) and total dry matter (TDM) were estimated from a harvest area of 1 × 4 m. Panicle number was counted from an area of 1 × 1 m, grain number was counted for 10 panicles, and the weight of 1000 grains was determined.

At Tapra, there was a significant difference in the yield of rice varieties between irrigated and rainfed conditions, but there was only a slight effect of lime application on grain yield. Thus, only the effect of lime on grain yield is shown for each variety. Other data are shown as the mean of treatments with and without lime application, and cultivars are compared under irrigated and rainfed conditions.

Results

Soil analysis

The soil at Ubon comprised 88.8% sand, 6.8% silt and 4.4% clay, and at Tapra 61.2% sand, 24.7% silt and 14.1% clay. The chemical properties of soil at Ubon and Tapra are shown in Tables 1 and 2 respectively. Before planting the rice plants at Ubon the soil pH was 3.9 and 4.0 under rainfed and irrigated conditions, respectively. This was lower than the pH of soil at Tapra, which was 4.5 and 4.6 under irrigated and rainfed conditions, respectively. Organic matter, total N and extractable K were lower, but available P was slightly higher at Ubon than at Tapra. After the rice harvest, soil pH at Ubon was increased by 1.1–1.2 units with lime application under both rainfed and irrigated conditions, while pH was raised by only 0.2–0.6 units at Tapra. There was only a slight change with lime application in soil organic matter and total N at both locations.

Rainfall and water level in the paddies

At Ubon rainfall increased after rice sowing, with a peak in late August (Fig. 1a). High rainfall resulted in high free water levels in the paddy in both rainfed and irrigated conditions (Fig. 1b). Free water level in rainfed conditions was slightly lower than in the irrigated condition, but the paddies were flooded three weeks after sowing, and the flooded condition continued until harvest.

At Tapra, rainfall was much less than in Ubon in July (Fig. 2a) and the experimental plot was not flooded on the transplanting date; therefore, for transplanting, water was supplied to both the irrigated and rainfed conditions. There was about 10–15 cm standing water under irrigated conditions. Rainfed paddies were not flooded until the middle of September except for transplanting, after which the flooded conditions remained for three days. At Tapra, rainfall was highest in early September (248 mm). The paddies were flooded in both irrigated and rainfed conditions, and the flooded conditions continued until harvest (Fig. 2b).

Plant height and phenological development

Lime did not have a significant effect on plant height at Ubon (Table 3). NSG19 was the tallest cultivar; KDML105 and IR57514 were medium and IR20 was the shortest. At Tapra, plant height of different varieties was of the same order as at Ubon. However, there was a significant effect of water stress at Tapra under rainfed conditions: plant height was reduced by 18% in IR20 and by 10–15% in other cultivars compared to the irrigated condition (Table 4).

Table 1. Chemical properties of soil at Ubon Rice Research Centre, wet season 1994.

Condition	Chemical properties				
	pH (1:1 H_2O)	Organic matter (%)	Total N (%)	Available P (ppm)	Extractable K (ppm)
Irrigated					
Before planting	4.0	0.381	0.0296	17.5	24
After harvesting					
– lime	4.2	0.5184	0.0264	32.0	na
+ lime	5.4	0.4664	0.0213	29.8	na
Rainfed					
Before planting	3.9	0.347	0.0208	17.4	18
After harvesting					
– lime	3.8	0.4538	0.0235	37.1	na
+ lime	5.0	0.4125	0.0213	34.8	na

na = not available

Table 2. Chemical properties of soil at Tapra, Khon Kaen, wet season 1994.

Condition	Chemical properties				
	pH (1:1 H_2O)	Organic matter (%)	Total N (%)	Available P (ppm)	Extractable K (ppm)
Irrigated					
Before planting	4.5	0.588	0.07	16	59
After harvesting					
– lime	4.8	0.496	0.05	11	47
+ lime	5.0	0.455	0.04	11	96
Rainfed					
Before planting	4.6	0.542	0.04	11	114
After harvesting					
– lime	5.0	0.469	0.04	9	25
+ lime	5.7	0.479	0.05	10	74

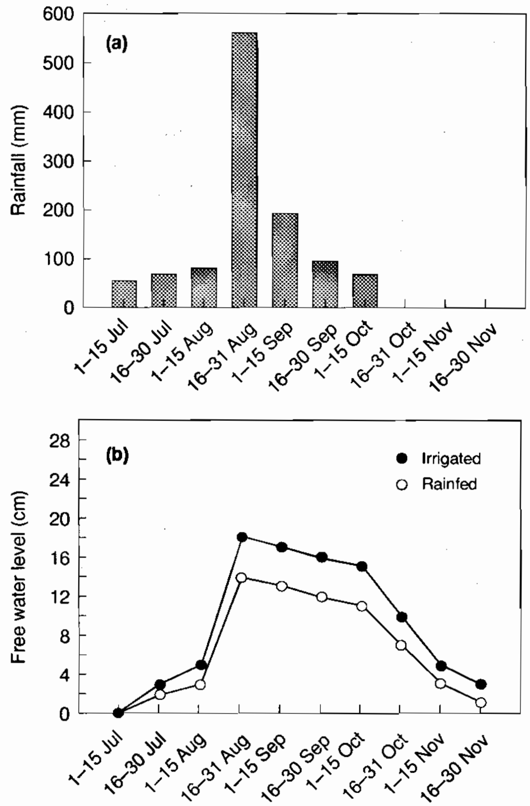

Figure 1. Rainfall (a) and free water level in the two treatments (b) at Ubon, Northeastern Thailand, wet season 1994.

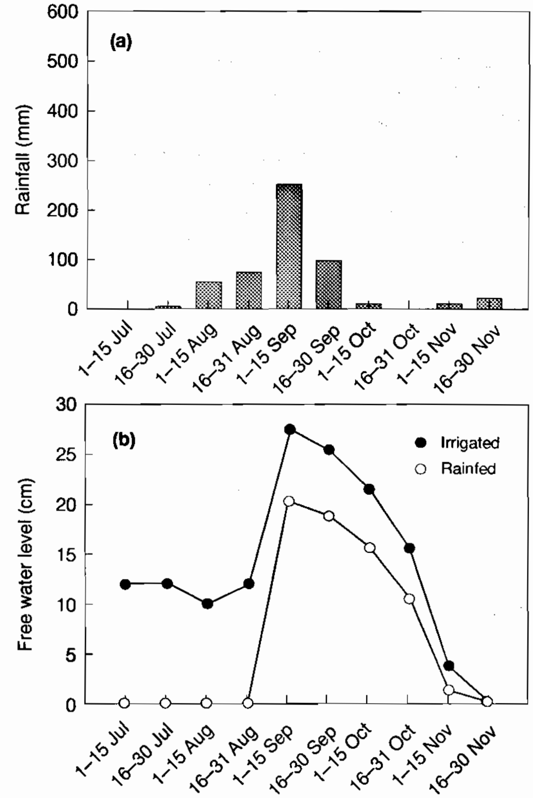

Figure 2. Rainfall (a) and free water level in the two treatments (b) at Tapra, Northeastern Thailand, wet season 1994.

Table 3. Plant height (cm) as affected by lime application at Ubon, wet season 1994.

Cultivar	– lime	+ lime	Average
KDML105	99b	90b	95b
NSG19	112a	116a	114a
IR57514	86c	89b	88b
IR20	74d	78c	76c

Note: Results followed by the same letter are not significantly different ($P < 0.05$)

Table 4. Plant height (cm) as affected by water availability at Tapra, Khon Kaen, wet season 1994.

Cultivar	Irrigated condition	Rainfed condition	Difference (%)
KDML105	149a	126b	15.4
NSG19	150a	133a	11.3
IR57514	128b	110c	14.0
IR20	122c	100d	18.0

Note: Results followed by the same letter are not significantly different ($P < 0.05$)

Lime did not have a significant effect on days to 75% flowering at Ubon. However, there were significant differences among the four cultivars (Table 5); KDML105, IR57514, NSG19 and IR20 took 111, 109, 106 and 104 days to flowering, respectively. At Tapra, lime application had no significant effect, but water stress delayed phenology by 3–8 days. NSG19 was the earliest-maturing variety, followed by IR57514 and IR20; KDML105 was the latest-maturing cultivar.

Table 5. Phenology of four varieties (days after sowing) at Ubon and Tapra, wet season 1994.

Phenology	Rice variety			
	KDML105	IR57514	NSG19	IR20
Ubon				
Days to 75% flowering	111a	109a	106b	104b
Days to maturity	141a	139a	136b	134b
Tapra — irrigated				
Days to 75% flowering	116a	100b	94b	103b
Days to maturity	144a	133b	126c	133b
Tapra — rainfed				
Days to 75% flowering	121a	106b	107b	111b
Days to maturity	148a	136b	133b	137b

Note: Results followed by the same letter are not significantly different ($P < 0.05$)

Grain yield, total dry matter and harvest index

At Ubon, lime had a significant effect on grain yield, with an increase of about 18% (Fig. 3a). Grain yields of KDML105, NSG19 and IR20 increased by about 20–25% with lime application. For IR57514, grain yield increase was only 10%, and was not significant. IR57514 had the highest average yield, of 1.98 t/ha, which was significantly higher than that of KDML105 and NSG19; IR20 had the lowest yield, of 1.24 t/ha. Lime had a significant effect on TDM of all cultivars, but the proportion of TDM increase was higher in IR20 and IR57514 than in NSG19 and KDML105 (Fig. 3b). Lime did not have a large effect on harvest index (Fig. 3c). There was a significant interaction of rice cultivar and lime application on harvest index. Harvest indexes of KDML105 and NSG19 were higher with application of lime, whereas harvest indexes of IR57514 and IR20 were higher without lime application.

At Tapra, lime had a slight effect on grain yield under irrigated conditions but did not show any positive effect under rainfed conditions except for IR20 (Fig. 4a). There was a significant interaction between lime and cultivar for irrigated rice. The application of lime increased grain yield of IR20 by up to 22% but of the other cultivars by only 6–9% under the irrigated conditions.

Lime had a significant effect on grain yield at Ubon as the application rate was higher and soil pH was lower than at Tapra. The result for IR20 at Tapra was similar to that reported by Verma and Tripathi (1987). They found that the application of lime did not increase grain and straw yield significantly under soil-water saturation, but did so under submergence. They reported that lime was responsible for decreasing iron content in the rice plant under both conditions, with a higher relative decrease under submergence than when saturated. We found that IR20 appears to be the most susceptible to acid soil as it responded to lime more than did other cultivars at either location. Although lime was applied at 1500 kg/ha at Ubon, the grain yield of IR20 was significantly lower than for IR57514. The yield may have been limited by low pH or low soil fertility, as water stress was not the limiting factor.

At Tapra, the average rice yield obtained in irrigated conditions was 24% higher than that in rainfed conditions. IR20 was the most sensitive to drought, with grain yield declining by 35% under rainfed conditions; the grain yields of IR57514, NSG19 and KDML105 were reduced by 25, 20 and 13%, respectively.

IR57514 is a promising line for rainfed lowland rice and had the highest grain yield under both irrigated and rainfed conditions. The average yields of IR57514 were slightly over 4 t/ha and 3 t/ha under the irrigated and rainfed conditions, respectively. The grain yield of IR20 was not significantly different from that of IR57514 under irrigated conditions, but it was significantly lower under rainfed conditions.

Water stress reduced TDM, but not harvest index (Figs 4b and c). Under irrigated conditions, the harvest indexes of NSG19, IR57514 and IR20 were not significantly different from each other; they were significantly higher than the harvest index for KDML105. There were no significant differences in harvest index among the four cultivars under rainfed conditions.

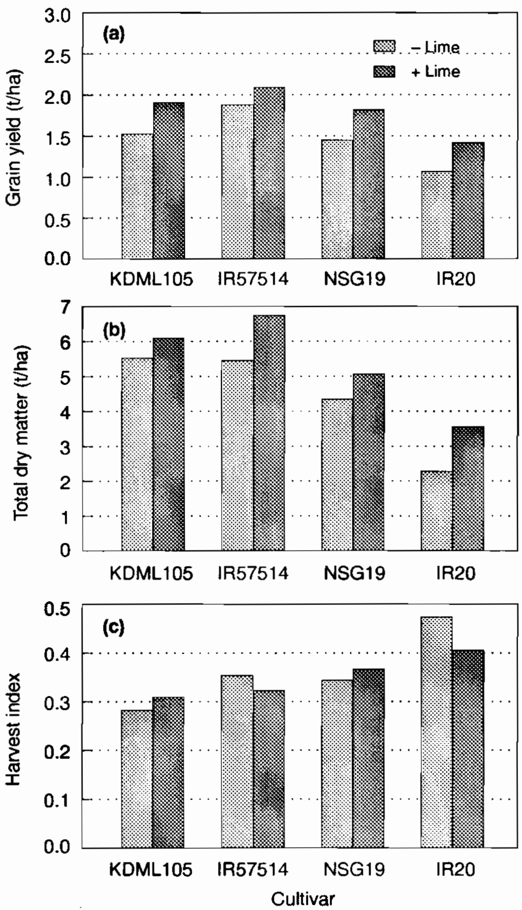

Figure 3. Grain yield (a), total dry matter (b), and harvest index (c) of four rice cultivars grown with or without lime application at Ubon, Northeastern Thailand, wet season 1994.

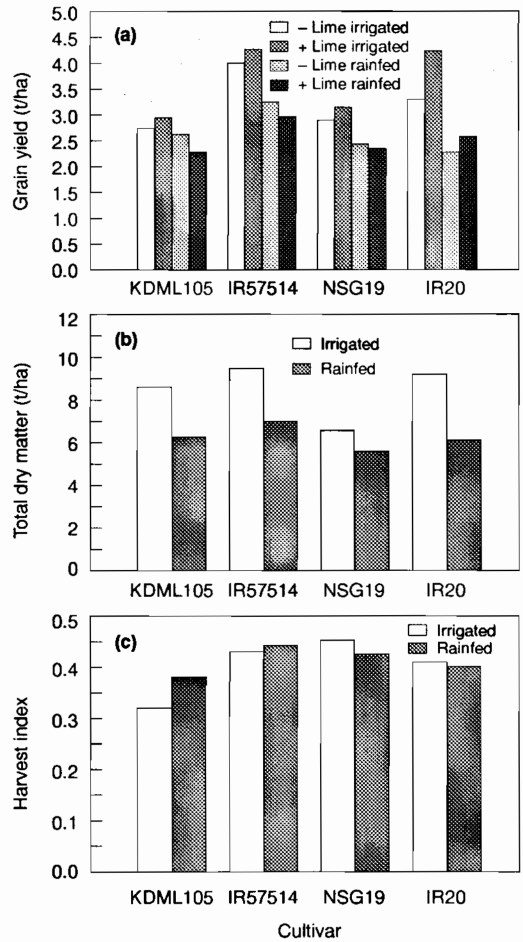

Figure 4. Grain yield (a), total dry matter (b) and harvest index (c) of four rice cultivars under rainfed and irrigated conditions at Tapra, Northeastern Thailand, wet season 1994. The effect of lime application is shown only for grain yield.

Irrigation had a large effect on phenology, TDM and grain yield at Tapra as there was no floodwater in the rainfed paddies for about six weeks after transplanting, until mid-September. Water stress in this period was mild, and there were no visible drought symptoms such as leaf death or leaf rolling. However, phenology of all cultivars was delayed, and panicle number and grain number were decreased. Grain yield of IR20, the cultivar most sensitive to drought, was reduced by up to 35%. Similar results were obtained by Ismunadji (1985). He reported that grain yield was significantly higher under submerged conditions than when the water content of the soil was maintained at field capacity. The rice plants grew taller under submerged conditions, and were harvested two weeks earlier than the plants grown at field capacity.

Yield components

Effects of lime application on yield components at Ubon are shown in Figure 5. Lime application did not have a large effect on yield components for most cultivars. IR57514 had the highest panicle number, followed by IR20 and KDML105. NSG19 had the smallest panicle number (Fig. 5a).

There was a significant interaction of lime application and cultivar on grain number per panicle. IR20 had the highest grain number per panicle when lime was applied. The number was increased by 28% compared to that with no lime application. Grain number of NSG19 was increased by 17% by lime application. Lime had almost no effect on grain number in KDML105 and IR57514 (Fig. 5b). IR20 had a significantly lower filled grain percentage than did the other three cultivars (Fig. 5c). The weight of 1000 grains of IR20 was significantly less than for the other three cultivars, and NSG19 had a significantly higher dry weight of 1000 grains than did the other three cultivars (Fig. 5d).

Yield components of four rice cultivars under irrigated and rainfed conditions at Tapra are shown in Figure 6. Under the irrigated condition, IR57514 had the highest panicle number but it was not significantly different from IR20 (Fig. 6a). KDML105 and NSG19 had a significantly smaller panicle number. Under rainfed conditions, IR57514 had a significantly higher panicle number than did other cultivars.

Under irrigated conditions, IR20 had the highest grain number per panicle, but it was not significantly different from IR57514 (Fig. 6b). KDML105 had the smallest grain number. Under rainfed conditions, grain number per panicle was significantly lower than in irrigated conditions, but the cultivar ranking was the same.

Filled grain percentage was not significantly different among the four cultivars except for NSG19 under irrigated conditions, in which the earliest-maturing cultivar had the lowest percentage of filled grain, due to bird damage (Fig. 6c). Under both irrigated and rainfed conditions, KDML105 and NSG19 had a significantly higher 1000-grain weight than did IR57514 and IR20, whereas the effect of water stress on 1000-grain weight was small (Fig. 6d).

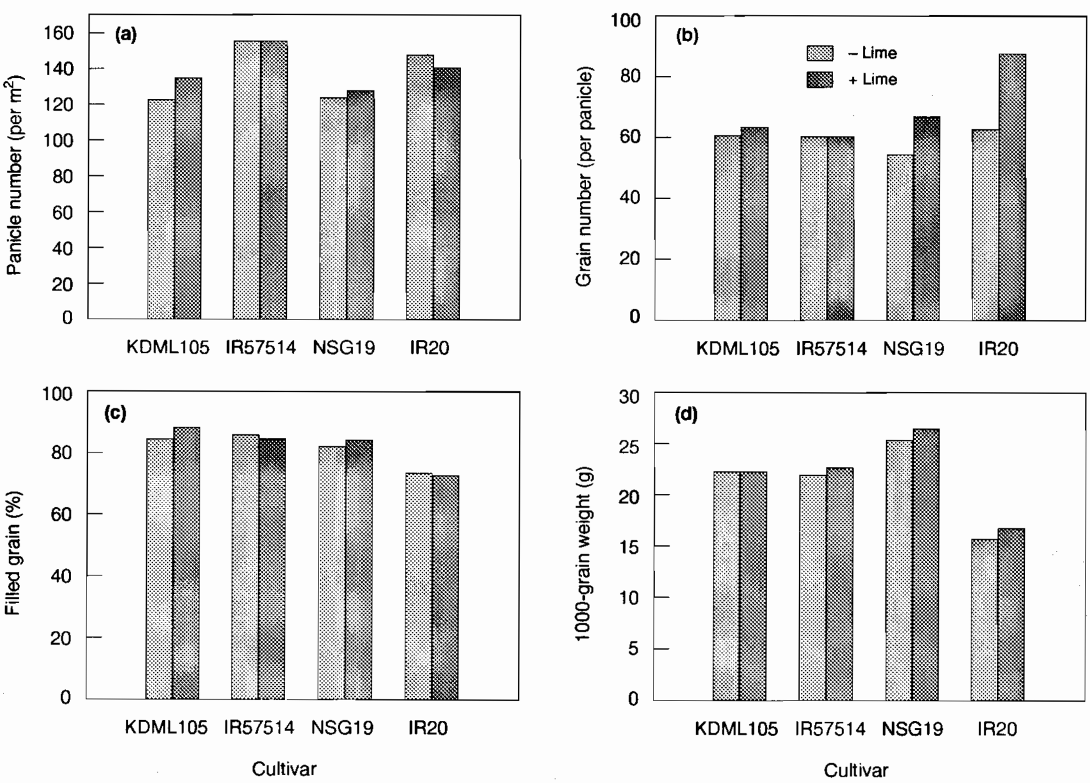

Figure 5. Panicle number (a), grain number per panicle (b), filled grain percentage (c) and 1000-grain weight (d) of four rice cultivars grown with or without lime application at Ubon, Northeastern Thailand, wet season 1994.

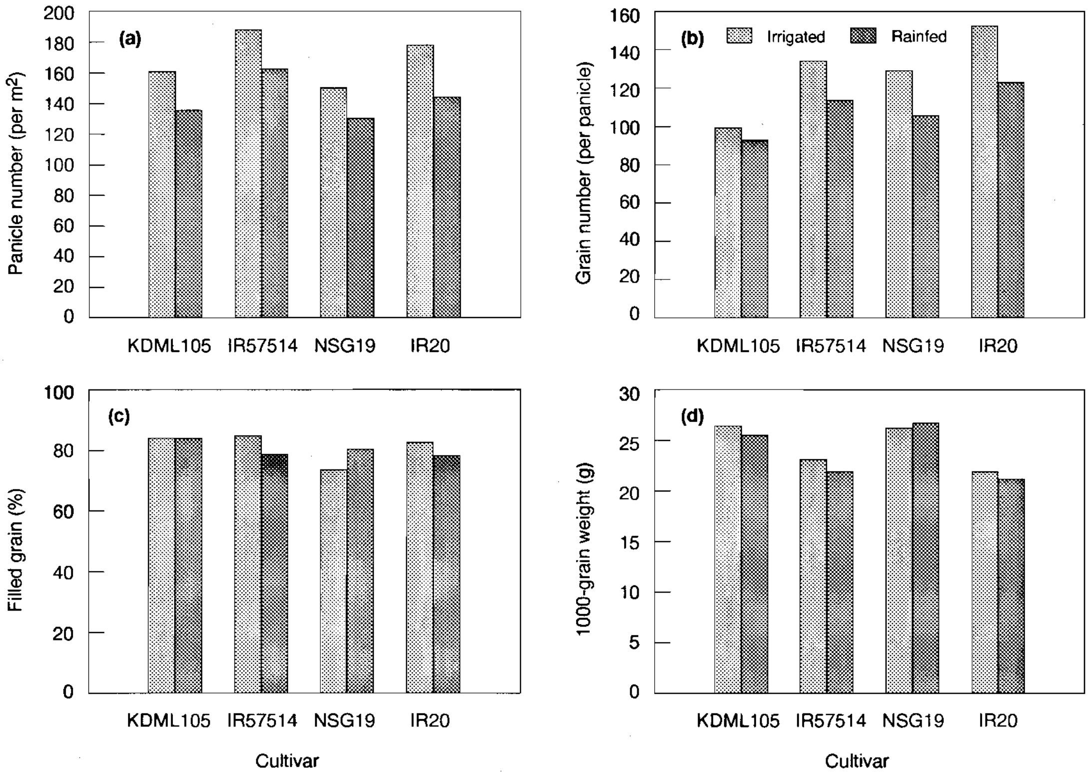

Figure 6. Panicle number (a), grain number per panicle (b), filled grain percentage (c) and 1000-grain weight (d) of four rice cultivars grown under irrigated and rainfed conditions at Tapra, Northeastern Thailand, wet season 1994.

Conclusions

Lime application increased average grain yield by up to 18% at Ubon, but only 5% at Tapra. The difference was associated with differences in soil pH and the amount of lime applied. IR20 appears to be more susceptible to low pH than the three other cultivars studied. Irrigation increased grain yield by up to 24% at Tapra, where there was no standing water for six weeks after transplanting under rainfed conditions.

Acknowledgments

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Effects of Fertiliser Application and Irrigation on Grain Yield of Rice Cultivars Grown under Lowland Conditions

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Abstract

Two lowland experiments were conducted to determine the effects of fertiliser application and irrigation on grain yield of six contrasting rice cultivars at Sanpatong, Northern Thailand. These cultivars were also compared in three other experiments to determine genotype-by-environment interaction for yield of lowland rice.

Without fertiliser application and irrigation, mean yield in each experiment was 1.3–1.6 t/ha. Yield responded to application of both farmyard manure and chemical fertiliser, and the effect of fertiliser was greater in rainfed than irrigated conditions. Despite no obvious water-stress symptoms in rainfed conditions, where free water level was sometimes below the soil surface, the yield almost doubled with irrigation, and the effect of irrigation was greater when no fertiliser was applied.

Among the 13 environments where the same four cultivars were grown, mean grain yield varied from just over 1.0 to 4.5 t/ha and significant genotypic variation was obtained in eight environments. Generally early-flowering cultivars (IR20 and NSG19) produced lower yield than medium- to late-flowering cultivars (IR57514-PMI-5-B-1-2 and KDML105). Late-flowering cultivars (E-Pad and Chiangsaen) generally performed better than the early-flowering cultivars. These differences among phenology groups were caused by the fact that the early-flowering cultivars produced lower total plant dry matter and a higher proportion of unfilled grain.

There was, however, significant genotype-by-environment interaction. Generally, there were larger differences in yield between cultivars in high-yielding environments where irrigation and fertiliser were applied, whereas the genotypic variation was much smaller in environments where there was no application of irrigation and fertiliser.

RAINFED lowland rice is grown on 37 million ha in South and Southeast Asia, which is 25% of the world's rice-growing area (IRRI 1995). In Northern Thailand a large part of the rice-growing area has been cultivated with low application of chemical fertiliser, the average amount of mixed fertiliser being 71 kg/ha (OAE 1994), despite the fact that most soils in the region are low in organic matter, available phosphorus (P) and cation exchange capacity (Jiraporncharoen 1993). Low average rice yield in Northern Thailand (2.5 t/ha) is to some extent associated with inadequate application of fertiliser.

Organic fertiliser such as farmyard manure is an alternative source of nutrients and appears to be more beneficial than chemical fertiliser for crops grown on sandy soils. Nutrients from farmyard manure become available gradually and hence for a long time during growth. In addition, organic fertiliser improves soil structure and soil moisture retention (FAO 1987), and this is beneficial for rainfed lowland rice.

Lack of adequate soil water is another major constraint for rice production in rainfed lowland ecosystems, particularly in Northeastern Thailand, where the deep percolation rate is high (Fukai et al. 1995). The rainfall pattern during the monsoon season is such that rice may be exposed to flood and drought

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within a growing season. In addition to the direct effect of water stress, the fluctuation of water level in rice paddies, especially the alteration of aerobic and anaerobic conditions, affects availability of some nutrients. Standing water in rice paddies increased the availability of nitrogen (N), P, silicon and molybdenum, while in non-submerged conditions P availability decreased (Ragland et al. 1987).

Rice genotypes may differ in their response to low soil fertility and drought. Some Thai cultivars, such as KDML105, are thought to adapt well to low soil fertility conditions. On the other hand, modern semi dwarf indica cultivars require a high rate of N fertiliser for high yield (De Datta et al. 1968). A number of studies have investigated the nature of drought resistance in different rice cultivars, and those suitable for rainfed conditions in Northeastern Thailand have been identified by Jearakongman et al. (1995). These high-yielding cultivars had a high harvest index under favourable growing conditions, with flowering time matching water availability, and an ability to maintain green leaves and some growth during drought. However, drought-resistant cultivars identified under high soil fertility may not be able to express their potential advantages when soil fertility is very low (Wongprasaid et al. 1996). Thus, rice cultivars which were selected under favourable conditions may not perform better than others do under adverse conditions such as drought and low soil fertility.

Several experiments were conducted to examine the effect of fertiliser and irrigation on the yield of several rice cultivars, and to identify any genotype-by-environment interactions. Findings may assist breeders in determining whether cultivars with drought resistance can be adequately selected under favourable soil conditions or whether selection should be done under various soil conditions.

Materials and Methods

Two types of lowland experiments were conducted at the Sanpatong Rice Experiment Station, Northern Thailand, latitude 18°16'N, longitude 98°50'E. In Experiment 1, 4–6 rice cultivars were compared to examine the effect of irrigation and fertiliser application in 1993 and 1994, whereas in Experiment 2 thirty-five cultivars, including those used in Experiment 1, were compared in 1992–94. The experimental site was an infertile, sandy loam soil which contained low organic matter, a moderate level of available P and very low extractable potassium (K). The chemical and physical properties of the soil are shown in Table 1.

Experiment 1

In each year, there were irrigated and rainfed trials which were separated by a 1.5 m wide laneway. In the irrigated trial, water level was always kept above the soil surface. In the rainfed trial, the soil was irrigated once for transplanting in both years but no irrigation was applied thereafter.

Each trial was designed as a split plot with three replications in 1993 and four in 1994. Fertiliser application was assigned in the main plots and cultivars in the subplots. Rice was transplanted at 3 seedlings per hill and hill spacing was 25 × 25 cm.

In 1993, there were two fertiliser treatments: nil and farmyard manure application. There were six cultivars: IR20, NSG19, KDML105, IR57514-PMI-

Table 1. Properties of soil at experimental site for Experiment 1, Sanpatong Rice Experiment Station, Northern Thailand.

	1993		1994	
	Irrigated	Rainfed	Irrigated	Rainfed
pH	6.1	6.5	5.9	6.7
Organic matter (%)	0.45	0.80	0.8	0.4
Total N (%)	0.04	0.03	–	–
Available P (ppm)	27.8	28.2	20.9	8.5
Extractable K (ppm)	–	–	28	21
Cation exchange capacity (meq/100 g)	–	–	9.3	9.6
Sand (%)	–	–	66.2	70.1
Silt (%)	–	–	17.0	14.4
Clay (%)	–	–	16.7	15.6

Table 2. Properties of farmyard manure applied in Experiment 1.

	Cattle (1993)	Poultry (1994)
pH	7.1	6.6
Organic matter (%)	28.8	45.3
Total N (%)	3.04	2.94
Total P (%)	4.0	1.8
Total K (%)	1.7	2.4

5-B-1-2, E-Pad and Chiangsaen. Farmyard manure at the rate of 6.25 t/ha was broadcast and incorporated in the soil 2 weeks before transplanting. Properties of the farmyard manure are shown in Table 2.

All cultivars were sown on 14 July and transplanted on 16–17 August. Plot size was 1.5 × 5 m. In 1994, there were three fertiliser treatments (nil, farmyard manure, and chemical fertiliser) and four cultivars (IR20, NSG19, KDML105 and IR57514-PMI-5-B-1-2). Farmyard manure was applied in the same manner as in 1993. Chemical fertiliser was applied as basal at 30-30-30 kg of N-P-K per ha one day before transplanting. Ammonium sulfate was applied at 30 kg N/ha at 40 days after transplanting. Sowing date was 20 July and transplanting date was 18 August. Plot size was 3 × 5 m.

The free water level above or below the soil surface was determined using 50-cm long PVC tubes with a 10-cm diameter. The tubes were inserted to 40 cm soil depth, and water level in the PVC tubes was determined frequently. Date of flowering was recorded when 75% of the panicles emerged, and harvesting was done at physiological maturity. Plant height was recorded before harvesting. Total dry matter (TDM) and yield components (panicle number, unfilled grain percentage, grain weight) were determined at maturity from a 0.5 m^2 sample area. Grain yield was determined from an area of 2 m^2 in 1993 and 6 m^2 in 1994, and was adjusted to 14% moisture content.

Experiment 2

In each of three years, 35 cultivars were compared in a randomised complete-block experiment with three replications, and four cultivars common to Experiment 1 were analysed to compare their performance in different growing environments. Sowing dates were 17, 20 and 19 July, and transplanting dates were 21, 20 and 25 August, for 1992, 1993 and 1994 respectively. Chemical fertiliser at 20-25-0 kg N-P-K/ha was applied as basal and 15 kg N/ha was applied as top-dressing at 30 days after transplanting. Crops were grown under rainfed conditions, except when main paddies were irrigated for transplanting in all years and also at booting stage in 1993 and 1994. Grain yield (at 14% moisture content) was determined from an area of 4 m^2 in each plot, which measured 1.5 × 5 m.

Results

Effect of fertiliser application and irrigation

In 1993, rainfall started in April and ended in October (Table 3) just before flowering of the medium and late cultivars KDML105, E-Pad and Chiangsaen. In the rainfed trial, water level fluctuated above and below the soil surface during September and October. There were, however, no severe water-stress symptoms such as leaf rolling and leaf death during this period. After standing water disappeared for the season, water level gradually decreased to 40 cm below the soil surface and beyond in November (Table 4).

Table 3. Monthly rainfall in 1993 and 1994 at the experimental site at Sanpatong, Northern Thailand.

Month	Rainfall (mm)	
	1993	1994
January	0	0
February	0	0
March	0	145
April	48	66
May	99	95
June	15	187
July	51	126
August	116	170
September	267	206
October	156	80
November	0	71
December	2	30
Total:		
Year	752	1174
During growing season	591	682

There were cultivar differences in height and number of days to flowering. Traditional cultivar E-

Pad was the tallest (mean across fertiliser treatments was 148 cm), followed by Chiangsaen (136 cm), KDML105 (124 cm), NSG19 (119 cm) and IR57514-PMI-5-B-1-2 (107 cm), whereas IR20 was shortest (90 cm). NSG19 flowered first, at 94 days after sowing, and E-Pad last, at 111 days after sowing. Chiangsaen and KDML105 also flowered late, at 110 days after sowing. IR57514-PMI-5-B-1-2 and IR20 had a similar number of days to flowering — 103 and 102 days, respectively. Flowering date was little affected by fertiliser treatment, whereas plant height increased by up to 15 cm with fertiliser or irrigation application. Thus, the plants to which fertiliser and irrigation were applied were commonly 25 cm taller than those without fertiliser and irrigation.

Table 4. Free water level above or below the soil surface in irrigated and rainfed trials in Experiment 1, Sanpatong, Northern Thailand, 1993.

Date		Free water level (cm)	
		Irrigated	Rainfed
November	4	7.3 above	7.8 below
	8	3.8 above	28.2 below
	10	3.2 below	9.5 below
	12	17.5 below	19 below
	15	More than 40 below	More than 40 below

In 1993, application of farmyard manure increased the yield of all cultivars in both irrigated and rainfed conditions (Table 5a). Without farmyard manure, the yield under irrigated conditions was much greater than that under rainfed conditions, but the response to farmyard manure application was less in the irrigated trial. Grain yield varied among cultivars in all conditions. High-yielding cultivars were KDML105, IR57514-PMI-5-B-1-2 and E-Pad in both irrigated and rainfed trials, whereas the earlier-flowering NSG19 and IR20 produced a lower yield in both trials. In the rainfed trial, the cultivar variation was much smaller in the treatment without farmyard manure, although cultivar by farmyard manure interaction was not significant in either trial. Responses of TDM at maturity to farmyard manure application and irrigation, and variation among cultivars, were similar to those for grain yield (Table 5b). Harvest index varied little among cultivars (0.47–0.50) or between the farmyard application and no application treatments (0.48–0.49) in either trial.

Application of farmyard manure increased panicle number, particularly in the rainfed trial (Table 5c). For a given fertiliser treatment, irrigation also increased panicle number. Whereas cultivar differences in panicle number were not related to the variation in grain yield, there was negative correlation between grain yield and proportion of unfilled grain among the six cultivars. Thus, two earlier-flowering cultivars (NSG19 and IR20) with low yield had a high proportion of unfilled grain (Table 5d). The effect of both farmyard manure application and irrigation on the proportion of unfilled grain, however, was small and non-significant.

In 1994, the amount and distribution of rainfall were better than in 1993, and no cultivars were subjected to severe water deficit. One week after transplanting, the plants were subjected to flash flooding and high water level, especially in the irrigated trial. This condition lasted for 14 days. KDML105 in the irrigated trial showed some flood damage. Disappearance of standing water in irrigated and rainfed conditions started at 83 and 69 days after sowing respectively. At 104 days after sowing, when the two later-flowering cultivars KDML105 and IR57514-PMI-5-B-1-2 flowered, water level was 15 cm below the soil surface in the rainfed trial. At 121 days after sowing, water level was below 40 cm soil depth in both trials.

In 1994, irrigation had a large effect on grain yield in the nil-fertiliser treatment, but had a smaller effect when fertiliser was applied (Table 6). In the rainfed trial, both chemical and farmyard manure application doubled the yield. In both irrigated and rainfed trials, yield was similar with chemical fertiliser and farmyard manure. The effect of fertiliser application was, however, small in the irrigated trial. It is possible that the flash flooding soon after chemical fertiliser application at transplanting caused nil-fertiliser plots to be contaminated with the chemical fertiliser to some extent, and this may have resulted in a small difference between nil-fertiliser and fertiliser treatments in the irrigated trial, and also a higher yield in the irrigated than the rainfed trial for the nil-fertiliser treatment. While responses to fertiliser applications appeared different between cultivars, there was no significant interaction between cultivar and fertiliser treatments in either the irrigated or rainfed trial. As for 1993, IR57514-PMI-5-B-1-2 produced a higher yield than did NSG19 and IR20. In 1994, however, the yield of KDML105 was similar to that of the earlier-flowering NSG19 and IR20, and was significantly less than that of IR57514-PMI-5-B-1-2. The flooding after

Table 5. Grain yield and yield components of six rice cultivars grown with no added fertiliser (nil) or farmyard manure (FYM) at Sanpatong, Northern Thailand in 1993.

Cultivar (C)	Irrigated			Rainfed		
	Fertiliser (F)			Fertiliser (F)		
	Nil	FYM	Mean	Nil	FYM	Mean
(a) Grain yield (kg/ha)						
IR20	3127	4098	3612	1031	2577	1804
NSG19	2940	3919	3429	1002	2092	1547
KDML105	3706	5100	4403	1367	3429	2398
IR57514	4556	5183	4870	1381	3458	2420
E-Pad	4052	5219	4635	1442	3479	2460
Chiangsaen	3560	4717	4138	1523	2669	2096
Mean	3657	4706	4181	1290	2951	2121
LSD (5%)	F*	681		F*	1266	
	C**	459		C*	535	
	F×C	ns		F×C	ns	
(b) Total dry matter (kg/ha)						
IR20	5710	8030	6870	2010	5650	3830
NSG19	5110	8890	7000	2190	3450	2820
KDML105	8700	10190	9440	2730	7420	5080
IR57514	8350	10740	9550	2870	8850	5860
E-Pad	7240	10990	9120	2990	6050	4520
Chiangsaen	7430	10550	8740	3270	5630	4450
Mean	7090	9820	8450	2680	6170	4430
LSD (5%)	F	ns		F*	1870	
	C**	1410		C	ns ($P = 0.06$, LSD 2000)	
	F×C	ns		F×C	ns	
(c) Number of panicles per ha (× 10^4)						
IR20	181	238	210	97	142	120
NSG19	121	110	116	69	100	85
KDML105	133	183	158	80	126	103
IR57514	143	151	147	75	123	99
E-Pad	114	141	128	56	112	84
Chiangsaen	85	104	95	53	69	61
Mean	130	155	142	72	112	92
LSD (5%)	F	ns		F**	21	
	C**	21		C**	26	
	F×C*	29		F×C	ns	
(d) Proportion of unfilled grain (%)						
IR20	24.5	29.1	26.8	16.0	23.6	19.8
NSG19	24.3	24.0	24.2	27.3	25.2	26.2
KDML105	10.3	7.4	8.9	12.7	7.3	10.0
IR57514	5.8	6.5	6.1	10.1	4.7	7.4
E-Pad	6.8	7.0	6.9	7.5	8.9	8.2
Chiangsaen	10.3	12.5	11.4	12.0	12.0	12.0
Mean	13.7	14.4	14.0	14.3	13.6	13.9
LSD (5%)	F	ns		F	ns	
	C**	2.5		C**	7.0	
	F×C	ns		F×C	ns ($P = 0.07$, LSD 5%)	

Note: A significant result is denoted by: * ($P < 0.05$); or ** ($P < 0.01$)

Table 6. Grain yield (kg/ha) of four rice cultivars grown with no added fertiliser (nil), chemical fertiliser or farmyard manure (FYM) application in 1994.

Cultivar (C)	Irrigated				Rainfed			
	Fertiliser (F)				Fertiliser (F)			
	Nil	Chemical	FYM	Mean	Nil	Chemical	FYM	Mean
KDML105	3414	3620	3649	3561	1564	2744	3460	2589
IR57514	3754	4092	4822	4223	2036	3664	3692	3131
NSG19	3047	4152	3490	3563	1446	2902	3107	2485
IR20	3287	3862	3707	3618	1464	2571	2971	2336
Mean	3376	3932	3917	3741	1628	2970	3308	2635
LSD (5%)	F*	452			F**	898		
	C**	387			C**	422		
	F×C	ns			F×C	ns		

Note: A significant result is denoted by: * ($P < 0.05$); or ** ($P < 0.01$)

transplanting may have affected the growth of KDML105 more than it did for the other cultivars. Treatment differences in yield components in 1994 were similar to those in 1993, and data are not shown.

Cultivar differences across 13 environments

The results of four environments (two water conditions × two fertiliser treatments) in 1993 and six environments (two water conditions × three fertiliser treatments) in 1994 for Experiment 1 were combined with those of the three environments (three years) from Experiment 2, and the grain yields of the four common cultivars (NSG19, KDML105, IR57514-PMI-5-B-1-2 and IR20) were analysed using the residual maximum likelihood method. The results (Table 7) show strong effects of environment and cultivar, but also significant interaction between the two.

Table 7. Analysis of variance of grain yield for four cultivars grown in 13 environments using the residual maximum likelihood method.

	DF	Mean squares	Significance[1]
Replication	2		
Environment	12	11.929	**
Replication × environment	26	0.724	
Cultivar	3	8.614	**
Cultivar × environment	35	0.525	*
Error	73	0.165	

[1] * = $P < 0.05$; ** = $P < 0.01$

IR57514-PMI-5-B-1-2 produced the highest grain yield and NSG19 the lowest in almost all environments (Fig. 1). Environments 1–13 are shown in order of the lowest mean yield to the highest yield. With the exception of environment 11 (1994 chemical fertiliser application in the irrigated trial), the difference in yield between IR57514-PMI-5-B-1-2 and the low-yielding cultivars was large in high-yielding environments. In lower-yielding environments (1–7), yield variation was generally small and non-significant in four out of the seven environments. An exception was environment 4 (Experiment 2 in 1994), where yield variation was large; this was caused by the very low yield of NSG19, probably as a result of water stress early in growth.

Discussion

The results indicate that an intermediate-flowering cultivar IR57514-PMI-5-B-1-2 was most suitable in this location in Northern Thailand. Early-flowering cultivars (IR20 and NSG19) produced a low yield in most conditions, mainly due to low TDM and the high proportion of unfilled grain. Lower dry-matter production of early-flowering cultivars has been demonstrated in lowland conditions in Northeastern Thailand (Jearakongman et al. 1995). Low assimilate availability before flowering of the short-duration cultivars could result in a shortage of differentiated sink (Ashraf et al. 1994) as well as a shortage of assimilate to fill grains after flowering. IR20 and NSG19 performed quite well in the very low soil fertility conditions of Ubon Ratchathani in Northeastern Thailand (Wongprasaid et al. 1996), but in Northern Thailand they performed poorly. In most environments of the present study, when there was no late-season drought, later-flowering cultivars such as KDML105 and IR57514-PMI-5-B-1-2 produced higher yields than did the early-flowering cultivars. In the Northern Thailand environment, where rainfall and soil characteristics are generally better than in Northeastern Thailand, the intermediate-flowering cultivars performed the best, followed by the late-flowering cultivars.

Although phenological development is mostly controlled by photoperiod and temperature, severe water stress could delay flowering (Yoshida 1981b; Lilley and Fukai 1994). Under the rainfed conditions of this experiment, flowering was not uniform, particularly in no-fertiliser plots. Some panicles could not be completely exserted, and this resulted in a small number of fertile panicles and hence low yield. IR20 appeared to be most affected.

To obtain high yield, application of chemical fertiliser or farmyard manure was necessary in both irrigated and rainfed conditions. Chemical fertiliser and farmyard manure were about equally effective in the 1994 experiment. Response to fertiliser in terms of yield was greater in the rainfed than in the irrigated trial in both years. Under rainfed conditions with low soil fertility, yield of all cultivars was strongly suppressed. Under irrigated conditions where soil was always submerged, all cultivars showed high yield, even in the no-fertiliser treatment. While the result in 1994 may possibly be affected by the no-fertiliser plots being contaminated by inorganic fertiliser from the nearby plots, the same results were obtained in 1993, when no contamination would have occurred. Submergence of soils increases the availability of P, K, calcium, silicon, iron and manganese, and this could be beneficial to irrigated lowland rice (Yoshida 1981a; De Datta 1981). When previously flooded soil is no longer submerged, pH decreases quickly (Ragland et al. 1987). The fluctuation of water level above and below the soil surface that was observed in the present experiments would have caused a change in soil pH and availability of some elements, such as P, as well as loss of some nutrients such as N. There were

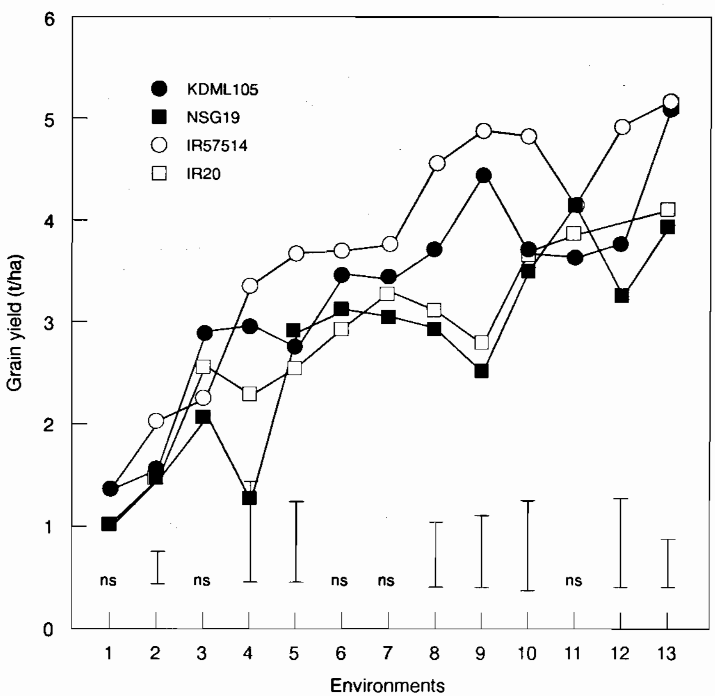

Figure 1. Grain yield of four rice cultivars grown in 13 environments. Bars indicate LSD 5% (ns = non-significant cultivar difference).

no severe water-stress symptoms in the rainfed crops in either year, but yield was increased greatly by irrigation. It thus appears that the loss of standing water during some stages of growth may not have caused severe water stress, but may have reduced yield through the reduced availability of some nutrients.

The present work has shown that the performance of rice cultivars varied with soil water status and soil fertility. Selection of lines in a breeding program should be made under specific soil conditions, with the rate of fertiliser application depending on the fertility of the target area of the breeding program.

Acknowledgment

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Effect of Growth Duration, Nitrogen and Sowing Date on Grain Yield of Australian Rice: A Modelling Approach

R.L. Williams*

Abstract

The duration of rice crops in New South Wales commonly extends for the entire period during which environmental conditions allow rice growth. This duration is often around 180 days (from sowing to harvest), and allows for maximum crop growth. Recently developed cultivars of shorter growth duration have a shorter vegetative phase. Short-duration cultivars increase the flexibility of rice rotations and reduce water use, thereby lowering production costs. However, the yield and management implications of reducing growth duration have not been fully investigated.

The likely impact on yield, and optimal management for the shorter duration rices, were examined by a simplified process crop model. The model simulates grain yield in response to sowing date, nitrogen (N) application and water depth during the early stage of pollen microspore development. A simulation experiment was conducted that combined 9 sowing dates, 13 N rates, 3 crop durations and 3 water depths over 41 years. The average yield response over the 41 years suggests that short growth duration led to a 1.0–2.2 t/ha lower yield than long duration for all sowing dates and water-depth combinations. The optimal sowing date for all growth durations was 18 October. With delay in sowing after this date, the yield of the long-duration type declined at a faster rate than the short-duration type. For short-duration types, the optimal N application rates were 25–50 kg N/ha greater than those for types with long growth duration.

THE Australian rice industry is based in the Riverina region of southeast Australia (35°S). The area receives an average rainfall of only 200 mm during the growing season; hence, the crop is fully irrigated. The Murrumbidgee and Murray river systems flow westward through the rice-growing area, supplying irrigation water from upper catchment dams in the Great Dividing Range. The region has distinct winter and summer seasons, allowing only one crop per year. The duration of the rice crop is limited by cool spring and autumn seasons, leading to a clearly defined optimal sowing time. Full-season cultivars are planted in early October, when temperatures first allow rice establishment. This enables full-season cultivars to go through the critical stages of pollen formation between panicle initiation and flowering in the warmest time of the year (Fig. 1).

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Average industry yield of all cultivars from 1991 to 1995 has been 8.5 t/ha, with the most adapted cultivar (Amaroo) yielding 9.1 t/ha for the same period. A number of growers have consistently achieved grain yields of more than 12 t/ha over the same period. These high yields were the result of full irrigation, mechanised field agronomy, lack of insect pests and diseases, high levels of radiation during the summer and absence of significant cold damage. The significantly lower grain yields for the 1996 season (6.4 t/ha average industry yield and 6.6 t/ha for Amaroo) were due to below-average minimum temperatures during the reproductive development of the crop, leading to significant floret sterility.

Rice cultivars with a shorter growing season have been sought by the Australian rice industry for a number of years. The advantages include increased flexibility in farm rotations, less water use (reducing costs) and less water percolation into the water table. The recent development of a short-duration type (Jarrah), which flowers three weeks earlier than the standard Amaroo, has prompted the need to investigate the yield potential of short-duration cultivars and to determine the management strategies necessary to achieve their full yield potential.

Reinke et al. (1994) analysed cultivars of differing maturity and found that the yields of a short-duration cultivar were less than those of long-duration cultivars at the optimum sowing time, but the yields were greater than those of the long-duration cultivars at later sowing times. These experiments were conducted in seasons in which the average industry yield was relatively low, and the results may not be typical of yield responses over a larger number of years.

The temperate rice yield model TRYM (Williams et al. 1994), developed and calibrated for the Australian rice industry, allows prediction of the yield performance of the rice cultivar Amaroo for a wide range of management options, including nitrogen (N) nutrition, sowing date and water depth. This paper reports the results of a computer-based simulation experiment to define the yield penalties associated with reducing growth duration and to suggest optimal management strategies for shorter-duration cultivars under New South Wales conditions.

Description of Model

TRYM estimates individual paddock rice yields in response to the management options of N nutrition, sowing date and water depth at the critical reproductive stage of early pollen microspore. The model is described in Williams et al. (1994) and is briefly described below.

The model simulates phasic development, N uptake, leaf area development and growth in daily time steps (Table 1). Grain yield is estimated as the product of maturity biomass and harvest index.

Table 1. Summary of relationships in the simulation model.

Quantity or process simulated	Factors
Phasic development	Temperature, photoperiod, plant N uptake
N uptake	Soil N mineralisation, fertiliser, temperature
Leaf area index (LAI)	N uptake, development
Intercepted radiation	Solar radiation, LAI
Growth	Intercepted radiation, temperature
Microspore temperature	Water depth, screen temperature
Harvest index	Microspore temperature, plant N status
Grain yield	Growth, harvest index, development

Maximum harvest index is estimated, in the absence of cold damage. The effect of cold damage on rice is based on the temperature of the developing panicle at early pollen microspore and the N status of the crop.

Low temperatures and increasing N uptake of the crop increase the level of cold damage. The estimation of harvest index in this paper is the same for all rice types.

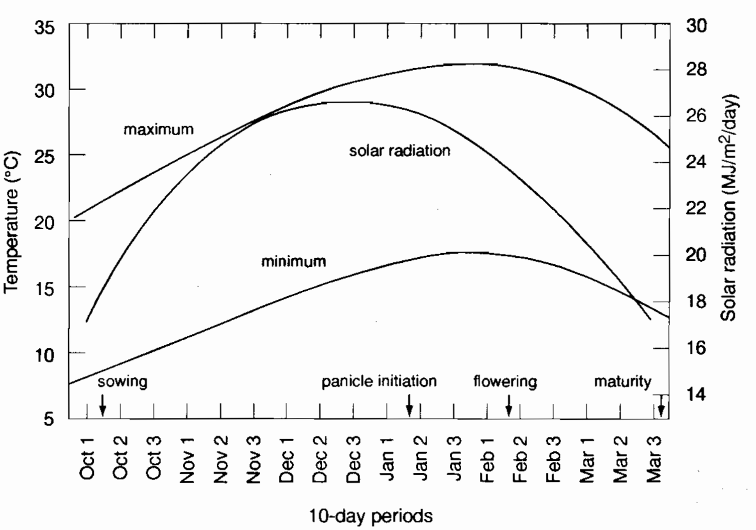

Figure 1. Long-term (41 year) average maximum and minimum temperature and solar radiation recorded at Griffith and average timings of phenological events for a full-season cultivar.

The model follows the structure of a simplified process model, which is characterised by the simplest structure consistent with physiological principles and simulates only those variables that can be measured. An optimiser is used to estimate the parameters that give the lowest errors of yield prediction and intermediate steps of growth and development. The process of optimisation has the advantage over the process of manual 'tuning' in that a model can be calibrated simultaneously on several attributes, such as the interaction of phenology and N status.

Model fit

The data set for calibration of the model represents environments which include wide ranges of N status, sowing dates, water depths and temperatures (Fig. 2). The calibrated model accurately predicts experimental yields in the New South Wales rice-growing area. Because the functional relationships are based on biological principles, it is suitable for limited extrapolation outside the range of data. During calibration, the model fitted the yield data with a root mean square (RMS) error of 0.8 t/ha for yields from zero to 13 t/ha. In the experiments used for calibration, the least significant difference (LSD) was 1.0 t/ha. The model's RMS error was 0.9 t/ha when tested on yield data from independent experiments yielding from 6 to 13 t/ha.

Simulation Experiment

The current crop model was linked to daily solar radiation and maximum and minimum temperatures for the last 41 years (from 1955 to 1996). A simulation experiment predicted crop development, growth and yield for a range of sowing dates, N application rates and water depth for three growth durations.

The simulations used parameters based on the long-duration cultivar Amaroo and two hypothetical short-duration types. In these types panicle initiation occurred 10 and 20 days earlier than Amaroo. Panicle initiation dates of the long-duration cultivar were fixed based on Amaroo crop observations, collated as the RiceCheck database. Panicle initiation dates were input to the model for all simulations, while flowering and maturity were estimated by TRYM. There were 13 N rates (0–300 kg N/ha in 25-kg increments) and nine sowing dates. The panicle initiation dates used for each cultivar and sowing date combination are presented in Table 2.

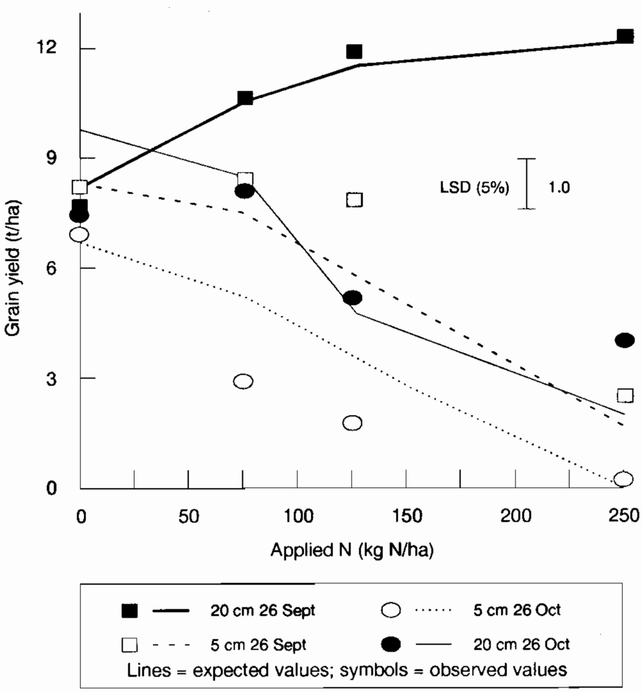

Figure 2. Observed and expected yield response of Amaroo rice to applied nitrogen at two sowing dates (26 September and 26 October) and two water depths (5 and 20 cm).

Table 2. Fixed date of panicle initiation (PI) for full-, medium- and short-duration cultivars used in the simulation experiment.

Sowing Date	PI date		
	Long duration	Medium duration	Short duration
3 Oct 93	28 Dec	18 Dec	8 Dec
8 Oct 93	1 Jan	22 Dec	12 Dec
13 Oct 93	11 Jan	1 Jan	22 Dec
18 Oct 93	16 Jan	6 Jan	27 Dec
23 Oct 93	19 Jan	9 Jan	30 Dec
28 Oct 93	23 Jan	13 Jan	3 Jan
2 Nov 93	25 Jan	15 Jan	5 Jan
7 Nov 93	27 Jan	17 Jan	7 Jan

The soil parameters for the model were set so that there was approximately 77 kg N/ha mineralised from sowing to flowering, and 42% recovery of applied N during the period from sowing to flowering in the long-season cultivar. Each simulation was also performed for three water depths at early pollen microspore stage. At this phenological stage, the rice crop is most sensitive to low minimum temperatures, which can lead to large yield reductions (Uchijima 1976). Floodwater covering the developing panicle at this stage protects it from low night temperatures and reduces cold damage by increasing panicle temperature by 7°C (Williams and Angus 1994).

The effect of three water depths (approximately 5, 12 and 25 cm), identified as deep, medium and shallow, were estimated. Under the deep-water treatment it was assumed that the developing panicle was totally immersed in the floodwater at the early stage of pollen microspore development. The shallow-water treatment assumed that the panicle was exposed to the ambient air, and the medium-water that the panicle was half immersed in the floodwater.

Response to nitrogen

The response to N was averaged across the 41 years of simulation for the three water depths and three growth duration types. There was an increase in yield associated with increased N application for all combinations of growth duration and water depth (Table 3).

Maximum average yields of more than 11 t/ha were achieved with the long-duration cultivar, with more than 200 kg N/ha applied and deep water. At maximum yield levels, the long-season cultivar had a yield advantage of 2.4, 1.8 and 0.6 t/ha over the short-duration type for the deep-, medium- and shallow-water treatments, respectively. The medium-duration type had a yield intermediate between the other two types.

Table 3. Simulated rice yield (t/ha) for three cultivars of differing growth duration (full, medium, short) and three water depths (deep, medium, shallow) at early pollen microspore in response to nitrogen application, averaged over 41 years (1955-96).

N applied (kg N/ha)	Deep water			Medium water			Shallow water		
	Full	Medium	Short	Full	Medium	Short	Full	Medium	Short
0	7.6	6.6	5.5	7.4	6.5	5.5	7.1	6.4	5.5
25	8.3	7.2	6.1	8.0	7.1	6.0	7.4	6.8	5.9
50	8.9	7.8	6.6	8.4	7.5	6.4	7.6	7.0	6.2
75	9.4	8.2	7.0	8.8	7.9	6.8	7.7	7.2	6.5
100	9.8	8.7	7.4	9.0	8.1	7.1	7.6	7.2	6.6
125	10.2	9.1	7.8	9.2	8.4	7.3	7.5	7.2	6.7
150	10.6	9.4	8.1	9.4	8.6	7.5	7.3	7.2	6.7
175	10.9	9.7	8.4	9.5	8.7	7.7	7.1	7.1	6.6
200	11.1	9.9	8.6	9.6	8.8	7.8	6.8	6.9	6.6
225	11.3	10.2	8.9	9.6	8.9	7.9	6.5	6.7	6.5
250	11.5	10.4	9.1	9.6	8.9	8.0	6.1	6.4	6.3
275	11.7	10.6	9.3	9.6	8.9	8.0	5.8	6.2	6.1
300	11.9	10.8	9.5	9.5	8.9	8.0	5.4	5.9	5.9

The simulated yield potential gap of about 2 t/ha between the full- and short-duration cultivar is similar to that observed by Reinke et al. (1994). They found that in the absence of cold damage, a short-duration cultivar (M101) yielded 1.8 t/ha less than the full-season cultivar M7, which has a similar phenology to Amaroo. The field trial also showed that the lower yield of the short-duration cultivar could not be compensated for by increased N application.

The simulated yields of all types decreased with lower water depths. The proportion of yield loss associated with shallow-water and cold conditions was less for the short-duration type than for the long-duration cultivar. This is because the short-duration type had lower N uptake at the critical temperature-sensitive stage, and because this stage occurred during a warmer time of the year.

Response to sowing date

At all sowing dates, the long-duration type yielded more than the other types. Maximum average yields were simulated for 18 October sowing for all three types and all water depth treatments (Table 4). As with the N response, the average yield penalty of short-duration types was relatively constant across the range of sowing dates examined.

Optimal Management

The optimal rate of N application was estimated for each cultivar, sowing date and water depth combination. The optimal rate of N application was defined as the point at which the yield increase with an additional 25 kg N/ha was less than 0.25 t/ha. At current prices this yield response gave a $2 gross return per dollar spent on N fertiliser.

Simulated optimal rates of N application for the short-duration type were consistently 25 kg N/ha greater than for the full-duration type with deep water (Table 5). The short-duration type required this higher rate of N to develop sufficient leaf area, in the shorter time to flowering, to intercept the full amount of radiation prior to and after flowering. Even with this higher rate of N application, the average yield of the short-duration type was 2 t/ha lower than for the long-duration type.

With lower water depths and optimal rates of N application, the yield and yield differential between the long- and short-duration types declined. Optimal N application rates were not affected significantly by sowing date; however, yields of all types declined significantly with delay in sowing from 18 October to 7 November. The rate of decline was faster for the long-duration type than for the short-duration type.

Conclusion

The simulated long-duration type had a consistently higher yield than the short-duration type. The yield advantage was 2.2 t/ha with deep water and 1 t/ha with shallow water. The greater yield potential of the long-duration type was due to the development of greater maximum leaf area index and the interception of more incident radiation during the longer growing season. This extra growth was converted to grain yield in crops that were protected from cold damage.

Table 4. Simulated rice yield (t/ha) for three cultivars of differing growth duration (full, medium, short) and three water depths (deep, medium, shallow) at early pollen microspore in response to sowing date, averaged over 41 years (1955-96).

Sowing date	Deep water			Medium water			Shallow water		
	Full	Medium	Short	Full	Medium	Short	Full	Medium	Short
3 Oct	9.85	8.56	7.19	8.62	7.83	6.69	6.86	6.67	6.04
8 Oct	9.96	8.68	7.35	8.71	7.88	6.83	6.87	6.64	6.10
13 Oct	10.76	9.57	8.27	9.46	8.44	7.58	7.24	6.76	6.51
18 Oct	10.79	9.63	8.41	9.56	8.63	7.63	7.22	7.05	6.48
23 Oct	10.59	9.47	8.25	9.40	8.56	7.49	7.07	6.98	6.36
28 Oct	10.43	9.39	8.18	9.24	8.45	7.50	6.90	6.85	6.44
2 Nov	10.00	8.98	7.77	8.82	8.16	7.21	6.65	6.66	6.33
7 Nov	9.63	8.63	7.44	8.50	7.96	6.98	6.51	6.63	6.24

Table 5. Optimal rates of applied nitrogen, and simulated average yield, for rice crops of differing water depth, sowing date and duration (full, medium, short), averaged over 41 years (1955-96).

Water depth	Sowing date	Full		Medium		Short	
		Optimal N (kg N/ha)	Yield (t/ha)	Optimal N (kg N/ha)	Yield (t/ha)	Optimal N (kg N/ha)	Yield (t/ha)
Deep	3 Oct	225	11.01	225	9.68	225	8.21
	8 Oct	200	10.85	225	9.78	225	8.36
	13 Oct	200	11.66	200	10.43	225	9.34
	18 Oct	200	11.66	200	10.49	225	9.47
	23 Oct	200	11.45	200	10.32	225	9.29
	28 Oct	200	11.28	200	10.21	225	9.19
	2 Nov	175	10.58	200	9.78	225	8.75
	7 Nov	175	10.18	175	9.16	200	8.39
Medium	3 Oct	100	8.64	125	7.96	125	6.75
	8 Oct	100	8.71	100	8.01	125	6.90
	13 Oct	100	9.47	100	8.62	125	7.70
	18 Oct	100	9.53	125	8.79	125	7.76
	23 Oct	100	9.41	100	8.71	100	7.60
	28 Oct	100	9.25	100	8.60	125	7.61
	2 Nov	100	8.84	100	8.27	125	7.27
	7 Nov	100	8.49	125	8.04	125	7.03
Shallow	3 Oct	25	7.24	50	6.73	75	6.06
	8 Oct	25	7.28	50	6.79	75	6.15
	13 Oct	25	7.82	50	7.26	75	6.74
	18 Oct	25	7.76	50	7.39	75	6.79
	23 Oct	25	7.65	50	7.30	75	6.67
	28 Oct	25	7.52	50	7.20	75	6.65
	2 Nov	25	7.23	50	6.92	75	6.42
	7 Nov	25	6.99	50	6.71	75	6.21

Maximum yields for all growth durations were obtained by planting on 18 October and yields declined with later sowing. The rate of yield decline was greater for the long-duration type than the short-duration type. Simulated optimal N application rates were 25–50 kg N/ha greater for the short-duration type.

The lower yield potential of short-duration rice types identified in this paper demonstrates the likely costs of growing shorter-duration rice types. The further development of shorter-duration types will necessitate an added emphasis on yield potential to make them attractive to growers.

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Breeding Strategies for Rainfed Lowland Rice: Suggestions for Future Research

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IN this discussion paper we attempt to suggest possible future research directions to those who are involved in activities related to plant improvement for rainfed lowland rice. Our suggestions are based on the papers published in these proceedings, but other publications were also used as sources of relevant information (IRRI 1995; Khush 1996; Mackill et al. 1996; Singh et al. 1996; and Zeigler 1996). An associated workshop investigating the analysis and exploitation of plant adaptation in crop improvement programs (Cooper and Hammer 1996) also provided a resource base on strategies appropriate for crop improvement in complex, heterogeneous agricultural systems. We have also relied heavily on discussions held during the workshop, particularly in the last session where we had an opportunity to discuss important future research issues for each of three areas of research: plant breeding, plant physiology and soils. Each group identified high priority future research areas that were discussed at the workshop. We have integrated the views expressed by each group and incorporated them into this discussion.

The suggestions listed below are for breeding strategies alone, and particularly breeding strategies for areas where drought and adverse soil conditions are major problems. Cultural practices to improve rice production under these conditions are considered to some extent, but the use of cultural practices or breeding methods to reduce the effects of diseases and pests is not included here. While we fully appreciate the importance of rice quality for human consumption, that aspect is also not discussed here. The focus is on increasing rice production from the rainfed lowland ecosystem.

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Characterisation of Target Environments for a Breeding Program

One of the key issues highlighted during the workshop is the need to recognise the diversity of rainfed lowland rice environments and the associated difficulties of developing effective plant improvement programs for such conditions. It is possible that many problems may be site specific, and the knowledge obtained in one site may have limited use for other regions. Thus, while we may 'think globally' we need to 'act locally' for the rainfed lowland ecosystem. We therefore need to develop a breeding program that can accommodate regional requirements and has sufficient resources to address the problems of particular regions. The first requirement is to characterise target environments in terms of their soils, hydrology and weather conditions and determine whether these factors contribute to genotype-by-environment (G×E) interactions for yield and other relevant traits. Any characterisation of the target population of environments of a breeding program must deal with the challenging task of integrating information from measurements on the biophysical resource base and G×E interactions for production characteristics.

The soils group considered that proper characterisation of soils within the target area of a breeding program is one of the most important issues. Once most typical soils are known and most important soil limitations identified, a plant breeding program can choose selection sites which are representative of the region. These sites may not be at research stations if soil types are not typical of the area or if soil management is different from typical rice paddies. It may be also possible for plant breeders to select rice lines that are adapted for specific soil limitations, if they are identified by the soil scientists.

Similarly, the importance of identification of the drought environment was suggested by the plant physiology group. Drought is often a major constraint for rainfed lowland rice, but plant types required depend on the type of drought (e.g. early versus late season, severe stress, intermittent stress). Late-season drought is considered the most important type of drought in Northeastern Thailand. Further research would allow determination of appropriate selection sites where late-season drought is likely to develop. If the problem is very severe, active selection at a controlled site (e.g. drought-screening facilities) may be used to enhance the particular character (i.e. resistance against late-season stress) required for the germplasm used in the breeding program.

The area covered by a breeding program may be modified according to the environmental characterisation analysis. Ideally the target area would have homogeneous biophysical characteristics and little or no G×E interaction for production characteristics. If environments differ greatly within a target area, the area may be divided into smaller units. Analysis of G×E interactions for grain yield is a central component of any attempt to subdivide the target area, and should be used to determine adaptation domains to be targeted by the breeding programs. If G×E interaction variance is large relative to the genotype variance component, then the area may be considered to be too heterogeneous and the causes of the interactions should be investigated. Cooperation among soil and plant scientists will be necessary to determine the appropriate target areas for a breeding program.

Determination of an Ideosystem for Direct Seeding

The rainfed lowland ecosystem is not static. Cropping practice changes with changes in the external environment, such as labour and fertiliser costs, and demand for particular types of rice. With the change in cropping practice, we may consider conceptual 'ideosystems' and the components that make up such ideal rice-growing systems. Two major systems are now obvious for large areas of rainfed lowland ecosystems: one based on the traditional transplanting system and the other based on direct seeding. In the transplanting system, rice is often planted late and traditional photoperiod sensitive cultivars are commonly used. For the direct-seeding system, and especially for direct dry seeding, seed can be sown early as the water requirement is less and the use of photoperiod insensitive cultivars would allow the crop to frequently escape late-season stress.

In order to develop rice cultivars that are adapted to direct seeding, the plant breeding group suggested the need to select lines for performance under direct-seeding conditions from F_2 onwards. The precise selection strategies need to be investigated, depending on the projected importance of direct seeding in the future for the area concerned, G×E interactions between the transplant and direct-seeding systems and the costs of the alternative breeding strategies. Social scientists can play a significant role in some of these areas. The possibility of seedling screening (e.g. for seedling vigour and submergence tolerance) should be investigated, as well as the possible role of molecular markers to assist selection of lines with the appropriate combinations of desirable traits.

The plant physiology group also made several suggestions for determination of ideosystems for direct seeding. Weed competition is considered a major problem with direct seeding and therefore physiological and morphological characters that could reduce the competitive advantage of weeds, such as early vigour and spreading tillers, need to be identified. Similarly, crop establishment is a greater problem under direct seeding than with transplanting, and both genotype requirement and cultural practice to promote rapid establishment need to be identified. The soils group considered it important to provide information on soil characters that affect performance of direct-seeded rice (e.g. soil texture) and soil management for direct seeding (e.g. weeds, water level). The change from transplanting to direct seeding will also require investigation into the optimal plant type, planting date and density, and seeding method (broadcasting/drilling). Seedlings are likely to encounter early-season drought, and therefore attributes conferring resistance against early-season drought (e.g. green leaf retention, early vigour) need to be identified.

The use of dry seeding of short-duration, photoperiod insensitive cultivars will provide an opportunity for double cropping of rice or rice followed by an upland crop in areas of generally favourable rainfall (e.g. more than five months with rainfall exceeding 200 mm per month). This will require research on identification of a suitable second crop that can mature on stored soil water in the early dry season. The first rice crop would mature in the middle of the rainy season (e.g. September) and this may require rice cultivars that can withstand heavy rainfall at flowering and grain filling. An ideosystem needs to be developed that maximises total output from a farm holding; for example, the use of a legume crop to maintain soil fertility (e.g. photoperiod insensitive rice/short duration chickpea in Bangladesh) would require increased research effort.

Identification of Plant Types Required for Rainfed Lowland Rice

The importance of matching the rice plant's phenology with the paddy water environment, to minimise the effect of drought, is well recognised. Use of early-flowering cultivars to escape from late-season drought is a most effective means of achieving high yield for rainfed lowland rice. Genotypic variation for phenology often explains a large part of the G×E interactions for yield of rainfed lowland rice. Thus, identification of the optimum time of flowering, using the available rainfall records, is essential for each region, and this may be facilitated by the use of a rice simulation model. The plant breeding group suggested separating genotypes into groups based on their photoperiod sensitivity. Considering the importance of phenology in determining grain yield in rainfed lowland rice, the plant physiology group suggested identifying the effects of drought stress, nutrition and their interaction on phenology as an important future research area. The availability of cultivars with a range in maturity date is important to the stability of production in many rainfed lowland regions, particularly where the slow nature of hand-harvesting requires that the crop be ready for harvest over an extended period to ensure that there is sufficient time to harvest the crop with the available labour. Thus, it is necessary to ensure that continued breeding effort is invested in the genetic improvement of late- and early-maturing cultivars.

There are other specific characters that may confer drought resistance, and these have been considered in detail in this workshop. Genetic variation for characters such as rooting depth, water extraction, leaf water potential and green leaf retention has been identified. However, their contribution to yield (drought resistance) under drought stress conditions needs to be demonstrated before routine selection is made using these characters. In addition, their practical inclusion in a routine breeding program could be facilitated by marker aided selection.

There has been considerable effort to develop genetic markers for the putative traits of hardpan penetration capacity, increased maximum rooting depth, and osmotic adjustment in doubled-haploid and recombinant inbred populations of rainfed rice. Thus, these areas of research have received added attention in recent years. This work, while not discussed at this workshop, was recently presented at the Third International Rice Genetics Symposium at the International Rice Research Institute (IRRI) in 1995. There is also a need for more detailed studies of the contribution (if any) of these traits to yield and stability, and of the environmental circumstances under which they can enhance performance. Advances are most likely with a balanced approach, combining the skills of breeding, biotechnology, physiology, agronomy and soils.

Notwithstanding these advances, our understanding of drought and drought stress in relation to the crop development stage needs to be improved so that other putative drought resistance characters may be identified for the most typical drought conditions in the target regions; thus characterisation of the drought environment, as discussed above, is required.

The soils group suggested identification of rice genotypes tolerant of soil limitations, such as low soil fertility and low soil pH, which are common in some areas of the rainfed lowland ecosystems, to be an important area of future research. There is good evidence for genetic variation in a number of specific soil nutrient related traits (Mackill et al. 1996). Some routine selections are made in the greenhouse at IRRI for tolerance to salinity, alkalinity, phosphorus (P) and zinc deficiency, and boron and iron toxicity by ranking lines against susceptible and tolerant cultivars on suitable soils. There is scope for research to better understand the basis of soil pH and nutrient availability problems on the coarse-textured soils of northeast Thailand and the Lao People's Democratic Republic (Lao PDR), especially in relation to fluctuating water availability. Again, marker aided selection may be helpful in ensuring progress for complex nutrient traits, such as a capacity of a root system to alter rhizosphere pH and local availability of P. At the same time, simple screens could be adapted from those used in the greenhouse at IRRI, so that screening may proceed immediately. Finally, we need a greater understanding of the relative importance of nutrients and water as limitations to yield in rainfed lowland conditions than we have at present.

Some papers in the proceedings from this workshop and elsewhere emphasised the importance of high yield potential (e.g. yield under no stress conditions) because cultivars with high yield potential generally do well in most conditions of rainfed lowlands. Selecting lines under well-watered conditions as part of the breeding program may result in a general increase in yield in the target environment. The success of recent irrigated rice cultivars in increasing yield potential is due to increased harvest index, often via semidwarfness. While very short-statured cultivars (e.g. RD23 in Thailand) may be more prone to flood damage, shorter plants generally do better in rainfed lowland conditions in Lao PDR. Therefore, it may be worth testing to find out whether the required plant types will differ among regions, and if so to identify suitable plant types for each major region of the rainfed lowland ecosystem. Use of experimental populations based on genotypes for differing plant types may assist identification of the desired recombinant plant types.

Whilst the focus of the research in northeast Thailand and Lao PDR is towards drought-prone subecosystems, submergence is a major challenge in other areas, such as east India. Generally, water depths are less than 70 cm in rainfed lowland paddies, and duration of submergence is less than two weeks. With the shift to direct seeding in northeast Thailand and Lao PDR, seedlings may have a higher probability of submergence even in these drought-prone environments. A capacity to tolerate short-term submergence would be beneficial. For short-term submergence, tolerant plants should lack a capacity to elongate, but should rely on a greater ability to utilise carbohydrate reserves in anaerobic respiration during the period of submergence (Mackill et al. 1996). Conversely, when submergence is prolonged or water depths are greater, an ability to elongate is beneficial for ensuring a continued supply of oxygen to submerged plant parts via the aerenchyma. Marker aided selection may assist identification of lines possessing the appropriate enzymatic pathways for tolerance to short-term submergence.

Emphasis on Interstation Testing

The large G×E interaction variance component for grain yield that has been found in some rainfed lowland rice experiments suggests that genetic progress for yield will continue to be slow if breeders continue to rely heavily on intrastation testing or intensive selection at one or a few sites at the expense of interstation and on-farm testing. The practice of intense intrastation selection prior to interstation and on-farm testing is extensively used in some rainfed lowland rice regions. Therefore, a major weakness of this plant breeding strategy, if yield improvement is the primary objective, is the limited testing of breeding lines for yield in multienvironment trials, particularly at the early generation stages of the breeding programs.

In addition to these research issues that were identified to be high priority areas, there were other issues discussed during the workshop that would make crop improvement research more efficient. The soils group pointed to the importance of collaboration between scientists of different disciplines (e.g. soil scientists and plant breeders). For example, researchers and extension personnel should discuss the relative merits of breeding for a specific soil limitation or the use of agronomic practices to overcome the limitations. Similarly, characterisation of experimental sites is important when transferring information from the experimental site to other sites. The site needs to be characterised for soil and weather conditions, but collection of plant growth data will enhance the value of the experiments.

A number of new techniques may be useful for the plant breeding programs of the rainfed lowland system and rice improvement in general. For example, molecular marker technology, G×E interaction analysis, crop simulation modelling and geographical information systems may assist with environmental characterisation. These techniques need to be advanced further and evaluated in relation to the needs of the breeding programs. Training of personnel in these and other areas is an important strategy for developing the human resource base required to implement strategies for achieving the projected gains in production that are required from the rainfed lowland ecosystem.

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