Hybrid Rice Technology
new developments and future prospects

SELECTED PAPERS FROM THE
International Rice Research Conference

Edited by **S. S. Virmani**

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Los Baños, Laguna, Philippines
Mailing address: P.O.Box 933, Manila 1099, Philippines

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

Los Baños, Philippines
Mailing address: P.O. Box 933, Manila 1099, Philippines
Phone: (63-2) 818-1926, 812-7686
Fax: (63-2) 818-2087
Email: IN%"Postmaster@IRRI.CGNET.COM"
Telex: (ITT) 40890 Rice PM; (CWI) 14519 IRILB PS;
(RCA) 22456 IRI PH; (CWI) 14861 IRI PS

Suggested citation:

Virmani, S S, ed. (1994) Hybrid rice technology: new developments and future prospects. Selected papers from the International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

ISBN 971-22-0053-1

Contents

Foreword

Most rice-producing countries have high population growth rates, low rice yields (except for China, Egypt and Indonesia) and low GNP. Resources for food imports are limited and food aid is only a temporary solution. The world annual rough rice production must increase from today's 520 million t to 563 million t by 2000 and to 764 million t by 2025.

However, for the leading rice-growing countries of South and Southeast Asia, the needed increase in rice production rate is even higher. To meet this challenge, research to increase rice productivity must receive high priority. Successful development and utilization of hybrid rice in China during the past two decades has demonstrated that rice yield potential can be increased by commercial exploitation of heterosis or hybrid vigor in this self-pollinated crop. Therefore, IRRI and national rice research programs are exploring the potential of this biological phenomenon to raise rice varietal yields. Results are encouraging and some national programs (e.g., India and Vietnam) have recently released rice hybrids for commercial cultivation.

This symposium is a follow-up to one held in China in 1986. Since then considerable progress has been made in research and development of hybrid rice. This second international symposium was held under the umbrella of the International Rice Research Conference. Eighty scientists and seed production experts from 18 countries, IRRI and FAO attended. Contributions covered breeding, biotechnology, seed production, agronomy, plant physiology, plant pathology, entomology and economics. Fourteen country reports and three reports on International Collaboration on Hybrid Rice were also presented by representatives of FAO, IRRI and China, respectively. This book is expected to become a valuable source of information on hybrid rice for the coming years.

We are grateful for the financial support from the Government of Italy to IRRI's Hybrid Rice Project which helped sponsor this symposium and the publication of the proceedings.

Klaus Lampe
Director General

Acknowledgments

The Organizing Committee of the symposium consisted of P. L. Pingali, M. Arraudeau, V. R. Carangal, T. R. Hargrove, K. L. Heong, S. S. Virmani, and W. Barsana. This volume was edited by Kate Kirk and Tess Rola.

Increasing yield potential in rice by exploitation of heterosis

L. P. Yuan

The degree of heterosis in different hybrid rice varieties has the following general trend: indica/japonica > indica/javanica > japonica/javanica > indica/indica > japonica/japonica. The yield potential of the best existing indica/indica hybrids developed by the CMS system, in terms of per day per unit area, is around 75 kg/ha (from seed to seed), about 15% higher than pureline varieties. The best two-line system indica/indica hybrids can outyield CMS indica/indica hybrids by 5-10%. Heterosis of japonica/javanica hybrids could be used to increase japonica hybrid yields. Their grain quality retains japonica characteristics. Indica/japonica hybrids possess the highest yield potential in both sink and source. Theoretically, they may have a 30% yield advantage over the best existing indica/indica hybrids. However, there are some problems in such intersubspecific hybrids—semisterility, plants too tall, very long growth duration, and many poorly filled grains. So far, most problems have been overcome through two-line breeding methods, except for the poor filling of a number of fertilized grains. The strategy of developing very high-yielding indica/japonica hybrids for commercial production is discussed.

Hybrid rice has helped China to increase rice production by nearly 200 million t from 1976 to 1991. Hybrid rice has a yield advantage of more than 30% over conventional pureline varieties (Table 1). In 1991, the area under hybrid rice was 17.6 million ha, 55% of the total rice area in China, and production of hybrid rice was 66% of the total rice output.

Although research on the commercial utilization of heterosis in rice has made tremendous gains during the last 20 yr, it is, from a strategic point of view, still in its infancy because the high yield potential of hybrid rice has not been fully tapped yet.

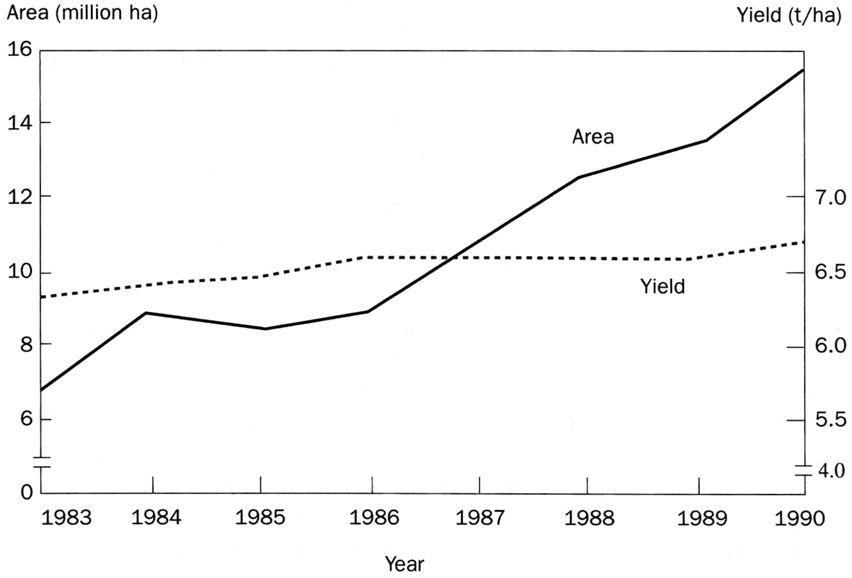
Strategies for developing hybrid rice will involve the following:

- Breeding methodology
  - Three-line method or CMS system

  - Two-line method or PGMS and TGMS systems
  - One-line method or apomixis system
- Exploitation of heterosis
  - Intervarietal hybrids
  - Intersubspecific hybrids
  - Distant hybrids (interspecific or intergeneric hybrids)

Table 1. Yields of hybrid and conventional rices from 1981 to 1990.

Year	Conventional (t/ha)	Hybrid (t/ha)	Hybrid over conventional (%)
1981	4.1	5.3	29.3
1982	4.4	5.9	31.9
1983	4.8	6.4	33.5
1984	5.0	6.4	28.8
1985	4.8	6.5	34.4
1986	4.9	6.6	35.9
1987	4.8	6.6	38.4
1988	4.5	6.6	45.5
1989	4.5	6.6	45.9
1990	4.6	6.6	41.4



1. Area and yield of hybrid rice in China from 1983 to 1990.

Breeding methodology

Three-line method or CMS system

Hybrid rice varieties used commercially are intervarietal hybrids produced by the CMS system. Many years of experience have proved that the CMS system, or three-line method, is an effective way of developing hybrid varieties and will continue to play an important role in the next decade. However, there are some constraints and problems in such a system. The most serious is that yields of existing hybrid rice varieties, including newly developed ones, have stagnated (Fig. 1). They have already reached their yield plateau, and further increase in yield potential is unlikely if no new methods and materials are invented and adopted.

Two-line method or PGMS and TGMS systems

Chinese rice scientists have been exploring new technological approaches to replace the CMS system and raise the yield ceiling in hybrid rice. So far, the most successful is the development of two-line method hybrids. This method is based on two new kinds of rice genetic tools, photosensitive (PGMS) and thermosensitive (TGMS) genic male sterile lines, which have been developed successfully in China. Male sterility is mainly controlled by one or two pairs of recessive nuclear genes and has no relation to cytoplasm. Developing hybrid rice varieties with these systems has the following advantages over the classical three-line or CMS system:

— Maintainer lines are not needed. The PGMS lines (under longer daylength) and the TGMS lines (under higher temperature) show complete pollen sterility and can thus be used for hybrid seed production. Under shorter daylength or temperate conditions, they show almost normal fertility and can be multiplied by selfing.

— The choice of parents for developing heterotic hybrids is greatly broadened. Studies showed that more than 97% of varieties tested (within subspecies) can restore such MS lines. In addition, PGMS and TGMS genes can be transferred easily to almost any rice lines with desirable characteristics.

— There are no negative effects due to sterile cytoplasm, and the unitary cytoplasm situation of WA will be avoided.

Exploitation of heterosis

Intervarietal F_1 hybrids

Breeding F_1 rice hybrids through two-line systems may be classified into two categories: intervarietal hybrids and intersubspecific hybrids. There are no genetic barriers or fertility problems in intervarietal hybrids, and the male sterility of PGMS or TGMS lines is controlled by simple recessive gene(s) which do not need a special R gene for fertility restoration; almost all normal varieties and lines within the same subspecies can restore fertility. Consequently, the probability of obtaining excellent intervarietal hybrid combinations through the two-line method is much greater than if the three-line method were used. A number of improved two-line system intervarietal rice hybrids have been successfully developed recently, and replicated tests, regional trials, and

Table 2. Yield of intervarietal rice hybrids produced by the two-line method in large demonstration fields, 1991.

Location	Season	Hybrid	Area (ha)	Yield (t/ha)	Percent of check
Tian-Dong County Guangxi Province	First crop	KS-9/03	470	9.5	+21
Sha County Fujian Province	Middle crop	W6111 S/Vary Lava	20	9.8	+18
Hunan Province	Second crop	W6154 S/Teqing	270	9.4	+14
Hunan Province	Second crop	Pei-Ai 64 S/Teqing	10	9.2	+12

farmers' field trials on a large scale have been carried out. The total planting area was 15,300 ha in 1991. The results were promising; some of them outyielded the best existing hybrids by 10-20%. Several examples are given in Table 2.

The highest yield of W6154S/Teqing in an experimental plot was 15.7 t/ha during a single crop season in Yunnan Province and 11.3 t/ha during the second crop season in Hunan Province. This hybrid variety has created new record yields in rice.

Intervarietal two-line system hybrids will be released to farmers in 1993; area to be planted will be 2 million ha in 1995.

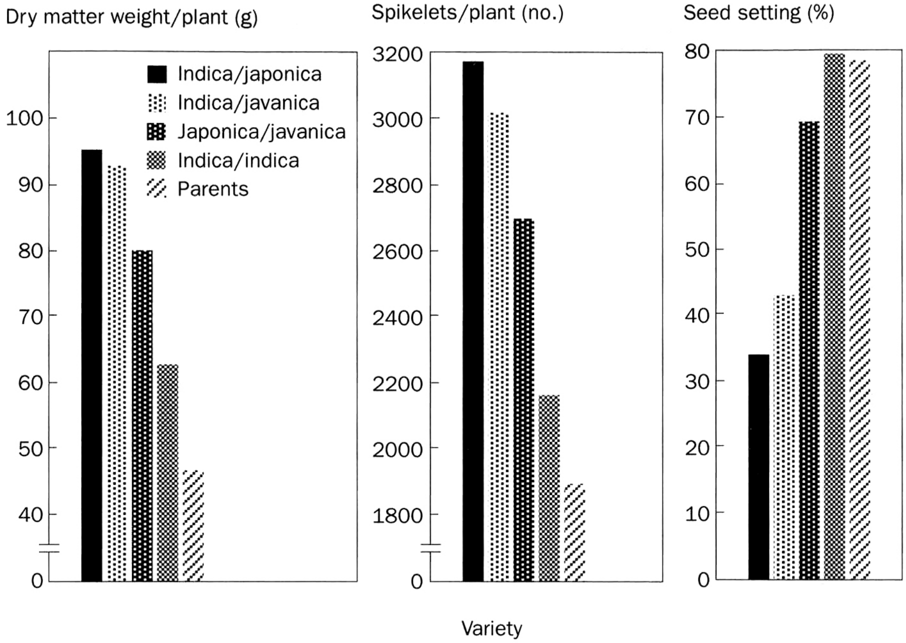
Intersubspecific F_1 hybrids

Our studies indicated that the degree of heterosis in different kinds of hybrid rice varieties has the following general trend: indica/japonica > indica/javanica > japonica/javanica > indica/indica > japonica/japonica (Fig. 2,3). The first three kinds are intersubspecific hybrids, the latter two are intervarietal.

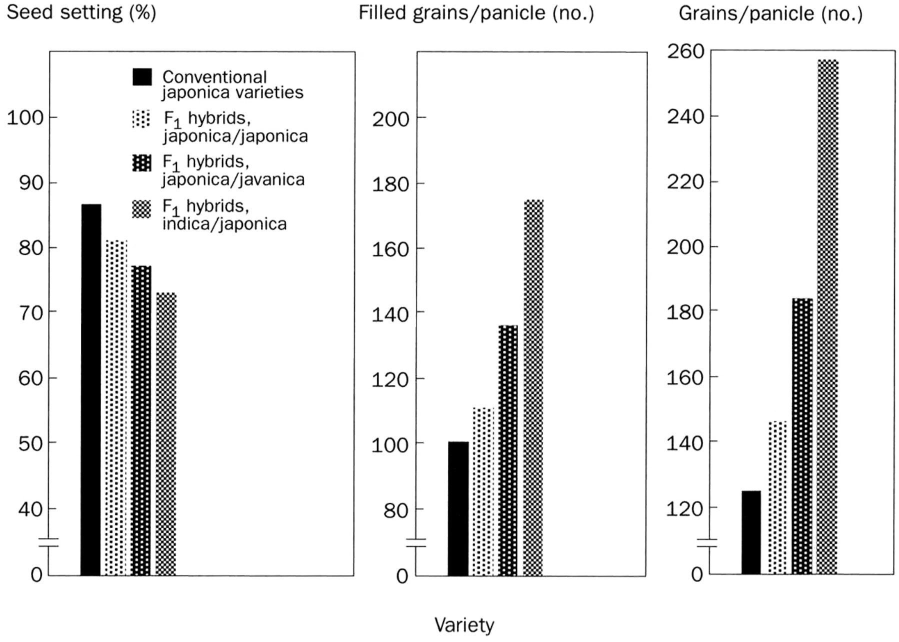
There are fewer fertility problems in japonica/javanica hybrids, and the grain quality of most javanica varieties is similar to that of japonica varieties in many aspects. It is therefore reasonable to assume that heterosis of japonica/javanica hybrids would be an effective approach for increasing japonica yields while retaining japonica-type grain quality. The development of indica/javanica hybrids may also improve grain quality as well as yield.

Indica/japonica hybrids possess the highest yield potential in both sink and source. Their theoretical yield may be 30% more than the existing highest yield of intervarietal hybrid varieties. Exploiting the strong heterosis in indica/japonica hybrids has been the major goal of our two-line system hybrid breeding program. However, in order to achieve it, four barriers normally found in such F_1 hybrids must be overcome: low seed setting rate, plants too tall, very long growth duration, and many poorly filled grains. So far, encouraging progress has been made.

By using wide compatibility (WC) genes, the low seed-setting rate caused by semisterility due to incompatibility between indica and japonica can be raised to nearly normal levels (Tables 3 and 4). A large number of japonica lines and several indica TGMS lines possessing WC genes have been developed.



2. Heterosis in different F_1 rice hybrids. Hunan Hybrid Rice Research Center, Changsa, 1988.



3. Comparison of economic characters in F_1 hybrids derived from types of indica and japonica varieties. Shenyang, 1990.

Table 3. The wide compatibility test of Pei-Ai 64 S (an indica TGMS line with WC gene), Changsha, China, 1989.

Female parent	Tester		F_1 seed setting (%)
	Nagjing 11	(Indica)	73.2
	IR36	(Indica)	81.1
	Xiang-Zao-Xian 1	(Indica)	76.4
	Milyang 46	(Indica)	75.0
Pei-Ai 64 S	Akihikari	(Japonica)	78.0
	Banila	(Japonica)	69.8
	Cheng-Te 232	(Japonica)	68.7
	Nong-Hu 26	(Japonica)	66.0
	Pei-Ti	(Javanica)	70.5
	Lun-Hui 422	(Javanica)	74.8
	CP SLO	(Javanica)	71.0
	CP 231	(Javanica)	70.0

Table 4. The wide compatibility test of Linggui 66 (a japonica line with WC gene), Hainan Island, 1992.

Male parent (japonica)	Tester (indica)	F_1 seed setting (%)
	Pei-Ai 64 S	95.53
Linggui 66	1356 S	88.29
	8902 S	85.23
	An-nong S	83.82
	645 S	83.15
	8526 S	65.28
	735 S	50.10
Shan You 55 (check)		91.93

Transferring an allelic dwarf gene (*Sd1*) into male as well as female parents can lower the plant height of indica/japonica hybrids to a semidwarf level, yet the hybrids still express very strong heterosis.

By crossing parental lines of different growth duration, (except for photosensitive late varieties), indica/japonica hybrids with medium and even shorter growth duration can be obtained.

Efforts are now focused on solving the last problem—i.e., the poor plumpness of a number of fertilized grains. It is expected that new breeding strategies will overcome this barrier within 2-3 yr.

Notes

Author's address: L. P. Yuan, Hunan Hybrid Rice Research Center, Changsha, Hunan, People's Republic of China.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Prospects of hybrid rice in the tropics and subtropics

S. S. Virmani

Cytoplasmic male sterile (CMS) lines were bred at IRRI in 1988-89 (IR58025 A, IR62829 A) and in India (Punjab male sterile lines) in 1990. Some of the hybrids bred subsequently outyielded the best check varieties in trials in the Philippines, India, Malaysia, and Vietnam. A maintainer breeding program at IRRI has resulted in considerably higher maintainer frequency. Genetically diverse CMS sources have been identified at IRRI (CMS-ARC and CMS-*Oryza perennis*) and in India (CMS-Kalinga) to overcome potential genetic vulnerability of hybrids. No restorer has yet been identified for CMS-*O. perennis* among elite cultivars. TGMS has been identified in Japan and at IRRI, and is being evaluated. Hybrid rice seed production technology for the tropics is now available. Future research should aim to a) develop new and genetically diverse CMS, maintainer, and restorer lines; b) exploit indica/tropical japonica heterosis utilizing wide compatibility genes; c) develop the two-line method of hybrid breeding using thermosensitive genic male sterility; d) improve the outcrossing potential of male sterile lines genetically; e) develop guidelines for agronomic management to maximize yield potential; and f) assess the economics of hybrid rice technology. The establishment of an international task force of hybrid rice, through a multilateral collaboration between IRRI and national agricultural research systems, would be beneficial.

In 1979, IRRI began to explore the prospects and problems of hybrid rice technology. Subsequently, some national rice research programs (India, Indonesia, South Korea, Malaysia, Philippines, Thailand, and Vietnam) also joined in this exploratory research. Hybrid rice research and development up to 1985 was reported by Yuan and Virmani (1988). Developing hybrid technology outside China was slower than anticipated, a major handicap being the lack of commercially usable cytoplasmic genetic male sterile (CMS) lines. These CMS lines were bred at IRRI by 1988-89 (IR58025 A, IR62829 A), and in India by 1990 (Punjab male sterile lines). Since there were plenty of restorers for CMS-wild abortive (WA) cytoplasm among elite inbred indica rice cultivars, experimental rice hybrids were quickly developed once the CMS lines became available. Some of these hybrids have significantly outyielded check varieties in trials in the Philippines, India, Malaysia, and Vietnam. Some heterotic hybrids have also been bred in India.

Hybrid rice seed production technology has been developed for the tropics and subtropics. It requires 15-20 g GA_3/ha and gives at least 1 t of hybrid seed and 1.5 t of pollen parent seed/ha. Seed yields can be increased to 2 t/ha by optimizing location, season, and cultural practices. With increased seed yield, and by identifying an effective substitute for GA_3, seed production costs could be reduced considerably. However, the economics of hybrid rice cultivation and seed production should be assessed. To use hybrid rice technology, national agricultural research system (NARS) should identify target areas and develop and/or strengthen seed production and distribution infrastructure in the public and/or private sector.

Heterosis studies

The presence of significant heterobeltiosis and standard heterosis for rice yield at IRRI has been reported by Virmani et al (1982), Ponnuthurai et al (1984), Virmani (1986, 1987), Yuan and Virmani (1988), Yuan et al (1989), Young and Virmani (1990), Peng and Virmani (1991), and Virmani et al (1991). Outside IRRI, similar results have been reported from South Korea (Koh 1987, Moon 1988), India (Parmasivan 1986, Ananda Kumar and Sreerangasamy 1986, Prakash and Mahadevappa 1987, Siddiq et al 1992), Indonesia (Suprihatno 1986, Subandi et al 1987), Pakistan (Cheema and Awan 1985, Cheema et al 1988), Malaysia (Osman et al 1987), and Vietnam (Luat et al 1985).

Table 1 summarizes yields of the best rice hybrids compared with those of the best available inbred rice varieties evaluated in replicated yield trials at IRRI during 1986–92. The best hybrids outyielded the best improved varieties (mean 5.2 t/ha) by about 17% on average. Yield advantages of some elite IRRI-bred rice hybrids evaluated in the Philippines, India, Vietnam, and Malaysia are presented in Table 2. Some of the hybrids—i.e., IR62829 A/IR29723-143-3-2-1R (IR64616H) and IR58025 A/IR29723-143-3-2-1 R (IR64615 H)—showed yield superiority in more than one location. Some heterotic rice hybrids have also been bred in India using IRRI and locally bred CMS lines (Siddiq et al 1994). Yield advantage of the hybrid IR64616 H was higher in a higher yielding environment than in a lower yielding environment (Fig. 1). These results clearly show that rice varietal yields could be increased by 15-20% beyond the levels of available inbred cultivars by developing and using F_1 rice hybrids, particularly under irrigated conditions with good water and fertilizer management.

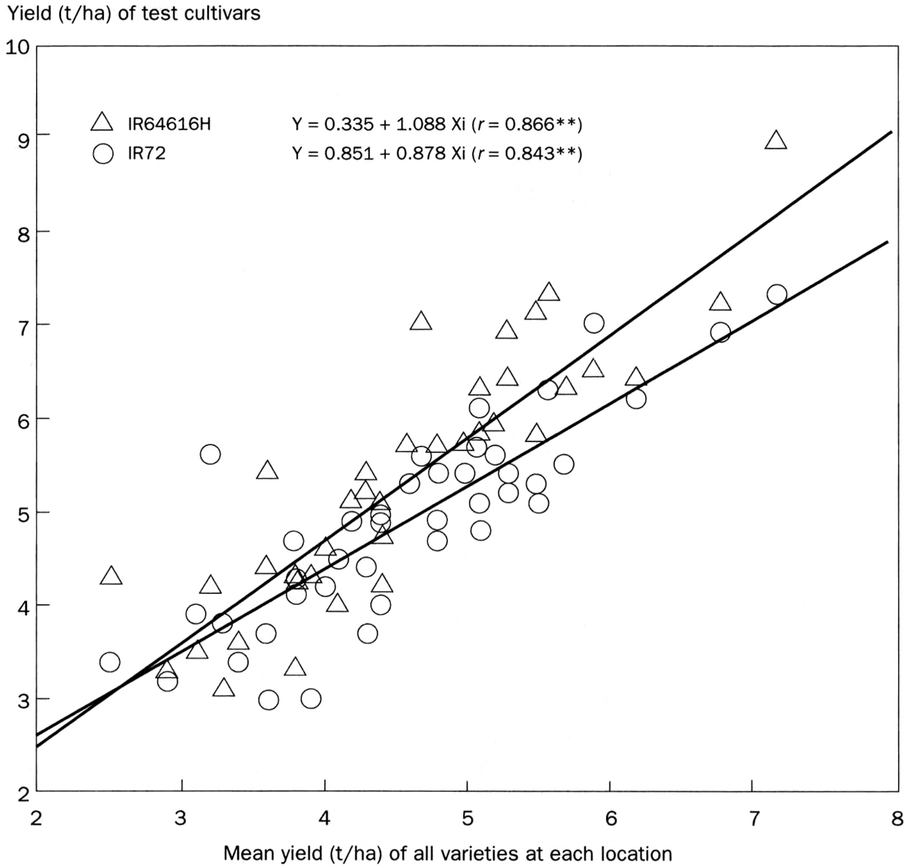
Elite rice hybrids have been found to possess disease and insect resistance and grain quality comparable with those of check varieties (Table 3). Thus heterotic rice hybrids with the required resistance and grain quality can be developed by choosing appropriate parental lines.

Increased yield in heterotic hybrids in rice is due to heterosis in spikelet number and, to some extent, heterosis for 1000 grain weight (Virmani et al 1982, Ponnuthurai et al 1984). Kim (1985) studied heterosis at three N fertility levels: 120,180, and 240 kg N/

Table 1. Comparison of highest yielding F_1 rice hybrids and inbreds in hybrid rice yield trials conducted at IRRI during 1986-92.

Season	Trial	Hybrid	Yield (t/ha)	Difference from the best check[a]	% of check	Growth duration (d)
1986 DS	I	IR54754A/IR46R	7.4	1.2*	119	126
	II	IR54754A/ARC 11353R	7.9	2.3*	142	133
1986 WS	I	IR54752A/IR64	3.9	1.0*	134	126
	II	IR19728A/IR25167-92	3.6	0.6*	120	122
	III	IR46830A/IR50R	4.1	0.7*	120	110
1987 DS	I	IR46830A/IR29723-143-3-2-1R	6.4	1.8*	139	112
	II	IR54752A/IR2797-125-3-3-2R	7.8	1.8*	130	130
	III	IR54752A/ARC 11353R	6.8	1.0*	117	128
1988 DS	II	IR46830A/IR9761-19-1R	4.8	0.0	100	108
	IV	IR54752A/IR64R	5.3	0.9*	120	120
	V	IR54752A/IR15324-13-3-3-2R	5.9	0.8ns	116	122
	VI	IR54752A/IR13146-45-2-3	6.8	1.1*	119	116
1988 WS		IR46830A/IR9761-19-1R	3.2	1.0*	145	105
1989 DS	I	IR54752A/IR9761-19-1R	6.3	1.5*	131	111
	II	IR54752A/IR28228-119-2-3-1-1R	6.5	1.0*	119	124
1989 WS	I	IR54752A/IR42686-C2-118-6-2R	3.1	0.4ns	114	120
	II	IR54752A/IR54742-22-19-3R	3.5	0.8*	131	136
1990 DS	I	IR62829A/IR9761-19-IR	4.0	0.6ns	117	110
	II	IR62829A/IR31805-20-1-3	4.5	-0.6ns	88	116
	III	IR58025A/IR10198-66-2R	4.8	0.5	112	116
	IV	IR58025A/IR29723-143-3-2-1R	5.6	1.0*	121	128
1990 WS	I	IR58025A/IR54752-22-19-3R	3.0	0	100	135
	II	IR58025A/IR40750-82-2-2-3R	3.2	0.2	107	126
1991 DS	I	IR62829A/IR35366-62-1-2-2-3	4.7	0.7*	118	112
	II	IR58025A/IR54745-2-45-3-2-4R	5.4	1.2*	128	122
1991 WS	I	IR58025A/IR19058-107-1R	6.4	1.2*	123	113
	II	IR62829A/IR47310-94-4-3-1R	5.1	1.1*	128	120
1992 DS	I	IR62829A/IR54883-43-1-3	6.4	0.5ns	108	112
	II	IR62829A/IR46R	7.2	0.7ns	111	115
	III	IR58025A/IR46R	6.3	0.8*	114	117
1992 WS	I	IR64608A/IR42686-C2-118-6-2	3.7	-0.6ns	86	111
	II	IR58025A/IR48725-B-B-141-2	4.3	0.2ns	105	116
	III	IR58025A/IR37712-90-3-3-3-2	4.1	0.4ns	111	119
	IV	IR58025A/IR54056-64-2-2-2	4.4	0.7*	119	126
	Mean	DS		6.0	0.9	118
		WS		4.0	0.6	115
	Grand mean		5.2	0.8	117	

[a] * = significant at the 5% level using LSD test, ns = not significant.



1. Regression of yield of IR4616 H and inbred check on location mean yield in National Coordinated Trials of irrigated rice cultivars in the Philippines. (Source: The Rice Varietal Improvement Group of the Philippine SeedBoard, PhilRice, 1990 WS, 1991 DS, 1991 WS, 1992 DS, and 1992 WS)

ha. Standard heterosis in spikelets per plant decreased as N increased from 120 to 240 kg/ha. Hybrids showed a greater potential sink size attained with lower N levels than inbred semidwarf cultivars.

Peng et al (1988) studied heterosis and isozyme divergence for six genes in indica rice, (*Est 9, Est 2, Amp 3, Sdh 1, Pgi 2,* and *Pgd 1*) to search for methods that would predict yield heterosis. However, they did not find any association between magnitude of heterosis in F_1s and isozyme variation among parents. These results were at variance with those of Deng (1982, 1984), which suggested that esterase and peroxidase patterns in the parents could be used to predict yield heterosis in rice. Peng et a1 (1988) attributed the cause of their contradictory results to the nature of the parental lines they used. These lines were elite rice cultivars bred at IRRI from complex crosses involving

Table 2. Yield advantage of some elite IRRI-bred hybrids in some national trials conducted in collaboration with IRRI, 1990-92.

Country	Year/ season	Location	Hybrid	Yield (t/ha)	%of best check
India	1990 WS	Mandya	IR58025A/!R9761-19-1R	9.3	112
	1991 DS	Mandya	IR58025A/IR29723-143-3-2-1R	7.0	125
		Hyderabad	IR62829A/IR1019&66-2R	6.8	128
	1991 WS	Hyderabad	IR62829A/IR10198-66-2R	7.0	117
		Maruteru	IR62829A/IR35366-40-3R	6.3	112
		New Delhi	IR62829A/IR35366-40-3R	11.6	123
		Hyderabad	IR62829A/IR28238-109-2R	5.2	121
		Mandya	IR58025A/IR40750-82-3R	6.4	121
			IR58025A/IR54742-22-19-3R	6.2	117
		Faizabad	IR58025A/IR40750-82-3R	4.6	126
	1992 WS	Hyderabad	IR58025A/IR34686-179-1-2-1R	7.3	109
		Mandya	IR58025A/IR32419-28-31-3	7.5	114
		Coimbatore	IR58025A/IR39323-182-2-33R	6.3	131
		Faizabad	IR58025A/IR46R	6.6	135
		Cuttack	IR62829A/IR46R	5.3	143
Vietnam	1990 WS	Omon	IR62829A/IR29723-143R	6.7	129
		Omon	IR58025A/IR29723-143R	7.6	146
	1991 DS	Omon	IR62829A/IR29723-143R	6.1	122
		Omon	IR58025A/IR29723-143R	6.0	120
	1991 WS	Omon	IR62928A/IR29723-143R	4.9	132
		Omon	IR58025A/IR29723-143R	4.6	124
	1992 WS	Omon	IR62829A/IR29723-143R	5.5	112
		Omon	IR58025A/IR21567-18-3R	6.2	112
		Omon	IR58025A/IR52287-15-2-3-2R	6.7	144
		Hanoi	IR58025A/IR29723-143R	5.1	150
			IR58025A/IR66R	5.1	150
			IR62829A/IR10198-66	5.7	167
Philippines	1992 DS	Nueva Ecija	IR58025A/IR32419-28-31-3	7.9	113
		Isabela	IR62829A/IR20933-68-21-1-2R	8.0	139
Malaysia	1990 DS	Bumbong Lima	IR62829A/IR29723-143R	5.8	141
			IR58025A/IR29723-143R	5.1	124
	1991 ws	Bumbong Lima	IR58025A/IR29723-143R	5.6	140
	Mean			6.4	128

parents from various geographical origins that allowed extensive recombination among genes. Consequently, linkage disequilibrium between isozyme markers and gene blocks involved in heterosis for yield might have disappeared. Also, the number of isozyme loci was small and therefore did not cover the rice genome comprehensively enough to detect such associations. Peng et al (1991) also studied the relationship

Table 3. Disease/insect resistance and grain quality characteristics of an elite rice hybrid compared with check variety (Phil Rice 1993).

Characteristic	Hybrid IR64616 H	Check IR72
Resistance to		
Blast	R[a]	S
Bacterial blight	S	I
Tungro virus	I	I
Yellow stem borer	I	I
Brown planthopper		
Biotype 1	I	R
Biotype 2	I	I
Biotype 3	I	R
Green leafhopper	I	I
Grain quality		
Amylose (%)	25.6	28.6
Gel consistency	Soft	Soft
Gel temperature	High/Int. /Low	High/Int. /Low
Hull (%)	20.9	20.9
Brown rice (%)	79.1	79.1
Milling recovery (%)	64.8	66.7
Chalky (%)	3.2	3.2
Grain type	Long slender	Long slender
Acceptability (%)		
Raw	85.3	79.0
Cooked	82.4	55.0

[a] R = resistant, S = suceptible, I = intermediate.

between heterosis and genetic divergence (measured using D^2 statistics) in rice. Correlation coefficients between magnitude of heterosis and degree of genetic divergence (D^2) were low. Heterotic and nonheterotic hybrids were found among crosses derived from parents showing different levels of genetic divergence. This study also did not show a relationship between heterosis and genetic divergence that could be used as a guideline for predicting heterosis in hybrid rice breeding programs.

Young and Virmani (1990) studied heterosis in rice over environments created by three N fertility levels (0,60, and 120 kg N/ha) and two seasons, wet (WS) and dry (DS). Substantial heterosis, heterobeltiosis, and standard heterosis were observedin different environments. The extent of heterosis was higher in WS (stress environment) than in DS (favorable environment). It was concluded that, by choosing parents carefully, hybrids possessing higher yield potential than inbreds could be developed for the tropics.

Young and Virmani (1989) also observed positive and negative effects of WA cytoplasm on heterosis for grain yield, days to flowering, and plant height. The first two effects were modified by environments; plant height was not. The study indicated the usefulness of evaluating diverse cytoplasmic sources in various nuclear genotypes bred for hybrid rice breeding programs.

Male sterility systems

Cytoplasmic genetic male sterility is the major system used to breed rice hybrids. Other systems (chemical male sterility, thermosensitive genic male sterility [TGMS], and photoperiod-sensitive genic male sterility [PGMS]) are still in the experimental stages.

Various CMS sources discovered in rice were compiled by Virmani and Shinjyo (1988), who also proposed their interim designations. The symbols assigned were interim because studies on the interrelationship between various CMS sources are limited, and it is possible that cytoplasmic factors derived from different rice cultivars may be genetically the same. Virmani and Shinjyo (1988) also proposed a model for identifying genetic differences among cytoplasms and restoring genes.

Since then, new CMS source—V20 B and Kalinga (Pradhan et al 1990)—and *Oryza perennis* (Acc. 104823) (Dalmacio et al 1992)—have been identified. It is interesting to note that V20 B is a maintainer of CMS-WA cytoplasm (the most extensively used CMS source in hybrid rice breeding) but is itself a source of CMS cytoplasm with a japonica rice cultivar; it should, therefore, have a different source of cytoplasm. Crosses of CMS lines (IR66707 A) possessing *O. perennis* cytoplasm with nine restorers of CMS-WA (Dalmacio et al 1993) showed almost complete pollen sterility (93-100%), indicating that the male sterility source of IR66707 A is different from WA sterility.

Experience at IRRI and in other countries has indicated that male sterility-inducing cytoplasmic factors are widely distributed in wild and cultivated rices. Therefore, development of CMS lines possessing diverse cytoplasmic and nuclear background is possible.

Successful use of a CMS line in breeding hybrids depends on its stability and adaptability across environments, the relative ease of restoration, its genetic diversity from restorer parents, its outcrossing potential, and its combining ability. Of hundreds of CMS lines developed in China over the years, fewer than 20 have been used to develop commercial rice hybrids (L. P. Yuan, Hunan Hybrid Rice Research Center, pers. commun.). Of the 40 CMS lines bred at IRRI during 1980-88, only three (IR58025 A, IR62829 A, and IR64608 A) possessed traits suitable for developing commercial hybrids (Virmani et al 1991). A number of CMS lines developed in India, Indonesia, South Korea, and Thailand (Virmani et al 1991) possessing WA cytoplasm are being evaluated for stability of pollen sterility, combining ability, and outcrossing potential to select those suitable for developing commercial hybrids. Evaluation at IRRI indicated that only a few (PMS1 A, PMS8 A, and PMS10 A) may be commercially useful.

Development of CMS lines depends on the frequency of maintainers identified among elite lines. Studies conducted at IRRI showed that frequency of maintainer lines was high among elite lines originating in Korea (using japonica rices), and low in India,

Table 4. Frequency of maintainers among elite lines and varieties of different origins in a testcross nursery, IRRI, 1990.

Origin	Lines tested (no.)	Maintainer frequency No.	Maintainer frequency %
IRRI	550	11	2.0
Bangladesh	22	–	0.0
China	4	–	0.0
Taiwan, China	16	1	6.2
CIAT	7	1	14.3
India	94	14	14.9
Indonesia	10	1	10.0
Korea	9	4	44.4
Pakistan	5	1	20.0
Philippines	10	–	0.0
Sri Lanka	21	2	9.5
Thailand	3	–	0.0
Vietnam	4	–	0.0
Total	750	35	4.7

Pakistan, Philippines, Indonesia, and Vietnam (using indica rices) (Table 4). Elite lines from IRRI showed very low frequency of maintainer lines. Maintainer frequency was somewhat higher for CMS lines with CMS-ARC cytoplasm than those with CMS-WA cytoplasm (Table 5). CMS lines V20 A, IR58025 A, and IR62829 A, which have the same cytoplasm but different nuclear genotypes, showed differences in maintainer frequency. Thus the genetic background of the CMS lines influenced their maintaining ability.

To enhance maintainer frequency for WA cytoplasm among elite lines bred at IRRI, a maintainer breeding program was initiated in 1989. We selected 277 promising lines from maintainer × maintainer crosses during 1991 to testcross with CMS lines with WA cytoplasm. About 70% of these lines were found to be maintainers and used for the CMS line conversion program by recurrent backcrossing (IRRI 1992). Backcross progenies derived from these maintainer lines have also shown higher stability for complete pollen sterility in comparison with backcross progenies derived from maintainer lines selected from conventional breeding programs (derived from crosses involving restorers, partial restorers, partial maintainers, and/or maintainers). The latter perhaps possess some minor fertility restorer genes. The maintainer breeding program at IRRI makes it possible to breed 20-30 CMS lines every year. These CMS lines are freely available to the national rice research systems collaborating with IRRI.

There are plenty of restorer lines for CMS-WA among indica rice cultivars and elite breeding lines (Table 6). The fertility-restoring ability of CMS-WA cytoplasm is sporophytic and governed by two genes, one of which has a stronger effect than the other (Govinda Raj and Virmani 1988). Allelism tests conducted for restorer (R) genes in some restorer lines showed that these lines differed in R gene content, and an appropriate combination of two R genes conferred full fertility in crosses with a CMS-WA line (Govinda Raj and Virmani 1988). The existence of such a high number of

Table 5. Maintainer frequency of different CMS lines among lines originating at IRRI and NARS, 1990 wet season.

CMS line	Cytoplasm	Lines tested (no.)	Origin	Maintainers	
				No.	%
IR54755 A	CMS-ARC	16	IRRI	0	0.0
		25	NARS	8	32.0
V20 A	CMS-WA	22	IRRI	0	0.0
		41	NARS	7	17.1
IR58025 A	CMS-WA	53	IRRI	5	9.4
		80	NARS	7	8.7
IR62829 A	CMS-WA	172	IRRI	3	1.7
		9	NARS	0	0

Table 6. Frequency of restorer lines among rice cultivars of different origins, IRRI, 1982-89.

Origin	Total tested (no.)	Restorer frequency (%)
IRRI	2320	36
India	70	21
Philippines	19	63
Indonesia	61	44
South Korea	53	53

diverse R genes explains the high frequency of restorer lines among elite indica breeding lines. No restorers have yet been identified for CMS line IR66707 A possessing *Oryza perennis* cytoplasm (Dalmacio et al 1992).

IRRI has also been collaborating with Japan to develop TGMS indica rices for breeding two-line hybrids in the tropics. This work is presented in a separate paper (Lu et a1 1994).

CMS restorer and TGMS lines possessing wide compatibility (WC) genes, which help to overcome indica/japonica hybrid sterility (Ikehashi and Araki 1984 1986), are being developed at IRRI to exploit indica/japonica heterosis.

Hybrid seed production

Guidelines for hybrid rice seed production have been outlined by Lin and Yuan (1980), Yuan (1985), and Virmani and Sharma (1993). The technology involves selecting seed and pollen parents with synchronized time of anthesis, timing seeding and planting so that they flower synchronously, clipping flag leaves, spraying gibberellic acid (GA_3), and practicing supplementary pollination. In a study conducted at IRRI to evaluate the effect of flag leaf clipping, GA_3 application, and supplementary pollination individually and in all possible combinations on hybrid seed yield, GA_3 application was the most effective (Virmani et al 1991). Application of GA_3 at 15-20% flowering stage improved panicle exsertion and duration of floret opening in CMS lines. Since GA_3 is expensive outside China, its use must be as economical as possible (Maruyama et al 1993). Prasad et al (1988) found 2% urea spray effective as a substitute for GA_3. However, its effect in subsequent trials was inconsistent. GA_3 cost could be reduced if countries interested in using it on a large scale consider producing it indigenously.

Yields of 1-2 t/ha of hybrid seed and 1.5-2.0 t/ha of pollen parent have been obtained at IRRI and in some national programs using available hybrid rice seed production technology (Table 7). With increased seed yield and by identifying methods to reduce GA_3 dosage or finding an effective substitute for GA_3, seed production costs could be reduced considerably. Parental lines with beneficial floral traits (longer duration of floret opening, exserted stigma, and large anthers) are being bred to increase cross-pollination and seed yields.

The NARS are identifying suitable areas and seasons for hybrid rice seed production. Public and/or private seed companies in the Philippines, India, and Vietnam are conducting these trials in collaboration with hybrid rice researchers.

Future research needs

Future research in hybrid rice should aim to develop large numbers of new and genetically diverse A, B, and R lines, and F_1 hybrids. Heterotic hybrids for Indonesia and Thailand are still to be identified for want of CMS lines adapted to local conditions. CMS lines should be derived from genetically diverse CMS sources to overcome the problem of potential genetic vulnerability of hybrids. Maintainer and restorer breeding populations should be established by deploying male sterility-facilitated recurrent selection procedures to isolate genetically diverse parental lines, which would give higher levels of heterosis. Restorer genes should also be tagged with molecular markers to facilitate marker-aided selection of restorer lines among elite lines. The two-line method of hybrid breeding should be strengthened by breeding TGMS lines. (Photoperiod-sensitive genic male sterility has limited prospects in the tropics where daylength differences are small.)

Table 7. Hybrid seed yields in tropics and subtropics obtained on CMS IR62829 A, 1990-91.

Location	Seed yield (t/ha)	Outcrossing rate (%)
IRRI	0.8-1.3	27-37
Philippines	0.8-1.2	23-43
India		
Northwestern	0.9-1.7	34.0
Southern	0.6-1.9	
Vietnam, southern	0.7-2.2	19-33

Indica/tropical japonica hybrids should be studied to enhance heterosis beyond current levels. A, B, R, and TGMS lines possessing WC genes should be developed in the genetic background of elite indica and tropical japonica rices. Since the incorporation of WC gene(s) in parental lines requires testcrossing with indica/japonica testers to confirm the presence of the WC gene, the breeding procedure becomes rather cumbersome; it would be extremely useful if morphological, isozyme, and/or molecular markers tagged with WC gene(s) were identified so that marker-aided selection for this trait could be used.

The outcrossing potential of male sterile lines could be increased by genetic improvements in floral traits that influence outcrossing. Studies should be conducted to identify those floral traits which affect outcrossing directly, so that these traits can be incorporated into CMS or TGMS lines using appropriate breeding procedures. Male sterility-facilitated recurrent selection, as practiced in Brazil (Neves et al 1993), can also be deployed for this purpose.

To optimize the use of hybrid rice technology, the NARS should identify target areas for hybrid rice cultivation and develop and or strengthen seed production infrastructure in the public and/or private sectors. Agronomic management strategies for seedbed management, planting density, fertilizer application, irrigation, drainage control, etc. should be developed for the target areas.

Since hybrid rice seed production technology is labor-intensive and requires special skills and inputs (e.g., GA_3), costs of seed production in the target areas should be determined to assess economic feasibility. Economists should also study the implication of higher seed costs (plus other inputs, if any) versus the extra yield for hybrid rice cultivation.

The pace of development and utilization of hybrid rice technology in countries outside China depends on the development of suitable hybrids, economical seed production practices, and the infrastructure to process, certify, and distribute hybrid seeds. With the progress made so far, countries such as Vietnam, India, and the Philippines should be able to extend hybrid rice technology to their farmers within a year or two. The establishment of an International Task Force on Hybrid rice, which would involve IRRI and interested NARS, would speed the development and use of hybrid rice technology in the tropics and subtropics.

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Notes

Author's address: S. S. Virmani, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Wide compatibility gene(s) and indica/japonica heterosis in rice for temperate countries

H. Ikehashi, Jiang-Shi Zou, Pal Moon Huhn, and K. Maruyama

F_1 sterility in indica-japonica hybrids is due to gamete abortion caused by an allelic interaction at a locus in chromosome 6. Some javanicas have a neutral allele at this locus. The gamete-abortion neutral allele $S\text{-}5^n$ (wide compatibility gene [WCG]) has been incorporated into japonica types and utilized to develop fertile indica-japonica hybrids. Genetic analyses indicate that a new locus between *Est-9* and *Rc* (red pericarp) in chromosome 7 is responsible for the hybrid sterility in some crosses between javanicas and a variety from the Indian subcontinent. The two S-loci indicate that hybrid sterility in most crosses is caused at one of the loci and that the alleles at the other locus remain neutral. A general system to identify S-loci is being developed. Some WCG lines for indica-japonica hybrids have been developed in China and Japan. Two experimental indica-japonica hybrids have been tested in Japan. Indica-japonica hybrids are sensitive to cold weather in temperate regions. In BT cytoplasm, which is effective in the japonica background, the *Rf* gene functions at gamete level, producing 50% fertile gametes and 50% sterile, lowering the ratio of fertile pollen, which aggravates cold damage in indica-japonica hybrids. The hybrid sterility shown in male gametes also lowers the pollen fertility in indica-japonica hybrids. Segregation distortion in many marker genes was observed in indica-japonica hybrids, implying that substantial numbers of male gametes are aborted in the hybrids. Genetic analyses as well as selection are important for developing hybrids with sound pollen. Synchronization of flowering between indicas and japonicas is necessary for seed production.

Levels of heterosis or yield increase in hybrids depend greatly on genetic distance between parents. Choosing good varietal combinations for significant heterosis among indica rices is not difficult, as there is adequate genetic diversity. The heterosis expected in hybrids between two japonica varieties is insignificant, as their genetic backgrounds are similar. Generally, hybrids between distantly related, high-yielding varieties will be most promising. However, hybrids between an indica and a japonica rice were thought to be impossible, until a genetic means to overcome the hybrid sterility was proposed by Ikehashi and Araki in 1985. They showed that gamete abortion by an allelic interaction at a locus caused the hybrid sterility, and that incorporation of a neutral allele into one of the parents may overcome the sterility. The neutral allele is now known as the wide compatibility gene (WCG).

A number of indica-japonica hybrids free of hybrid sterility were developed by incorporating WCG into japonica or indica varieties. The new series of hybrids have shown a significant yield increase in China and Japan.

The restorer gene is very rare in japonicas. Another advantage of indica-japonica crosses is that the indica-restoring gene can be used directly for japonica cytoplasmic male sterile (CMS) lines. If hybrid varieties cannot be obtained by direct crosses between indicas and japonicas, the restorer gene should be transferred from indicas to japonicas.

Intersubspecific hybrids are expected to improve on some undesirable characters of indicas, e.g., cold sensitivity, and to add tolerance in adverse conditions. Some successful instances are reported in the breeding of experimental inter-subspecific hybrids. There are also research reports indicating accompanying problems, such as pollen sterility and synchronization of flowering between indica and japonica rices, which flower at different times. Solutions to those problems are being studied at many research centers.

Genetics and breeding for indica-japonica hybrids

There has been significant progress in the genetic analysis of WC and in the breeding of experimental indica-japonica crosses since the possibility of indica-japonica hybrids was indicated by Ikehashi and Araki (1986).

Screening and breeding of WC lines

It is now widely confirmed that the sterility of indica-japonica hybrids is due to gamete abortion caused by an allelic interaction at a locus in chromosome 6, where indica and japonica have $S\text{-}5^{i}$ and $S\text{-}5^{j}$, respectively, and some javanicas have a neutral allele, $S\text{-}5^{n}$. The $S\text{-}5^{i}/S\text{-}5^{j}$ genotype shows gamete abortion, but $S\text{-}5^{n}/S\text{-}5^{i}$ and $S\text{-}5^{n}/S\text{-}5^{j}$ do not. The S-5^{n} allele (WCG) has been incorporated into japonica types and successfully used for obtaining indica-japonica hybrids (Araki et al 1988, Ikehashi 1991).

Since the possibility of overcoming hybrid sterility for indica-japonica hybrids was reported, a number of Chinese researchers have screened WC varieties with three indica testers, Nanjing 11, IR36, and Nante Hao, and three japonica testers, Akihikari (Qiouguang), Zhao-sha-keng, and Ballila. Any varieties showing more than 70% fertility in crosses to the testers are selected as WC varieties. Scientists in the provinces of Jiangsu, Hunan, Fujian, Guizho, Zhe Jian, and others have developed some WC lines. A breeding line developed in Jiangsu Province, 02428, showed good fertility in crosses to a large number of indicas and japonicas on the basis of S-5^{n}, and is being used for intersubspecific hybrids (Table 1). The line developed from 02428 showed a high level of heterosis when crossed to indicas (Table 2). The yield of the new hybrid was 10% greater than indica hybrid Shan You 63. S-5^{n} was confirmed with gene markers of *C* and *Est-2* in three-way crosses—02428/IR36//Ballila and 02428/Nanjing 11// Nankeng 34.

Table 1. Main agronomic characters of F_1 hybrids between indica PGMS and japonica wide compatibililty line (J-WCL). Nanjing, 1989 (Wang and Zou 1990).

Hybrid	Plant height (cm)	Panicle length (cm)	Spikelets/ panicle (no.)	Seed set (%)	Yield	
					t/ha	Index(%)
Early I-S/J-WCL	93	24.2	240	15.6	1.9	23
Medium I-S/J-WCL	116	24.7	276	74.6	10.3	127
Ya You 2 (I/J)	120	25.2	210	71.2	11.1	136
Shan You 63 (check)	112	26.6	186	82.2	8.2	100

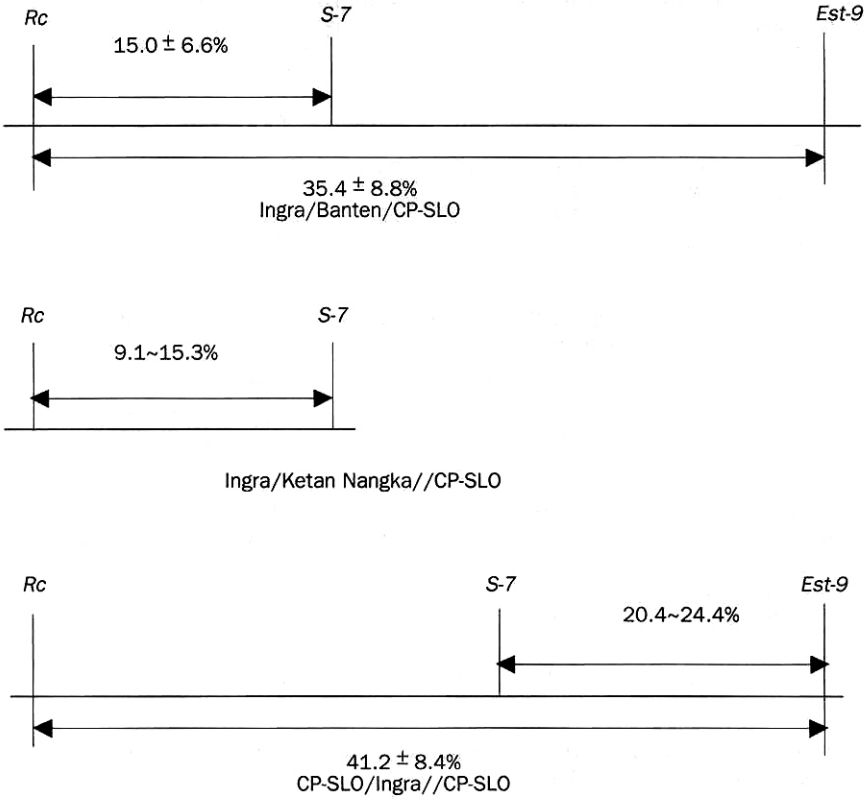
Table 2. Main characters and their heterosis of F_1 hybrids crossed with 024828 Xuan, Nanjing (Wang et al 1991).

Hybrid	Plant height (cm)	Panicle length (cm)	Spikelets/ panicle (no.)	Seed set (%)	Yield	
					t/ha	Index(%)
Indica/japonica						
NJTG-2/02428 Xuan	121	27.0	384.6	73.6	63.9	118.6
Sijiuqing 6/02428 Xuan	125	28.5	302.4	82.9	61.8	114.7
Suweon 787/02428 Xuan	126	26.3	283.0	90.0	54.0	100.2
Japonica/japonica						
Zaodanba/02428 Xuan	105	20.0	280.5	83.6	55.7	103.3
78B/02428 Xuan	94	23.7	246.2	93.1	60.7	112.6
Indica/indica						
Shan You 63 (check)	111	28.1	213.3	87.5	53.9	100.0

Table 3. Seed set of F_1 hybrids between Pel Ei 64 S and three varietal groups. Changsha, 1989 (Yuan 1990).

Subspecies	Variety	Fertility rate of F_1 (%)
Indica	Nanjing 11	73.2
	IR36	81.1
	Shan Zao Xian	76.4
	Milyang 46	75.0
Japonica	Qiouguang	78.0
	Ballila	69.8
	Chengte 22	68.7
	Longhu 26	66.0
Javanica	Peidi	70.5
	Lunhui 422	74.8
	CPSLO 17	71.0
	CP231	70.0

Similarly, CPSLO and others were used to develop WC lines in some provinces in China. At the China National Rice Research Institute at Hangzhou, a japonica line, M105-9S, and indica tester, Gui Hua Hang, were pollinated with 67 varieties, and eight WC varieties were selected (Luo et a1 1990). At the Hunan Hybrid Rice Research Center, a PGMS indica line with WCG was developed, Pei Ey 64 S, which showed high levels of fertility in its crosses to a japonica variety (Table 3).



1. Linkage map for new locus and its marker genes.

Identification of additional loci for hybrid sterility

So far, the WCG seems to solve the problems of hybrid sterility between indicas and japonicas. But there are some exceptional varietal combinations with two donors of WCG which still show hybrid sterility (Ikehashi et al 1990).

Yanagihara et al (1992) identified a new locus between *Est-9* and *Rc* (red pericarp) in chromosome 7, which is responsible for hybrid sterility in some crosses between javanicas and a variety from the Indian subcontinent (Fig. 1). With the finding of the two S-loci, it is clear that hybrid sterility in most crosses is caused at one of the loci and the alleles at the other loci remain neutral. A general system to identify S-loci is being developed to find other S-loci, whose presence has been suggested by some crosses.

Performance of indica-japonica hybrids

Despite the enthusiasm for indica-japonica hybrids, not much data on the evaluation of their field performance in China and Japan exist. Numerical data here are cited mostly from the limited studies in China and in Japan. Further assessment of yield data is necessary.

Yield potential of intersubspecific hybrids

Prior to the breeding of intersubspecific hybrids, yield potential of indica-japonica hybrids in Hunan Province, China, and Korea were evaluated with the assumption that the yield potential could be estimated by compensating for yield losses due to hybrid sterility.

A Korea-IRRI collaborative experiment was conducted at Suweon Crop Experiment Station, Korea, to examine heterosis for observed and potential yields in a set of crosses among different varietal groups (indica, japonica, and Tongil) developed from indica-japonica crosses. Thirty-seven F_1 hybrids (I/J=7, I/J=8, J/T=12, I/I=2, J/J=4, and T/T=4) made at IRRI were evaluated, along with 13 parents and check cultivars. Data were gathered from five plants in the middle row. The potential grain yield was calculated by the number of panicles x number of spikelets x grain weight x mean fertility in homozygous check varieties (IR50, Suweon 351, and Suweon 332). Yield components of the F_1 hybrids between and within the three varietal groups and their homozygous parents were measured (Table 4). Between F_1 groups, the highest grain yield was 9.6 t/ha in the F_1 of indica/Tongil crosses, followed by 9.2 t/ha for japonica/Tongil (Table 4). Potential yield was greatest in indica/japonica, 15.3 t/ha; followed by indica/indica, 15.0 t/ha; and japonica/Tongil, 14.7 t/ha. Large differences between estimated and potential yields were primarily due to low fertility in the remote crosses and late heading.

Performance of intersubspecific hybrids

Kanto Kou 1 and Ouu Kou 1, two experimental indica-japonica hybrids, were developed using an experimental line, Nekken 2, as a CMS parent. Nekken 2 is a sister line of Nekken 1, which was developed by incorporating WCG from a javanica rice, Ketan Nangka, into a japonica variety and registered as Norin PL9 (Araki et al 1990). The performance of Ouu Kou 1 was tested at the Tohoku Agricultural Experiment Station, where the hybrid was developed (Table 5). Ouu Kou 1 gave an average yield

Table 4. Group mean of grain yield (rough rice) and the associated characters In the F_1 crosses between and within different varietal groups, indica (I), japonica (J), and tongil (T), Suweon. Korea-IRRI collaborative trials.

F_1 group	Days to heading	Culm length (cm)	Panicle length (cm)	Panicles/ plant (no.)	Spikelets/ panicle (no.)	1000 grain weight (g)	Fertility (%)	Harvest index (%)	Grain yield (t/ha)	
									Estimated[a]	Potential[b]
Whole	116	95	26	15	189	26.0	72	43	9.0	14.2
I/J	118	117	28	14	193	29.3	66	38	8.6	15.3
I/T	120	78	27	15	182	25.7	83	47	9.7	13.5
J/T	112	104	25	15	197	25.7	66	40	9.2	14.8
I/I	126	82	29	17	193	24.5	67	45	8.0	15.0
J/J	112	90	24	16	176	25.2	79	49	9.1	13.4
T/T	116	75	24	16	182	23.8	73	44	8.4	12.9

[a] Calculated from the actual grain yield of five sampled plants each of three replications. [b] Calculated by the multiplication of number of panicles, number of spikelets, grain weight and mean fertility of homozygous check varieties (IR50, Suweon 351 and Suweon 332).

Table 5. Performance of Indica-japonica hybrids at Tohoku Agricultural Experiment Station for 1988-91 (Higashi et al unpubl.).

Hybrid/ variety	Year	Date of heading	Culm length (cm)	Panicle length (cm)	Yield of husked rice (t/ha)	Yield index
Ouu Kou 1[a]	1988	13 Aug	79	21.4	9.5	138
	1989	10 Aug	96	24.6	6.9	109
	1990	9 Aug	87	21.8	7.3	115
	1991	9 Aug	81	20.2	5.2[b]	87
Akihikari (control)	1988	11 Aug	71	18.6	6.9	100
	1989	7 Aug	87	18.9	6.4	100
	1990	7 Aug	75	17.8	6.4	100
	1991	4 Aug	78	17.5	6.0	100

[a] Ouu Kou 1:hybrids between Nekken 2 and Xinqingai 1. [b] Yield reduced by severe cold damage.

Table 6. Multilocation performance test of an indica-japonica hybrid, Ouu Kou 1, in 1990-91 (Higashi et al, unpubl.).

Hybrid/ variety	Place	Date of heading	Culm length (cm)	Panicle length (cm)	Yield of brown rice (t/ha)	Yield index
			1990			
Ouu Kou 1[a]	NARC	8 Aug	90	23.6	7.0	143
Kanto Kou 1[b]		8 Aug	85	22.6	6.4	131
Akihikari		6 Aug	74	19.8	4.9	100
Koshihikari		12 Aug	89	19.5	5.2	106
Ouu Kou 1	Hokuriku	1 Aug	94		7.7	112
Kanto Kou 1		31 Jul	91		7.6	110
Akihikari		25 Jul	80		6.9	100
Todorokiwase		31 Jul	92		6.6	96
			1991			
Ouu Kou 1	Ehime	13 Jul	87	22.3	6.5	110
Koshihikari		23 Jul	87	19.6	6.0	100
Akitakomachi		14 Jul	80	19.2	4.9	82
Ouu Kou 1	Ibaraki	6 Aug	74	22.1	6.4	139
Kanto Kou 1	Upland	12 Aug	66	20.9	4.9	106
Tsukuba hata mochi		8 Aug	95	22.7	4.6	100
Ouu Kou 1	Iwate	6 Aug	84	21.9	6.0	112
Akihikari	Kennan	2 Aug	82	18.3	5.4	100
Toyonishiki		10 Aug	95	18.5	5.0	93
Ouu Kou 1	Hukui	22 Jul	84	22.4	6.7	117
Akihikari		17 Jul	77	18.4	6.0	104
Hukuhikari		20 Jul	82	20.1	5.7	100
Ouu Kou 1	Hurukawa	30 Jul	75	20.1	2.7[c]	46
Kanto Kou 1		5 Aug	71	17.9	1.6[c]	27
Chiyohonami		6 Aug	84	18.9	5.9	100

[a] Ouu Kou 1:hybrids between Nekken 2 and Xinqingai 1. [b] Kanto Kou 1:hybrids between Nekken 2 and H87-53. [c] Yield reduced by severe cold damage.

increase of 20% for 1988-90 but was severely affected by the cold weather in 1991. The performance of Ouu Kou 1 was also tested at several other stations in 1990-91 (Table 6). It gave an average yield increase of 22% at six sites, excluding the one affected by the cold weather in 1991.

Many hybrid varieties were tested at the National Agricultural Research Center (NARC), where Kanto Kou 1 was developed, in 1991 (Table 7). All the hybrids were developed using Nekken 2 as the CMS line. Eight hybrids, including Ouu Kou 1, were obtained using indica varieties as restorers and gave an average yield increase of 10%, with a maximum of 26%. Six hybrids using breeding lines selected from indica-japonica crosses, including Kanto Kou 1, also gave an average yield increase of 10% with a maximum of 23%.

Table 7. Performance of hybrids between CMS Nekken 2 and indica varieties or C lines. NARC, Tsukuba, 1991 (Maruyama et al unpubl. data).

C line/ variety	Date of heading	Culm length (cm)	Panicle length (cm)	Yield (t/ha) Paddy	Yield (t/ha) Brown rice	Yield index
			F_1: CMS Nekken 2/an indica variety			
Xinqingai[a]	9 Aug	101	24.0	7.9	6.4	119
IR58	7 Aug	103	25.5	8.1	6.5	122
UPR103	13 Aug	97	26.0	7.7	6.0	113
Qing-erai	10 Aug	102	26.0	7.4	5.8	109
Jingmeiai	3 Aug	103	24.0	6.7	5.2	98
Hongyangai	8 Aug	101	23.0	7.4	5.9	111
Gaya	10 Aug	101	26.0	8.3	6.7	126
Qingqing	9 Aug	101	26.0	5.2	4.2	78
			F_1: CMS Nekken 2/a breeding line			
H87-53[b]	9 Aug	95	24.0	7.8	6.2	116
H87-50	8 Aug	101	23.0	8.2	6.6	123
H87-56	8 Aug	89	24.0	7.0	5.6	104
H87-24	4 Aug	96	24.0	7.7	6.2	115
H89-2	4 Aug	86	22.5	7.3	5.8	108
H90-36	5 Aug	92	22.5	6.1	4.9	91
			Control—restoring lines			
H87-24	6 Aug	67	24.5	7.0	5.5	103
H87-35	11 Aug	62	28.0	6.3	4.9	91
H89-22	5 Aug	70	23.0	5.6	4.4	103
H90-36	18 Aug	75	21.5	6.2	4.9	91
H90-90	5 Aug	67	21.0	5.4	4.0	75
			Control/parent varieties			
Nekken 2	6 Aug	79	20.0	6.1	5.0	93
Akihikari	3 Aug	89	18.0	6.5	5.3	100
Qingqing	14 Aug	74	23.0	6.7	5.3	98
Xinqingai	13 Aug	70	24.0	7.3	5.8	108

[a] Ouu Kou 1 is the F_1 hybrid between CMS Nekken 2 and Xinqingai. [b] Kanto Kou 1 is the F_1 hybrid between CMS Nekken 2 and H87-53.

Summarizing the initial tests, the indica-japonica hybrids selected gave a yield increase of 20% at high yield levels, ranging from 7 to 9 t/ha. The yield increase is not necessarily higher than that expected from evaluating potential yields. However, the parents of the hybrids may not have been high yielders themselves. The yield level of Nekken 2 is far below the present high-yielding japonicas because this experimental line was developed primarily to test the effect of WCG.

Progress in China

After the development of WC line 02428, a number of indica-japonica hybrids were tested in Jiangsu Province, China. Indica-japonica hybrids between early-indica-type PGMS lines, such as W6111 S, W6154 S, and 2177-1 S, and japonica WC varieties 02428, 02428 Xuan, and Rinnkai 422, were tested in Nanjing, China. Some indica-japonica hybrids showed extremely delayed flowering, but indica-japonica crosses with medium indicas, such as Milyang 23, Soku 64-S, BG 90-2 S, and IR24 S, flowered at the same time as the parents and gave an average increase of 27% (Table 8).

Most of the hybrids were superior to the parents. In performance tests on 7,000 ha in Jiangsu Province, China, an indica-japonica hybrid variety, Yayu 2 (3037/02428), gave a yield increase of 15% over Xiyu 2, a popular hybrid rice of indica origin. The 3037 is an indica cultivar selected from BG90-2, from which a PGMS line, 3037 S, has been developed. JW103 was developed for 02428. Presently, 3037/JW103 is being tested widely, together with other hybrids by the two-line method. A large-scale test of a hybrid between an indica variety and 02428 reported a yield increase of 26% (Table 8). Similarly, at the Hunan Hybrid Rice Research Center, an experimental indica-japonica hybrid, Erjiuqing indica (TGMS)/DT713 (japonica WC variety), was tested. This hybrid gave a yield increase of 47% against an indica hybrid V-You 6 (Table 9). According to initial trials in Hunan and Jiangsu, insufficient grain filling seems to be

Table 8. Performance of indica/japonica (Xaoxiandang/02428) hybrid compared with an indica hybrid Shan You 63 (Zou et al 1989).

Hybrid	Location	Panicles/ m^2 (no.)	Spikelets/ panicle (no.)	Seed set (%)	Yield	
					t/ha	Index (%)
Zaoxiandang/02428	Nanjing	192	294.8	69.6	9.7	126
Zaoxiandang/02428	Yxing	182	347.8	79.6	10.9	
Shan You 63 (check)		246	155.1	3.5	7.7	100

Table 9. Performance of Erjiuqing S (indica TGMS)/DT713 (japonica) hybrid compared with an indica hybrid. Changsha, 1989 (Yuan 1990).

Hybrid	Plant height (cm)	Panicles/ plant (no.)	Spikelets panicle (no.)	Seed set (%)	Yield	
					t/ha	Index (%)
Erjiuqing S/DT713	110	15.1	205.9	75.4	12.2	147.2
V-You 6 (check)	103	17.2	112.5	83.2	8.3	100.0

a problem in the intersubspecific hybrid, which often produces too many spikelets. Poosr grain filling is being solved by an improved fertilizing system.

Problems associated with indica-japonica hybrids

Although progress toward the development of intersubspecific hybrids is remarkable, testing the new hybrids inevitably reveals new problems.

Synchronization of flowering time

Indicas usually flower about 1 h earlier in the morning than do japonicas. This difference in flowering time makes hybridization between the two types difficult. In Nanjing, this was solved by selecting a japonica mutant, 02428 Xuan, which flowers earlier than the original type. The line, which was found in a population of 02428 in Jiangsu Province in 1987, was crossed with many indica and japonica varieties, and showed WC and good levels of heterosis compared to indica hybrid Shan You 63 (Table 2).

Strong photoperiod sensitivity in F_1

Some F_1 hybrids become photoperiod-sensitive despite nonphotoperiod-sensitive parents. For instance, both 02428 and Nante Hao flower early, but their hybrids flower later, due to sensitivity to short daylength. Some indicas, particularly those from China, seem to possess a photoperiod-sensitive gene, *Se,* in chromosome 6, which is suppressed by another gene in the F_1 (Araki et al, unpubl.). Selection of parent indicas without the suppressed photoperiod-sensitive gene may be the solution.

Plant height

Even when both parents are semidwarf, their F_1 hybrid often shows tall stature and lodging. Selection of plants shorter than ordinary high-yielding varieties seems to be important in choosing parents for intersubspecific hybrids. Use of the dominant dwarfing gene is also promising.

Cold tolerance

Indica-japonica hybrids show poor cold tolerance. In BT cytoplasm, which is effective in the japonica background, the *Rf* gene functions at gamete level, producing 50% fertile gametes and 50% sterile. Inevitably, the ratio of fertile pollen is lowered. Reduced pollen fertility was shown to aggravate cold damage to indica-japonica hybrids, as shown in Tables 5 and 6. A two-line system may solve this.

Hybrid sterility revealed in pollen

Lower fertility of male gametes due to hybrid sterility is another factor in sensitivity of indica-japonica hybrids to cold weather. Segregation distortion in many marker genes observed in indica-japonica hybrids suggests very frequent gamete abortion.

In a study of male gamete abortion, one or two marker genes on chromosomes 3, 4, 6, 7, 8, 11, and 12 of the twelve rice chromosomes were tested for segregation distortion in indica-japonica hybrids. Marker genes on chromosomes 3, 7, 8, 11, and 12 showed clear segregation distortion. The distortion was not related to the proportion of normal pollen. Germinability of pollen was below 10% in the hybrids, although 45-55% of the pollen grain appeared morphologically normal (Lin et al, unpubl.). The frequent occurrence of segregation distortion and the low germinability of pollen suggest that most pollen produced by indica-japonica hybrids is not functional. The fact that segregation distortion of a marker may be positive or negative, depending on the cross combination, suggests the existence of multiple alleles, including distortion-neutral alleles. The latter would mitigate pollen sterility in certain loci. Genetic analyses and selection for sound pollen are especially important in developing indica-japonica hybrids.

Conclusion

The potential of indica-japonica hybrids has been demonstrated in China, Korea, and Japan. Some selected intersubspecific hybrids gave yield increases of 15-20% at fairly high yield levels. Further improvements in parent lines will give a steady increase in hybrid performance.

The enhanced yield of indica-japonica hybrids may also be a target for rice breeding in tropical Asia, where many traditional upland rices are WC or japonica type. If male sterile indica parents become available in the form of TGMS in a two-line system which allows any parent combination, intersubspecific hybrids will be developed by choosing local, mostly japonica, types. TGMS lines will be best utilized where there are tropical highlands and tropical plains, as in Indonesia and Colombia. In Latin America and Africa, where japonica-like types are widely cultivated, indica-japonica hybrids have more potential. In Brazil, japonicas with a high outcrossing ratio have been developed by population breeding (Pericles et al 1990). This may also provide a promising tool for intersubspecific hybrids.

There are a number of problems inherent in indica-japonica hybrids. So far, these are being solved by innovative approaches. Further basic studies may find better solutions.

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Notes

Authors’ addresses: H. Ikehashi, Faculty of Horticulture, Chiba University, Matsudo, 271-Japan; Jiang-Shi Zou, Institute of Food Crops, Jiangsu Academy of Agricultural Sciences; Pal Moon Huhn, Crop Experiment Station, Suwon, 441-100, Korea; and K. Maruyama, National Agricultural Research Center, Tsukuba, Ibaraki, 305 Japan.

Citation infomation: Virmnani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Breeding tropical japonicas for hybrid rice production

G. S. Khush and R. C. Aquino

The experience of the last 15 yr indicates that only a small proportion of the hybrid rice combinations evaluated so far show higher yields than the best conventional cultivars. Moreover, the heterotic combinations have a yield advantage of only about 10-15%. Lack of heterotic hybrids and the limited amount of heterosis in heterotic hybrids are perhaps the main reasons for the slow development of hybrid rice technology outside China. Indica-japonica hybrids show 25-30% higher heterosis in yield, but this heterosis is harder to exploit. A japonica improvement program may help.

The amount of heterosis depends on the genetic distinctiveness of the two parents. The more distantly the parents are related, the higher the heterosis. Rice hybrids grown in China and the experimental hybrids under tests in other countries are based on indica rice germplasm. There has been a massive international exchange of indica germplasm during the last 25 yr through international nurseries. This has led to the narrowing of genetic distinctiveness in the improved germplasm of various breeding programs, hence the lack of heterosis in many hybrid combinations.

Indica and japonica germplasm, however, have remained distinct, and there has been very little gene flow between these two varietal groups. Hybrids between indica and japonica parents show 25-30% higher heterosis in yield. The commercial exploitation of this heterosis is hampered because of the following limitations:

- Intervarietal hybrid sterility
  It is well-known that most hybrids between indica and japonica varieties show varying levels of sterility. This intervarietal sterility has been the subject of numerous investigations in the past (Kato et al 1928; Oka 1958, 1988).
- Poor adaptability of temperate japonicas in the tropics
  The japonica cultivars from temperate regions (China, Japan, and Korea) are not adapted to the tropics. They show poor growth and flower precociously. Moreover,

they are highly susceptible to tropical insects and diseases. This poor adaptation of the japonica parents to the tropics is expressed in their F_1 hybrids with indicas.

- Taller stature and lodging susceptibility of indica/ japonica hybrids
  Improved indica cultivars grown in the tropics and subtropics have short stature conditioned by recessive *sd-1* gene (Aquino and Jennings 1966, Suh and Heu 1978) and they resist lodging. However, the improved temperate japonicas have been selected for short stature on the basis of polygenic variation and have the normal allele at the *sd-1* locus. Consequently, indica/japonica hybrids have tall stature and are thus susceptible to lodging.
- Poor grain quality of indica/japonica hybrids
  All the temperate japonicas have short, bold grains with low amylose and low gelatinization temperature. Most of the improved indicas, on the other hand, have medium long or long grains, with intermediate to high amylose and intermediate to low gelatinization temperature. Because of these extreme differences in the grain properties of parents, the grain quality of the indica/japonica hybrids is poor.

To overcome the above limitations and to exploit indica/japonica heterosis, we have started a japonica improvement program.

Overcoming the problem of intervarietal sterility

A wide compatibility (WC) gene was reported in some tropical rice cultivars, such as Ketan Nangka and CPSLO 17, by Ikehashi (1982) and Ikehashi and Araki (1984). Indica/japonica hybrids in which one parent has a WC gene show normal fertility. Many cultivars with WC genes have now been identified—BPI 76, Palawan, N22, and Moroberekan (Ikehashi and Araki 1984, Araki et al 1986, Ikehashi and Araki 1987, Ikehashi et al 1990, Kumar and Virmani 1993). We have started to incorporate WC genes in our improved japonica germplasm. Some of the parents with WC genes are listed in Table 1 and are being used for this purpose.

Developing japonica germplasm adapted to tropics

It was widely believed that japonicas were confined to temperate areas and indicas were limited to the tropics. On the basis of morphoagronomic studies, Oka (1958) concluded that japonicas and the so called javanicas from Indonesia are closely related.

Table 1. Donors for different traits for the tropical japonica improvement program.

Trait	Donors
Wide compatibility	Ketan Nangka, Moroberekan, CPSLO 17, N22
Short stature	MD2, Shen-Nung 89-366
Blast resistance	Moroberekan, Pring, Ketan Ararn, Mauni
Bacterial blight resistance	Loas Gedjeh, Ketan Lurnbu, Tulak Bala
Green leafhopper resistance	Pulut Cenrana, Pulut Senteu, Tua Dikin
Tungro resistance	Gundil Kuning, Djawa Serut, Jimbrug
Long grains	Azucena, Jhum Paddy 7, Rodjolele, Karang Serang 55

On the basis of allelic variation at 15 isozyme loci of 1,688 traditional rice cultivars, Glaszmann (1987) divided the rice germplasm into six groups. He clearly showed that temperate japonicas and javanicas belong to the same group. We refer to the latter as tropical japonicas. Crosses between temperate and tropical japonicas are fully fertile. We have systematically evaluated the germplasm from Southeast Asia (Vietnam, Thailand, Myanmar, Philippines, Malaysia, and Indonesia) and have identified numerous tropical japonicas. All of these have tall stature and are adapted to the tropics. We have also identified donors for disease and insect resistance within the tropical japonica germplasm (Table 1). The only donors that have not been found in the japonica germplasm are those for brown planthopper (BPH) resistance, but we have incorporated *Bph*-3 gene for resistance to BPH into japonica germplasm through backcrossing.

Introducing the dwarfing genes for lodging resistance

We have identified short-statured japonicas with *sd-1* genes. MD-2, a tropical japonica from Madagascar, and Shen-Nung 89-366, a temperate japonica from China, are short-statured cultivars with the *sd-1* gene and are being used as donors for short stature. We have selected short-statured progenies from the crosses of tropical japonicas with these short-statured donors.

Improving the grain quality of tropical japonicas

Temperate japonicas have uniformly low amylose, low gelatinization temperature, and short bold grains. There is very little variation for these traits within the temperate japonica germplasm. However, considerable variation exists for these traits in the tropical japonica germplasm. We have identified tropical japonica cultivars with long or medium long and slender grains, as well as intermediate amylose content and intermediate gelatinization temperature (Table 1). These are being used as parents to develop long-grained japonicas with intermediate amylose and intermediate gelatinization temperature.

Summary

The overall objective of this program is to develop improved japonicas adapted to the tropics, having WC genes, short stature conditioned by *sd-1,* multiple resistance to diseases and insects, and grain quality similar to that of improved indicas. These improved japonicas will be used to produce indica/japonica hybrids which hopefully will have 25-30% heterosis.

We have already produced some breeding lines which are adapted to the tropics but they still lack disease and insect resistance and have poor grain quality. These lines are being evaluated to

- study the extent of the heterosis in their F_1 hybrids with improved indicas,
- identify which are maintainers and restorers,

- detect/incorporate WC genes in them, and
- observe their floral behavior and compare it with that of improved indica parents.

It is hoped that breeding lines in the tropical japonica germplasm which are suitable for hybrid rice production and have a yield advantage of 25-30% over the best conventional cultivars will become available within the next 4-5 yr.

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Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Current status of two-line method of hybrid rice breeding

X. G. Lu, Z. G. Zhang, K. Maruyama, and S. S. Virmani

Photoperiod-sensitive genic male sterile (PGMS) rice could shift the development of rice hybrids from the three- to the two-line method. Thermosensitive genic male sterility is another tool for the two-line system. Fertility alteration of PGMS is simultaneously regulated by both photoperiod and temperature. Photoperiod regulates the fertility alteration within a certain temperature range. The span of the range varies as the sterility genes are transferred to different genetic backgrounds. A line with a wide temperature range of photoperiod sensitivity is desirable. The two-line method has helped in developing promising intervarietal group (indica/japonica) hybrid combinations. In 1991, two-line hybrids were planted to 20,000 ha throughout China. The two-line method has been exploited commercially in China since 1992.

To date, cytoplasmic male sterility (CMS) has been found to be the most effective system for developing rice hybrids in China and elsewhere. However, this system is cumbersome as it involves three lines (CMS, maintainer, and restorer). Its use is also restricted to those germplasms where maintainers and restorers are abundant. Continuous use of a CMS system risks potential genetic vulnerability of the hybrids to a biological stress. Shi et al (1981, 1985, 1986) reported a novel genic male sterility in rice which was found to revert back to fertility under certain photoperiods. It was called photoperiod-sensitive genic male sterility (PGMS). Subsequently, temperature-sensitive genic male sterility (TGMS) was also discovered (Zhou et al 1988, 1991; Maruyama et al 1990a,b; Yin et al 1990; Wu et al 1991; Virmani and Voc 1991) which reverted to partial or full fertility under certain temperature regimes. Based on these systems, Yuan (1987) put forward a new strategy of hybrid rice breeding which did not involve a maintainer line, hence it was called the two-line method. Any fertile line could be used as pollen parent to develop a rice hybrid. This paper highlights the current status of research on the two-line method of hybrid rice breeding.

Types of environment-sensitive genic male sterility in rice

Environment-sensitive genic male sterile (EGMS) lines are divided into two groups—photothermosensitive genic male sterile (PGMS) and thermosensitive genic male sterile (TGMS), depending on the environmental conditions under which fertility alteration takes place.

Photothermosensitive genic male sterility

Male sterility observed in line Nongken 58 S belongs to this category. This line shows complete pollen sterility in long-day conditions under certain temperature regimes, but revert to fertility under short-day conditions. The critical stage for fertility reversion ranges between rachis branching and spikelet primordia differentiation to the pollen mother cell formation stage (Yuan et al 1988). Critical daylength is 13.75-14.00 h/d; a daylength shorter than 13.75 h causes seed set ranging from 7.2 to 71.0% (Zhang et al 1987). Seed set increases as daylength decreases. When daylength is 14.00 h/d or longer, these lines show sterility; highest seed set was only 1.7% (Zhang et al 1987). Twilight has the same effect as daylength on inducing fertility alteration in such lines (Zhang and Yuan 1989).

He et al (1987) observed that temperature change during a day could also modify fertility alteration. Male sterile lines, developed by transferring the male sterility gene from Nongken 58 S to different genetic backgrounds, were evaluated under different daylength and temperature regimes. Fertility alteration was found to be regulated by both daylength and temperature conditions (Zhang et al 1992a). Table 1 presents seed setting percentage on selfed panicles of two male sterile lines, Nongken 58 S (japonica type) and W6154 S (indica type), under various daylength and temperature regimes.

Data suggest that in the sterile line Nongken 58 S, there is no absolute photosensitive or absolute thermosensitive sterility. The fertility alteration is a result of an interaction between photoperiod and temperature. When the temperature is above a certain point, pollen becomes sterile, and when it is below another certain point, pollen becomes fertile, regardless of the photoperiod. We refer to these two temperature points as the critical temperature for fertility induction (upper limit) and the critical temperature for sterility induction (lower limit). The temperature span between the two critical temperature points is the temperature range in which the pollen fertility alteration is regulated by photoperiod conditions. Even within the temperature range of photoperiod sensitivity, temperature conditions can still affect the critical daylength for fertility alteration and the degree of fertility alteration as well. Under short-day conditions, the critical daylength for fertility alteration becomes shorter and fertility decreases as the temperature rises, and it becomes longer with higher fertility as the temperature falls. Thus the effects of photoperiod and temperature on fertility alteration are interdependent and inseparable (Zhang et al 1992b).

The conditions for sterility gene expression–e.g., critical daylength for fertility alteration, critical temperature points, temperature range of photoperiod sensitivity, and intensity of interaction between photoperiod and temperature—are different among male sterile lines derived from Nongken 58 S by transferring the sterility gene

Table 1. Spikelet fertility of PGMS lines grown under various daylength and temperature conditions (Zhang et al 1992).

Temperature (°C)	Spikelet fertility (%) under daylength (h:min)						
	13:00	13:20	13:40	14:00	14:20	14:40	15:00
Nongken 58 S							
22	25.4	23.8	21.6	19.7	24.6	26.5	24.7
24	61.8	57.7	43.5	24.6	18.5	7.9	1.7
26	54.6	45.9	32.7	7.5	0.0	0.0	0.0
28	42.8	32.7	12.4	0.0	0.0	0.0	0.0
30	21.5	12.3	1.2	0.0	0.0	0.0	0.0
32	0.0	0.0	0.0	0.0	0.0	0.0	0.0
34	0.0	0.0	0.0	0.0	0.0	0.0	0.0
W6154 S							
22	19.4	16.9	17.9	21.5	21.8	23.0	19.5
24	56.8	49.5	29.6	27.8	30.6	28.5	28.7
26	43.2	24.8	15.4	20.1	17.9	12.8	16.4
28	1.3	0.0	0.3	0.0	0.0	0.0	0.2
30	0.0	0.0	0.0	0.0	0.0	0.1	0.2
32	0.0	0.0	0.2	0.0	0.0	0.0	0.0
34	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Guangliuai 4 (check)							
22	25.4	25.9	27.9	30.4	31.8	32.5	31.3
24	56.8	54.5	53.9	56.8	54.2	57.8	57.2
26	72.0	76.3	77.4	68.9	70.6	71.0	71.5
28	67.9	67.4	71.9	75.3	68.5	68.1	65.4
30	56.8	61.5	54.3	53.8	51.0	50.6	48.4
32	42.9	42.0	39.6	35.6	38.7	34.7	32.5
34	7.4	5.7	4.3	4.8	5.2	2.3	2.8

into various genetic backgrounds (Yuan 1990; Zhang et al 1992a,b; Zhou et al 1991; Xue and Zhao 1990; Sun et al 1991). These conditions may eventually determine the usefulness and utilization of a line in hybrid rice seed production (Zhang et al 1990, Yang et al 1989, Li et al 1989). In general, the critical temperature for fertility induction is the factor responsible for sterility fluctuations under long-day conditions. If the critical temperature for fertility induction of a line is not low enough, there may be problems with self-fertilization, which would affect the purity of the hybrid seed. Similarly, the critical temperature for sterility induction is the key factor responsible for male sterile line multiplication in short-day conditions. If the critical sterility temperature point is not high enough, it is very difficult to multiply the sterile line seeds in short-day seasons under the high temperatures which often occur in rice-growing areas.

The critical daylength for fertility alteration and the intensity of the interaction between photoperiod and temperature are the main factors in controlling the adaptability of a line. A line with a longer critical daylength for fertility alteration could be used in high latitudes and, conversely, a line with a shorter critical daylength for fertility alteration could be used in low latitudes. Consequently, a line with a strong interaction effect between photoperiod and temperature could be adapted to wider regions, a higher temperature may complement the short photoperiod in low latitudes, and a longer photoperiod could complement the low temperatures in high latitudes. For hybrid rice seed production, the ideal sterile line would have a low critical temperature point for fertility induction, a high critical temperature point for sterility induction, a wide temperature range of photoperiod sensitivity, and a strong supplementary effect between photoperiod and temperature (Yuan 1992b, Zhang and Yuan 1992).

Thermosensitive genic male sterility

Many other male sterile types which demonstrate fertility alteration have been obtained besides Nongken 58 S. Examples are Annong S, Hennong S, R59T S, Norin PL 12 and IR32364-1-3-2. According to preliminary data, the pollen fertility alterations are mainly regulated by temperature; photoperiod has an effect only in some cases. High temperature induces sterility and low temperature induces fertility or semi-sterility (Sun et al 1989, Wu et al 1991, Yang et al 1989, Zhou et al 1991, Virmani et al 1992, Maruyama et al 1992). However, the critical temperatures vary greatly as the sterile genes are from different sources.

Regions where thermosensitive sterile lines can be utilized in hybrid seed production are limited because lower temperatures may cause the sterility to fluctuate if its critical temperature is high. Contrarily, multiplication of the sterile line will be affected by high temperatures if the critical temperature is low, due to greater instability of temperature than photoperiod in nature.

Among thermosensitive sterile lines, there is another type of fertility alteration which is sterile under lower temperatures and fertile under higher temperatures. For instance, IVA shows pollen sterility in high altitude locations and becomes fertile at low altitudes (Zhang et al 1991a).

Sources of photothermosensitive male sterility

Since Shi (1981) reported the Hubei PGMS rice, breeders have found many lines with pollen fertility alterations. Some male sterile lines were spontaneous mutants (Yin et al 1990), others were developed by irradiation breeding (Maruyama et al 1991, Virmani et al 1992) or were selected from filial generations following hybridization (Zhou et al 1991) (Table 2). This suggests that photo- and/or thermosensitive genetic male sterility is a widespread phenomenon in nature and can be obtained in many ways.

Norin PL 12 (Maruyama et al 1990a,b; Virmani 1992) was developed in Japan by irradiation with 20 kr of gamma rays. It is completely sterile under 31/24 °C, partially fertile under 28/29 °C, and completely fertile under 25/18 °C (Maruyama 1990b, Virmani 1992).

IR32364-20-1-3-2B (Virmani et al 1992) was developed at IRRI in an indica rice variety. It shows complete sterility at 32/24 °C, but is partially fertile at 27/21 °C and 24/18 °C in the phytotron.

EMGS (Oard et al 1991, 1992; Rutger et al 1989) was developed by ethyl methane sulfonate treatment in the USA. It is highly sterile during July in California and its fertility increased fivefold when ratooned plants from the field were grown in a growth

Table 2. PGMS and TGMS lines developed in China, Japan, the USA, and IRRI[a].

Line	Varietal group	Developed by	Developed at	Fertility alteration conditions
Nongken 58 S	Japonica	Spontaneous mutation	Hubei, China	Long day 14.00
Annong S	Indica	Spontaneous mutation	Hunan, China	High temperature 27 °C
Hennong S	Indica	Cross breeding	Hunan, China	High temperature
5460 S	Indica	Irradiation	Fujian, China	High temperature 28-29 °C
R59T S	Indica	Irradiation	Fujian, China	High temperature
IR32364-20-1-3-2B	Indica	Irradiation	IRRI	High temperature 27 °C
poNorin PL 12	Japonica	Irradiation	Japan	High temperature 28 °C
IVA	Indica	Cross breeding	Yunnan, China	Low temperature 24 °C
Dianxin 1A	Japonica	CMS	Yunnan, China	Low temperature 22 °C
EGMS	Japonica		USA	Long day
X88	Japonica	Cross breeding	Japa n	Long day 13.75

[a] Nongken 58 S, EGMS, and X88 are PGMS lines: the rest are TGMS lines. [b] Environment-sensitive male sterile mutant.

chamber with a 12-h daylength (Oard et al 1991). The fertility alteration of EGMS was mainly controlled by daylength.

X88 was developed by cross-breeding in Japan. Its fertility alteration was regulated by daylength during 10-25 d before heading with sterility over 13.75 h/d and fertility below 13.50 h/d (Satoh et al 1992).

In China, scientists developed a number of TGMS lines. Annong S, which was found in Hunan, shows sterility under high temperature and fertility under low temperature, its critical temperature is 27 °C (Tan et al 1990). 5460 S and R59T S, which were developed in Fujian, show fertility under 27/22 °C but sterility under 33/28 °C (Yang and Wang 1990, Sun et al 1989).

The TGMS system is considered to be more useful than the PGMS in tropical areas where daylength differences are small but temperature differences between low and high altitudes exist (Virmani et al 1992).

Breeders in Yunnan, China, have developed another type of TGMS, IVA, which is opposite in characteristics to those previously mentioned. It is sterile under low temperature (24 °C) and fertile under high temperature (27 °C) (Zhang et al 1991a). Dianxin 1A (Jiang 1988) behaves similarly to IVA in terms of its fertility alteration.

Breeding of PGMS and TGMS

The sterility standard

Breeders in China have set a standard for the male sterile lines to be used in two-line hybrid rice breeding. Besides high combining ability, high outcrossing potential, and high disease and insect pest resistance, there is a system of fertility standards based on photoperiod and temperature conditions of rice areas in China:

- At least 1000 identical plants should be tested and the proportion of sterile plants should be 100%,
- Pollen sterility on the sterile plants should be ≤ 99.5%,
- The lines should have clearly defined fertility alteration conditions, and the continuous period for inducing complete sterility should last for at least 30 d in a year,
- Seed setting percentage should be more than 30% during fertility induction, and
- The critical temperature for sterility induction should be 23 °C or below for PGMS and 23.5 °C for TGMS.

Procedures and methods for developing male sterile lines

The major methods for sterile line development in China are hybridization followed by pedigree selection or anther culture and irradiation. Current studies on fertility alteration of PGMS and TGMS lines reveal several key points in sterile line breeding.

Diversity between parents should be large. The sterile genes from both PGMS and TGMS need different conditions to alter pollen fertilities when they are transferred into various genetic backgrounds. Most current PGMS lines are from Nongken 58 S; other sources, such as Annong S, should be used in breeding to broaden the genetic base.

Selection pressure should be strengthened. Selection of sterile plants in earlier generations may be conducted in high altitudes (23-25 °C) to select sterile plants with a relatively low critical temperature for fertility induction. This may be the key point for selecting lines with low critical temperatures for fertility induction that will be stable for sterility and can be successfully utilized in commercial hybrid seed production. Such lines will be TGMS if they show sterility under short-day (12-13 h) and high-temperature (28-30 °C) conditions, and PGMS if they show sterility under long-day (14-15 h) and low-temperature (23-25 °C) conditions.

Sterile lines must be tested in a phytotron at long days (14- 15 h) and short days (12-13 h) and four temperature treatments (23, 24, 25, and 26 °C) to determine their critical temperature for sterility/fertility induction and responsive types (whether they are PGMS or TGMS). Such tests may also be useful for predicting the adaptability of the lines.

Classification of sterile lines developed by cross-breeding

Many Chinese breeders have used Nongken 58 S as a gene source to breed PGMS lines. A number of indica (Lu et al 1987, 1989) and japonica PGMS (Yuan 1990) lines have been developed since 1988, and their conditions for fertility alteration have been studied (Table 3). The lines may be divided into four types, according to the characteristics of fertility alteration. (Zhang 1992).

Nongken 58 S type

Lines belonging to this group have been a relatively low critical temperature for sterility induction, a high critical temperature for fertility induction, and a wide

Table 3. Photothermo reactions of PGMS lines.

Line	Subspecies	TRPR[a]	CLL[b]	Developed at
Nongken 58 S	Japonica	24-30	13.75-14.00	Hubei
5088 S	Japonica	22-30		Hubei Agricultural Academy
7001 S	Japonica	22-30	13.50-14.00	Anhui Agricultural Academy
31111 S	Japonica	22-28		Huazhong Agricultural University
1541 S	Japonica	22-28		Hubei Yichang Agricultural Institute
Peiai 64 S[c]	Indica	22-24	13.00-13.30	Hunan Hybrid Rice Center
M901 S[c]	Indica	24-26		Fujiang Sanming Agricultural Institute
HN5-2S	Indica	24-26		Hubei Agricultural College
8906 S	Indica	24-26	13.25-13.45	Wuhan University
8902 S	Indica	27-30	13.25-13.45	Wuhan University
8912 S	Indica	26-30	13.25-13.45	Wuhan University
N5047 S	Japonica	26-30		Hubei Agricultural Academy
9044 S	Japonica	28-32		Hubei Agricultural Academy
Shuangguang S	Japonica	28-32		Hunan Hybrid Rice Center
WD-1S	Japonica			Wuhan University
C407	Japonica			China Agricultural Academy
AB0195	Japonica			Wuhan Dongxihu Agricultural Institute
6334 S	Japonica	24-30	13.75-14.00	Huazhong Teachers University
W6154 S	Indica	24-26	13.00-13.30	Hubei Agricultural Academy
W7415 S	Indica	24-26	13.00-13.30	Hubei Agricultural Academy
8801 S	Indica			Hubei Xiantao Agricultural Institute
K14 S	Indica			Guangxi Agricultural Academy
K7 S	Indica			Guangxi Agricultural Academy
K9 S	Indica			Guangxi Agricultural Academy
2177 S	Indica			Anhui Guangde Agricultural Institute

[a] TRPR = temperature range of photoperiod sensitivity, critical daylength for fertility alteration at 26-27 °C. [b] CLL = critical daylength for fertility alteration (Zhang et al 1992 b). [c] WC = wide compatibility variety.

temperature range of photoperiod sensitivity. In the rice-growing areas of central and southern China, their fertility alteration is photoperiod-sensitive and they can be multiplied easily, but it is still slightly risky to use them in hybrid seed production because a slight reduction in temperature will induce some fertility in the male sterile line. This type includes 31111 S, 5088 S, 1541 S, 7001 S, and others. From the photothermosensitivity characteristics, this type can be used in hybrid seed production, especially 5088 S and 7001 S which have lower critical temperatures for fertility induction and which show more stable sterilities under changeable natural conditions.

Peiai 64 S type

Peiai 64 S has a low critical temperature for sterility induction and a low critical temperature for fertility induction, with a narrow temperature range of photoperiod sensitivity. It has stable sterility in large areas of China and can be used in hybrid seed production without problems, but its multiplication is difficult, which limits its wide utilization. This type involves 735 S, HN5-2 S, 8906 S, M901 S, K-14 S. It can be used in hybrid rice development if the multiplication can be carried out commercially.

8902 S type

8902 S type has a high critical temperature for sterility induction and a relatively high critical temperature for fertility induction. The sterile line can be multiplied with a high yield, but hybrid seed production involves risks as the sterility is unstable when the temperature decreases in the long-day season. 5047 S and Shuanguang S are similar to 8902 S.

W6154 S type

W6154 S has a high critical temperature for sterility induction and a low critical temperature for fertility induction. It shows almost complete thermosensitive sterility in natural conditions. The fertility alteration can be significantly induced by photoperiod within the temperature range of photoperiod sensitivity, but the alteration is not complete. This type includes W7415 S and 8801 S. They can be used as thermosensitive sterile germplasm in the tropics.

To date, the ideal type of sterile line, with a low critical temperature for fertility induction, a high critical temperature for sterility induction, and a wide temperature range to allow for interaction with photoperiod, is not available. Such lines would be safe for both hybrid seed production and sterile line multiplication. They will become available in the near future (Yuan 1992a).

Selection of two-line hybrid combinations

In China, two-line hybrid rice breeding has two main areas, selection of intervarietal hybrid combinations and intervarietal group (indica/japonica) hybrid combinations.

Selection of intervarietal combinations

The yield criteria for an intervarietal combination by the two-line method are percentage increases of 5-10% and a growth duration similar to that by the three-line method using cytoplasmic male sterility (CMS). In contrast to CMS, PGMS or TGMS can combine with other cultivars without the need for maintainers and restorers (Yuan 1990), so the newest cultivars from conventional breeding can be used as soon as they become available. Some intervarietal combinations by the two-line method have been selected since 1989.

Japonica combinations include N5047 S/R9-1, 5088/R187, 5088 S/R9-1, 31301 S/1514, and 7001 S/Lunhui 422. They have been planted on 4000 ha as a late-season crop in the Yangtze River Valley in 1991. General grain yields were 6.8-7.5 t/ha, 10-15% higher than Ewan 5 and Eyi 105, leading japonica cultivars with the same growth duration as the combinations. The yield increase was not significant compared with that of Shanyou 63, a leading indica combination of CMS. The influence of homocytoplasmic restorer lines could not be eliminated from japonica hybrid breeding as the BT (Chinsurah Boro II) CMS source was used. Therefore, the area of three-line japonica hybrids planted decreased from 200,000 to 100,000 ha by 1991. Japonica sterile lines of PGMS have stable sterility, and japonica rice is in great demand in Chinese markets. It is estimated that japonica hybrids developed by the two-line method will spread widely in the Yangtze River Valley in the near future, partially replacing CMS indica hybrids and conventional japonica cultivars.

Indica combinations include W6154 S/Teqing, W6154 S/312, W6154 S/Tesanai, K9 S/03 (Jingguang 1), Peiai 64 S/Xiangzaoxian 1,5460 S/Minghui 63 (Guangyou 6063), and 8902 S/Minghui 63. These combinations cover 30,000 ha in the Yangtze River Valley and south China. Yields are generally 8.3-9.8 t/ha, the highest being more than 11 t/ha, 5-10% higher than that of Shanyou 63 and Shanyougui 33 which are the leading hybrids developed by the three-line method. Chinese breeders are trying to develop more useful indica PGMS or TGMS lines with stable sterility and which are easy to multiply.

The planted area of two-line hybrids is expected to reach about 2 million ha in China by 1995.

Selection of intervarietal group hybrid combinations

Oryza sativa L. is divided into three varietal groups, indica, japonica, and javanica. According to Yuan (1992b), yield potentials of hybrid rices in China are in the order indica/japonica > indica/javanica > japonica/javanica > indica/indica > japonica/japonica. The yield potential of indica/japonica is 30% higher than that of the current combinations between cultivars. Thus one of the targets of the two-line hybrid rice breeding method is to exploit the indica/japonica heterosis.

In China, hybrid breeding with the two-line method is also divided into two areas: a) selection of indica/javanica and japonica/javanica combinations, for which the criteria for yield is 10-15% higher than existing hybrids; and b) selection of indica/japonica combinations, with a yield increase target of 20%.

Source, selection, and breeding of lines with wide compatibility (WC). China has introduced some WC varieties—e.g., Ketan Nangka, CPSLO 17, Calotoc, Aus 373, and Dular. A variety testing system has been set up, using three indica cultivars (Nanjing 11, IR36, and Nantehao) and three japonica cultivars (Zaoshajing, Akihikari, and Balilla) for WC testing (Gu et al 1991). With the help of this system, Chinese scientists have screened many WC materials from rice germplasm resources. The major ones are 02428, Peidi, Pangxiegu, MCP231-2, PC311, Pecos, Peiai 64, Lunhui 422, T984, China 91, Haomei, DT7-1-3, and Vary Lava 1312 (Luo and Yuan 1989, Zhou 1989, Li et al 1990, Hong et al 1988, Wang et al 1990). Among them, 02428, Lunhui 422, and Vary Lava 1312 are directly exploited in intervarietal group hybrid breeding. In addition, many WC lines with desirable agronomic characters were derived from CPSLO 17 and 02428, which included indica, japonica, and javanica types, with different growth durations (Li 1990).

IRRI has identified a number of varieties, e.g., BPI 76, Lambayegue 1, Dular, Moroberekan, PBMNI, Palawan, and Fossa HV that possess WC genes (Vijaya Kumar and Virmani 1992).

Combining the PGMS gene with the WC gene in one line to breed a WC-PGMS line. Successful examples are Peiai 64 S, W 901 S, and 3105 S. Peiai 64 S, an indica line, has the PGMS gene from Nongken 58 S and the WC gene from Peidi (Luo et al 1992). 3105 S, a japonica line, has the WC gene from CPSLO 17. These kinds of sterile lines are ideal genetic tools because they can be used in both intervarietal and intervarietal group hybrids.

Breeding for intervarietal group hybrid combinations. 3037/02428 (Yayou 2) is a good intersubspecies combination produced using chemical emasculation. About 1000 ha in Jiangsu, China, were planted, and the hybrid outyielded Shanyou 63 by 15%. At present, 3037 is being converted to 3037 S (PGMS line) and some hybrid seed has been produced. W6111 S/Vary Lava 1312 (Yayou 1) and W6154 S/Vary Lava 1312 have been bred by crossing selected PGMS or TGMS lines with WC line. They have been planted on 150 ha and have yielded 9.8-11.3 t/ha.

Problems of intervarietal group hybrid combinations. There are many problems in intervarietal group hybrid breeding. These problems and their solution are listed below:

- F_1 sterility or semisterility. This is overcome by incorporating WC gene (s) in one of the parents.
- Tall plant stature of hybrids due to different semidwarf genes present in indica and japonica parents. This can be overcome by selecting parents possessing the allelic semidwarfing genes.
- Very short or very long growth duration of F_1s. This can be overcome by selecting parents with similar growth duration.
- Shattering of F_1s. Transferring a dominant gene for nonshattering into one of the parents overcomes this.
- Nonsynchronous anthesis of indica and japonica parents. This is overcome by breeding sterile lines with longer glume-opening duration and exserted stigma.
- High frequency of incompletely filled grains. In Guangdong, China, for example, W6154 S/PC311 was estimated to yield 12.8 t/ha in its milk stage, but only 50% of the grains filled well and the yield was 9.3 t/ha at maturity. Similarly, W6154 S/Vary Lava 1312, in Fujian, China, was estimated to yield 12-15 t/ha in its milk stage but the harvested yield was only 9.8-11.3 t/ha. Chinese breeders are trying to solve this problem by choosing both parents with plump grains (Yuan 1992a), although the mechanism of incomplete grain filling is not known.

In conclusion, it can be stated that the two-line method promises to increase hybrid rice breeding efficiency. If stable PGMS and TGMS lines become available, this system could replace the CMS system.

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Notes

Authors' addresses: X. G. Lu, Hubei Academy of Agricultural Sciences, Wuhan, Hubei 4300064, People's Republic of China; Z. G. Zhang, Agronomy Department, Huazhong Agricultural University, Wuhan, Hubei 430070, People's Republic of China; K. Maruyama, Heterosis Breeding Laboratory, National Agricultural Research Center, Kannondai, Tsukuba 305, Japan; and S. S. Virmani, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Application of biotechnology in hybrid rice

D. S. Brar, T. Fujimura, S. McCouch, and F. J. Zapata

Major advances have been made in biotechnology over the last decade, particularly in tissue culture and the molecular biology of higher plants. The techniques of anther culture, embryo rescue, protoplast fusion, molecular markers, and DNA transformation offer great potential in hybrid rice improvement. Developments include regeneration of rice plants from indica and japonica protoplasts, use of protoplast fusion to produce cytoplasmic hybrids (cybrids) and to transfer cytoplasmic male sterility (CMS) into elite breeding lines, establishment of a comprehensive restriction fragment length polymorphism map, production of transgenic rices, and transfer of genes for bacterial blight, blast, and brown planthopper resistance from wild species into cultivated varieties. A new CMS line, IR66707 A, has been developed. Apomixis offers the potential for permanent fixation of heterosis and development of true-breeding hybrid varieties, thus removing the need to produce hybrid seed every crop season. Embryo rescue and protoplast fusion techniques could be used to transfer gene(s) for apomixis from related wild species and genera into rice. Somatic embryogenesis offers the potential for artificial seed production, another way to exploit hybrid vigor without having to produce new hybrid seed. However, artificial seed technology in rice is still in its infancy. Molecular markers would make the identification of genes associated with heterosis possible. Tagging genes for wide compatibility, thermosensitive genic male sterility, fertility restoration, and apomixis with molecular markers would facilitate the transfer of such genes into elite breeding lines and pave the way for cloning these useful genes.

The phenomenon of heterosis has been exploited successfully in commercial hybrids of various crops, such as maize, sorghum, cotton, pearl millet, and, more recently, rice. Commercial exploitation of heterosis to increase rice yields has been demonstrated successfully in China, where 15 million ha out of a total 32.5 million ha of riceland were planted with F_1 hybrids in 1990 (Virmani et al 1991). Hybrids yield about 20% higher than inbred rices. The yield increases of hybrids have been achieved mainly through the principles of classical Mendelian genetics and conventional plant breeding methods.

The development of hybrid rice in China became possible with the discovery of a male sterile plant from the wild rice, *O. sativa f. spontanea,* on Hainan Island. While productivity has improved substantially, genetically homogeneous hybrids are especially vulnerable to pest attack, as was highlighted by the 1970-71 outbreak of southern corn leaf blight (*Cochliobolus heterostrophus*) on all US corn hybrids carrying T-type cytoplasmic male sterility (CMS). To overcome such problems, diversification of the CMS source is essential.

Recent advances in biotechnology, particularly in tissue culture and molecular biology, have opened new avenues in hybrid rice breeding. Developments include the regeneration of indica and japonica rice plants from protoplasts, production of somatic hybrid and cytoplasmic hybrid (cybrid) plants and transfer of CMS into elite breeding lines through protoplast fusion, DNA transformation and production of transgenic rices with new genetic properties, establishment of a comprehensive restriction fragment length polymorphism (RFLP) map consisting of more than 600 DNA markers, tagging of more than 20 genes of agronomic importance, and transfer of genes for bacterial blight, blast, and brown planthopper resistance from wild species across crossability barriers.

These advances in biotechnology offer great potential for hybrid rice improvement (Table 1). Some of the techniques and their applications are discussed below.

Table 1. Application of biotechnology in hybrid rice improvement.

Technique	Application
Anther culture	Extraction of high-yielding inbred lines from superior F_1 hybrids. Purification of male sterile, maintainer, and restorer lines.
Embryo rescue	Overcoming incompatibility to produce hybrids between wild and cultivated species. Deriving backcross progenies to develop alloplasmic lines for diversification of CMS sources. Transfer of genes for apomixis from wild species into elite breeding lines of rice.
Protoplast fusion	Expeditious transfer of CMS into elite breeding lines. Development of cybrids between otherwise sexually incompatible species.
Somatic embryogenesis	Production of artificial seeds for mass propagation of true-breeding hybrid varieties.
Molecular markers	Tagging genes for wide compatibility, fertility restoration, thermosensitive male sterility, apomixis, and identifying QTLs for heterosis to facilitate marker-based selection. Choosing parents based on RFLP diversity to obtain highly heterotic combinations.
Genetic transformation	Transfer of cloned genes governing apomixis for producing true-breeding commercial hybrids. Exploitation of genetically engineered nuclear male sterility and fertility restoration systems to produce hybrid varieties.

Anther culture

Anther culture is an important tool for developing homozygous lines and shortening the breeding cycle of new varieties, and can be used to extract high-yielding purelines from commercial F_1 hybrids.

In conventional breeding, a cross is made between desired parents and the segregating populations from F_2-F_7 must be grown to develop true-breeding homozygous lines. In contrast, lines derived through anther culture can be multiplied and evaluated in the immediate generation. The technique has been used successfully to produce improved cultivars of rice. More than one dozen varieties and 100 improved strains of rice have been developed in China through anther culture breeding (Brar and Khush 1993).

The technique consists of culturing anthers on a semisolid or liquid medium. The cultured anthers produce calli, or, in some cases, form embroids. These calli or embroids are regenerated into haploid plants. Dihaploid (DH) lines are produced by colchicine application, which doubles the chromosome number of the regenerated haploid plants. In rice, colchicine application is not necessary since more than 50% of haploids show spontaneous chromosome doubling. The seeds of DH lines are multiplied and evaluated for their agronomic performance.

Extraction of high-yielding inbred lines from superior F_1 hybrids

Anther culture of superior F_1 hybrids could be used to extract high-yielding homozygous lines. Fixation of certain favorable gene combinations in DH lines from such heterotic hybrids could lead to the development of high-yielding inbred lines, thus supplementing the varietal improvement programs. Similarly, anther culture could be used to purify male sterile, maintainer, and restorer lines.

Embryo rescue

The genus *Oryza,* to which cultivated rice belongs, has about 24 wild species. These wild species are an important reservoir of useful genes for resistance to biotic and abiotic stresses, including CMS. However, several crossability barriers limit the transfer of such genes from wild species into cultivated rice. Among these barriers, embryo abortion is the most frequent. Embryo rescue is an important technique for overcoming this in interspecific crosses.

Cytoplasmic diversification through wide hybridization

Embryo rescue of wild × cultivated hybrids could lead to the development of an array of alloplasmic lines with the cytoplasm of various wild species and the nuclear genome of the recurrent rice parent. These alloplasmic lines would enable diversification of CMS sources.

We have developed a new CMS line, IR66707 A, from direct crosses of *O. perennis* AA genome species with *O. sativa* cv. IR64. This line has *O. perennis* (Acc. 104823) cytoplasm and IR64 nuclear genome and is completely stable for male sterility. Genetic tests show that the male sterility source of IR66707 A is different from wild abortive (WA) cytosterility, one of the sources commonly used in hybrid rice breeding (Dalmacio et al 1992). Southern hybridization with mitochondrial DNA-specific probes showed identical RFLP patterns in 40 combinations (5 enzymes x 8 probes) involving *O. perennis* and IR66707 A. The findings indicate no major rearrangement in the mitochondrial genome of IR66707 A. The CMS is probably caused by modified transcription or translation of messenger RNA, not by modification of the mitochondrial genome. The technique has potential for production of hybrids and cytoplasm transfer from divergent species and genera such as *Leersia, Hygrooryza,* and others.

Transfer of wild apomixis genes

Apomixis refers to the development of an embryo without the union of egg and sperm. It is a natural method of producing genetically identical plants through seed, and offers the potential for developing true-breeding hybrid varieties. This would avoid the cumbersome and expensive process of producing fresh hybrid seed every crop season.

Apomixis has been reported in more than 250 plant species (Hanna 1987, 1991). Some apomictic species, such as *Pennisetum, Cenchrus, Poa,* and others. have been investigated extensively. At IRRI, several accessions of wild species of *Oryza* have been screened for apomixis through embryo sac analysis. Results are largely negative. Similarly, traditional varieties of rice have been screened for twin seedlings. The frequency of twin seedlings was low; however, twinning is not necessarily indicative of apomixis. Once apomictic gene(s) become available in wild species, embryo rescue will be important in their transfer into cultivated rice varieties.

Protoplast fusion

Transfer of CMS to elite breeding lines requires 5-7 repeated backcrosses. Protoplast culture has made it possible to transfer CMS within several months. Some notable examples of successful CMS transfer by protoplast fusion include tobacco, *Brassica,* citrus, and, more recently, rice.

Protoplasts of the donor CMS line are exposed to high doses of irradiation and fused with the iodoacetamide-treated protoplasts of the recipient line. Irradiation inactivates the nucleus, while chemical treatment with iodoacetamide prevents cell division. As a result, metabolically complementary cells are capable of developing into plantlets after fusion treatment. The donor-recipient method has been used successfully to transfer CMS sources into fertile lines of rice (Yang et al 1989, Kyozuka et al 1989). The method does not require the use of a selectable cytoplasmic marker of the donor.

Protoplasts of several indica and japonica rices have been regenerated into mature plants (Uchimiya et al 1991, Zapata et al 1992). These findings have broadened the scope for producing somatic hybrids and cybrids in rice through protoplast fusion (Akagi et al 1989). Success in protoplast culture has also made the direct transfer of CMS into elite rice breeding lines possible, thus avoiding the cumbersome process of backcrossing. Protoplast technology could be used to produce alloplasmic lines of rice having cytoplasm from various wild species and related genera. These lines could have diverse CMS sources, thus overcoming the hybrids' genetic vulnerability to disease and insect pests.

Production of cybrids and transfer of CMS into elite breeding lines

Somatic hybrids have been produced through protoplast fusion between cultivated rice and four wild species (Hayashi et al 1988). The production of cybrids following protoplast fusion is one of the most exciting developments. In cybridization, the nuclear genome of one parent is combined with the organelles of a second parent. In effect, organelles are transferred from one parent to the other in a single step. Protoplast fusion provides a unique opportunity to produce cybrids and recombine cytoplasmically inherited traits. Cybrids have been produced through protoplast fusion in several species. The cybridity is confirmed on the basis of mitochondrial DNA restriction patterns, morphological traits, and isozyme and cytological tests.

Yang et al (1988a, 1989) produced cybrid plants in rice by electrofusing gamma-irradiated protoplasts of A-58 CMS and iodoacetamide-treated protoplasts of the fertile cultivar Fujiminori. Cybrids had the peroxidase isozyme of the fertile parent (Fujiminori) but had four plasmidlike DNAs (B1, B2, B3, and B4) from the sterile A-58 CMS parent in their mitochondrial genomes. Cybrids produced through protoplast fusion using the donor-recipient method had the mitochondrial genome of the CMS line and the nuclear genome of the fertile variety (Akagi et al 1989). Kyozuka et al (1989) also used the donor-recipient method and transferred CMS of Chinsurah Boro II, an indica rice, into japonica variety Nipponbare. Akagi and Fujimura (1992) have developed an efficient and highly reproducible system for transferring CMS into an array of breeding lines. The method inactivates protoplasts of the recipient parent with 3 mM of iodoacetamide for 15 min, and those of the donor (CMS) parent with a high dose of X-rays (125 kr). Using this method, indica CMS has been introduced into 35 japonica cultivars.

Somatic embryogenesis

One of the major concerns of cultivating hybrid varieties is that farmers cannot use seed from the harvest for their next crop, and thus have to buy new seed for each crop. Moreover, the cost of hybrid seeds is 5-20 times that of seeds of inbred varieties. Possibilities for true-to-type multiplication of hybrid rice are being explored through two approaches: 1) production of artificial seeds through somatic embryogenesis, and 2) development of apomictic hybrid rice through wide hybridization and genetic engineering techniques.

Production of artificial seeds and mass propagation of true- breeding hybrids

Artificial seeds, consisting of somatic embryos enclosed in a protective coating, are being proposed as a low-cost, high-volume propagation system. The objective is to produce clonal seeds at a cost comparable with that of producing hybrid seed by conventional methods. Artificial seeds can be produced through somatic embryogenesis. This is the process by which somatic cells develop through the stages of embryogeny to give whole plants without gametic fusion. Somatic embryogenesis has been reported in more than 150 plant species. Somatic embryos have been induced from a variety of plant tissues, such as germinating seedlings, shoot meristems, young inflorescence, nucellus, leaf, anther, root, and others. The procedure involves establishing embryogenic cell cultures, followed by encapsulating of mature somatic embryos to serve as planting material.

Artificial seed technology involves various stages for the production of somatic embryos and their utilization as commercial propagules (Redenbaugh et al 1988):

1) optimization of a somatic embryogenesis system from cultured cells,
2) optimization of embryo maturation,
3) automation of embryo production,
4) production of mature synchronized embryos,
5) encapsulation of embryos with necessary adjuvants,
6) coating of encapsulated embryos,
7) optimization of greenhouse and field conditions for conversion of embryos to plants, and
8) delivery system for artificial seeds.

Although major advances have been made to understand the role of auxins and cytokinins in inducing embryogenesis from cultured cells, maturation of embryos, and germination of embryos into plantlets (Merkle et al 1990, Redenbaugh 1990, Fujii et al 1992), the technique has not been used commercially. Recently, Fujii et al (1992) were successful in celery, where embryos planted directly in the field showed 1% plant regeneration. Successful conversion of coated and naked somatic embryos of celery planted in the field indicates the possibility of using artificial seeds as a supplement to natural seeds.

In rice, the research on artificial seeds is still in its infancy. Efficient procedures are needed for inducing somatic embryogenesis from cultured cells of elite hybrids, and proper synchronization in somatic embryo development. Automated, large-scale liquid culture systems (bioreactors) have yet to be developed. Furthermore, seed coat materials with the proper protective qualities and dormancy still need to be identified.

Synthetic seed technology in rice has vast potential for exploitation of hybrid vigor, as it would permit the multiplication and large-scale propagation of superior hybrids. However, long-term research is needed before this technology becomes available for commercial propagation of true-breeding rice hybrids.

Molecular markers

The knowledge of the genetic architecture of rice is essential in genetic and breeding research. The classical genetic map is based on morphological mutant markers. The map based on molecular markers has inherent advantages over the classical map. Molecular markers, including both DNA markers and isozymes, are discrete, codominant, nondeleterious, and unaffected by the environment. Moreover, molecular markers are numerous and thus can cover the entire genome. In rice, comprehensive molecular maps consisting of more than 600 DNA markers are available (McCouch et al 1988, Tanksley et al 1992, Saito et al 1991). Several genes governing agronomically important characters have been tagged with molecular markers.

Molecular markers provide a unique opportunity to tag genes for use in hybrid rice breeding. Examples include genes for WC, TGMS, fertility restoration, and quantitative trait loci (QTL) for heterosis.

Tagging WC genes

Exploitation of genetic variability through indica/japonica crosses is hindered by the increased sterility of hybrids. Wide compatibility genes overcome the partial sterility commonly encountered in the progeny of indica/japonica crosses (Ikehashi and Araki 1988). Tagging WC genes with molecular markers would facilitate the transfer of such genes into elite breeding lines and the development of fertile indica/japonica hybrids.

Allelic interaction at the S-5 locus is reported to confer partial spikelet sterility of F_1 hybrids between indica ($S\text{-}5^i$) and japonica ($S\text{-}5^j$) rices, while heterozygotes containing a third allele ($S\text{-}5^n$) in combination with either $S\text{-}5^i$ or $S\text{-}5^j$ are fully fertile (Ikehashi and Araki 1984). As part of the IRRI-Japan Shuttle Research Project, linkage analysis based on molecular and morphological markers was conducted to determine the location of the S-5 locus on the molecular map of rice. A population of 198 plants derived from a three-way cross with IR36 (indica), Akihikari (japonica), and a WC variety, Nekken 2, (IR36/Nekken2//Akihikari) was planted at an experimental farm of the National Agricultural Research Center in Japan and used to evaluate fertility, morphological markers, and to do RFLP analysis. The S-5 locus is known to be located on chromosome 6 in the region of the morphological markers chromogen (C) and Waxy (wx). Polymorphism was detected for *Pgi-2, Est-2,* RZ516, CDO475, CDO96, RG213, RG424, and RZ247. DNA from 163 segregants derived from this three-way cross was digested and used for Southern blotting at IRRI. RFLP analysis with nonradioactively labeled probes confirmed tight linkage between RG213, *Est-2,* C, and S-5 (IRRI 1993). In addition, three distinct molecular weight bands were detected at RG213, corresponding to the respective parents in the cross. This allows unequivocable determination of the parental origin of the allele at this locus. RG213 is suggested for use in marker-assisted, seedling-stage assays for WC where fertile indica/japonica hybrids are desired in the breeding program. Liu et al (1992) used isozyme and RFLP markers to tag a WC gene. The WC gene was reported to be 9.1 map units from RG213 and 5.9 map units from *Est-2.* Similarly, tagging of genes for thermosensitive male sterility and fertility restoration will assist in transferring such genes into elite breeding lines, thus enhancing the efficiency of hybrid rice breeding.

Tagging gene(s) for apomixis

Unlike other traits, screening for apomixis is very laborious and difficult. Molecular markers offer great potential for tagging genes governing apomixis. Recently, attempts have been made in *Pennisetum* to tag apomictic reproduction with molecular markers (Ozias-Akins et al 1993). Apomixis in the genus *Pennisetum* is well-studied (Hanna 1991). One of the wild hexaploid species, *P. squamulatum* ($2n = 42$), is an obligate apomictic. Amphiploids ($2n=42$) were produced from the cross *P. glaucum*

× *P. purpureum*. These amphiploids were crossed with *P. squamulatum* and backcrossed three times to tetraploid pearl millet. An apomictic BC_3 progeny (2n = 29) was derived, with one to seven aposporous embryo sac(s) (Dujardin and Hanna 1989). Ozias-Akins et al (1993) identified RFLP and randomly amplified polymorphic DNA (RAPD) markers that demonstrate introgression of DNA from the apomictic species *P. squamulatum* in the BC_3 line. Cosegregation of apomictic reproduction and molecular markers was observed in BC_4 progeny. Two markers, UGT 197 and POC-04, were reported to be tightly linked with apomixis. Because of the lack of detectable recombination between the alien chromosomes and the pearl millet genomes, mapping resolution was not achieved. Once the gene(s) for apomixis become available in rice, molecular markers will enhance the efficiency of transfer of such apomictic genes into elite breeding lines.

Tagging QTL for heterosis

Restriction fragment length polymorphism markers are powerful molecular markers in QTL mapping. Wang et al (1993) identified several QTLs governing blast resistance in rice. Experiments have been initiated at IRRI to map QTLs for heterosis in a population derived from a cross of indica (IR64) and japonica (Azucena) varieties. Once QTLs with a major effect on heterosis for grain yield become available, this is expected to facilitate the development of highly productive hybrid varieties.

Stuber et al (1992) mapped QTLs associated with seven agronomic traits, including grain yield, in a cross between two widely used elite maize inbred lines, B73 and Mo 17. Both point analysis and interval mapping were used to identify QTLs on over 3,000 field plots (nearly 100,000 plants). This study demonstrated that heterozygous, rather than homozygous, marker loci were often most closely associated with the highest yielding progeny. These results suggest that overdominance plays a role in heterosis and that QTL analysis is capable of identiying specific regions of the genome that contribute to the heterotic response.

Choice of parents based on RFLP diversity

Exploitation of heterosis among genetically divergent germplasm is important in hybrid breeding. In well-studied systems, such as maize, heterotic groups have been established by relating the heterosis observed in crosses to the origin of parents, morphological traits, geographic origin, and, to a limited extent, isozyme diversity. Isozymes provide only limited information because relatively few polymorphic marker loci are available in elite germplasm. DNA markers, which are numerous in number and can cover the entire genome, have thus been suggested to help overcome many of the problems associated with morphological or isozyme markers.

Restriction fragment length polymorphism markers have been used to characterize genetic diversity (Ishii and Tsunewaki 1991; Wang and Tanksley, 1989; Wang et al 1992). Knowledge of genetic diversity is helpful in choosing parents for hybrid rice breeding, but it does not allow breeders to make accurate predictions about the most productive hybrid combinations. Lee et al (1989) supported the use of RFLP in understanding the relationships among maize inbreds. Smith and Smith (1991) demonstrated that RFLP diversity among maize hybrids was correlated with genetic distance, based on multigenic traits such as pedigree, F_1 yield, and yield heterosis. Messmer et al (1992) used RFLP markers to evaluate genetic diversity among flint and dent maize lines. In 1990, Melchinger and coworkers reported that random probing with RFLP was of limited use in predicting the heterotic performance of single crosses between unrelated lines, but Melchinger et al (1991) suggested that RFLP data can be used for assigning inbreds into heterotic groups and quantifying genetic similarities between related lines. These reports suggest that random probing is useful in assessing genetic distance. However, the ability to predict which combinations of inbreds will produce the most productive hybrids is more likely to evolve from QTL analysis, which is aimed at identifying specific associations between genetic loci and heterotic yield responses.

Molecular basis of CMS

Cytoplasmic male sterility is an important trait used in F_1 hybrid seed production in rice. It is maternally inherited. Extensive molecular and genetic evidence indicates that the genetic information for CMS is encoded by mitochondrial DNA (Lonsdale 1987).

Mitochondrial DNA modifications associated with CMS have been reported in rice (Kadowaki et al 1986, 1988, Mignouna et al 1987). Small linear and circular DNA molecules have been found in CMS lines of several plant species. Yang et al (1988a) found plasmidlike DNAs (B_1, B_2, B_3, and B_4) from the sterile A-58 CMS parent in their mitochondrial genomes. Precise understanding of the molecular basis of CMS could explain the cause of CMS instability and lead to the development and incorporation of stable CMS sources into rice varieties.

Genetic transformation

Major advances in genetic transformation have been made using *Agrobacterium* and direct DNA transfer methods and in the production of transgenic plants (Uchimiya et al 1989). Availability of embryogenic cell suspensions, efficient protoplast regeneration, and DNA transfer methods have been key factors in the successful production of transgenic rices (Toriyama et al 1988, Yang et al 1988b, Shimamoto et al 1989, Christou et al 1991, Datta et al 1992, Wu et al 1992). The prospects for producing genetically engineered hybrid rices have also widened.

Some useful genes governing apomixis, genetic male sterility, and fertility restorations need to be cloned and transferred into elite breeding lines of rice. Transfer of gene(s) for apomixis could lead to a major breakthrough in developing true-breeding rice hybrids. Attempts are being made to clone such genes from apomictic species such as *Pennisetum* and *Cenchrus.* Genes for nuclear male sterility (*barnase*) and fertility restoration (*barstar*) have already been cloned and transferred into crops such as tobacco and rape seed (Mariani et al 1990, 1992). These two genetically engineered genes are being exploited as an additional system for producing hybrid varieties. Both genes inhibit chimeric ribonuclease, *barnase* leads to the destruction of the tapetal cell layer and consequently to male sterility. *Barstar* can selectively restore fertility of male sterile plants. The TA29-*barstar* gene suppresses TA29-*barnase* gene expression by protein-protein interactions, protects tapetal cells from *barnase* cytoxicity, and restores male fertility. The *barstar* gene also acts as a dominant restorer of male fertility in tobacco.

The availability of such genetically engineered male sterility and fertility restoration systems provide new opportunities in the development of hybrid rice varieties.

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Notes

Authors' addresses: D. S. Brar, Plant Breeding, Genetics and Biochemistry Division, International Rice Research Institute, P.O. Box 933, Manila, Philippines; T. Fujimura, Mitsui Toatsu Chemicals, Inc. 1144 Togo, Mobara Shi, Japan; and S. McCouch and F. J. Zapata, Plant Breeding, Genetics and Biochemistry Division, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

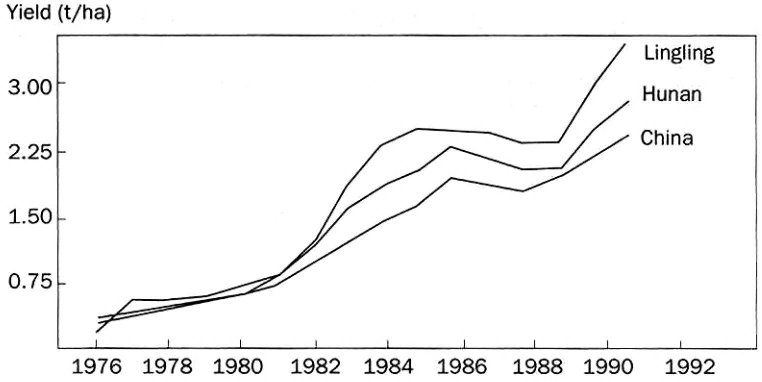
Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Advances in hybrid rice seed production technology

Huang Peijin, K. Maruyama, H. L. Sharma, and S. S. Virmani

The price of hybrid rice seed must be reduced by increasing yield and lowering production costs. Much effort has been put into improving seed production technology. In China, improved techniques have increased hybrid seed yield from 0.27 t/ha in 1976 to 2.3 t/ha in 1991. Synchronization of flowering among parental lines is vital for pollination. At IRRI, seedling age at transplanting was found to a be major determining factor in flowering synchronicity. Flowering in CMS, maintainer, and restorer lines was delayed by 2-3 d by spraying 25 ppm 2,4-D or 2% urea solution at the panicle initiation stage. It was, however, advanced by spraying KNO_3 (200 ppm) or 1% phosphate solution. Several means of raising yield have been practiced in China. The major points of the improved techniques are: a) avoiding flag leaf clipping by skillful spraying of gibberellic acid (GA_3); b) widening the row ratio; c) closer transplanting, two or three seedlings per hill for A line instead of one; d) doing supplementary pollination at anther dehiscence: and e) controlling kernel smut. GA_3 is expensive. Costs can be reduced by using an ultralow-volume (ULV) sprayer instead of the traditional knapsack sprayer. Dosage is reduced from 45 to 15 g GA_3/ha with comparable outcrossing rates and seed yields. By mixing the seeds of both parents, mechanized production becomes easier. This method ensures a higher ratio of seed set on the male sterile plants. The seeds are harvested as a mixture of pollinator seeds and hybrid seeds, and can be separated if they are different from the pollinator seeds in color, size, or other traits. If a female sterile pollinator is made available, only hybrid seeds will be harvested. Another possible method for separation is to incorporate a herbicide-sensitive gene in the pollinator, so that it can be eliminated by spraying that particular herbicide just after pollination. In this way, only hybrid seeds will be harvested.

Since commercial production of hybrid rice began in China in 1976, tremendous efforts have been made to improve seed production technology. In 1992, 187,000 ha were used for hybrid rice seed production in China. Hunan Province had 22,000 ha and average



1. Hybrid rice seed production in China, 1976-91.

yield was 2.7 t/ha. In Lingling Prefecture, there were 2,400 ha and the average yield was 3.2 t/ha. The ultimate aim is to make hybrid rice seeds cost the same as self-pollinated varieties. But this cannot be realized until an excellent apomict is developed. Until then, seed production technology using male sterile lines must be developed and utilized.

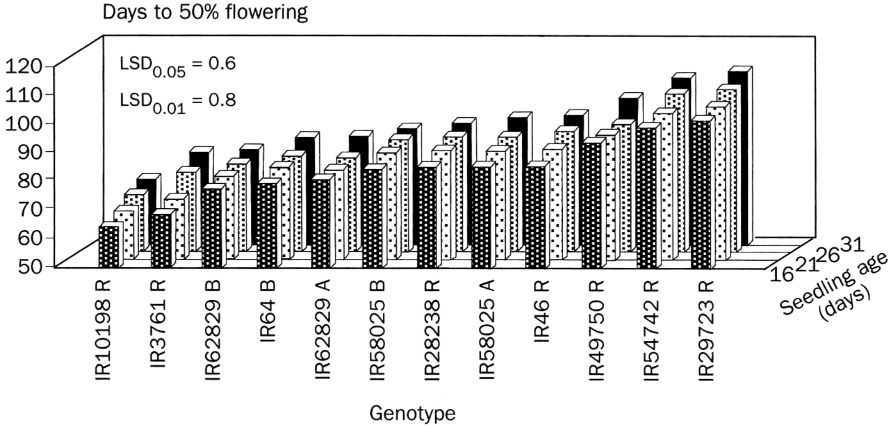
Hybrid rice seed production in China

Hybrid rice seed production has been increasing steadily since 1976 due to improved seed production techniques (Fig. 1). The key factors for this increase are choice of field, synchronization of heading and flowering of parents, row ratio and row orientation, field management, leaf clipping, gibberellic acid (GA_3) application, and supplementary pollination (Mao 1988).

Lingling Prefecture has the highest hybrid seed production in Hunan Province, which in turn has the highest in China. The technical improvements responsible have been identified. In 1984, skillful spraying of GA_3 made flag leaf clipping unnecessary, and seed yields increased from 0.8 t/ha in 1982 to 2.25 t/ha in 1991. Widening row ratios, closer transplanting with multiple seedlings, supplementary pollination at the peak time of anther dehiscence, and control of kernel smut disease increased seed yield to 3.2 t/ha. The new seed production techniques were demonstrated in 130 ha in 1991. The average rate of seed set was 58.3% and the average yield was 4.5 t/ha. In the highest seed yield plot, rate of seed set was 66.7% and the yield was 5.8 t/ha.

Synchronization of flowering

Yields from hybrid rice seed production plots are directly influenced by synchronization of parental flowering. Heading dates of seed and pollen parents with different growth durations can be adjusted by differential seeding and transplanting. However, in spite of differential seeding of seed and pollen parents (Yuan 1985) and staggered



2. Days to flowering in CMS, maintainer, and restorer lines of rice as affected by seedling age.

planting of pollen parents (Xu and Li 1988), synchronized flowering is sometimes not achieved due to differences in field management practices and fluctuations in weather conditions. It is, therefore, necessary to identify the management practices that result in nonsynchronization and identify corrective measures which would help to enhance or delay flowering as necessary.

Effect of seedling age on days to flowering

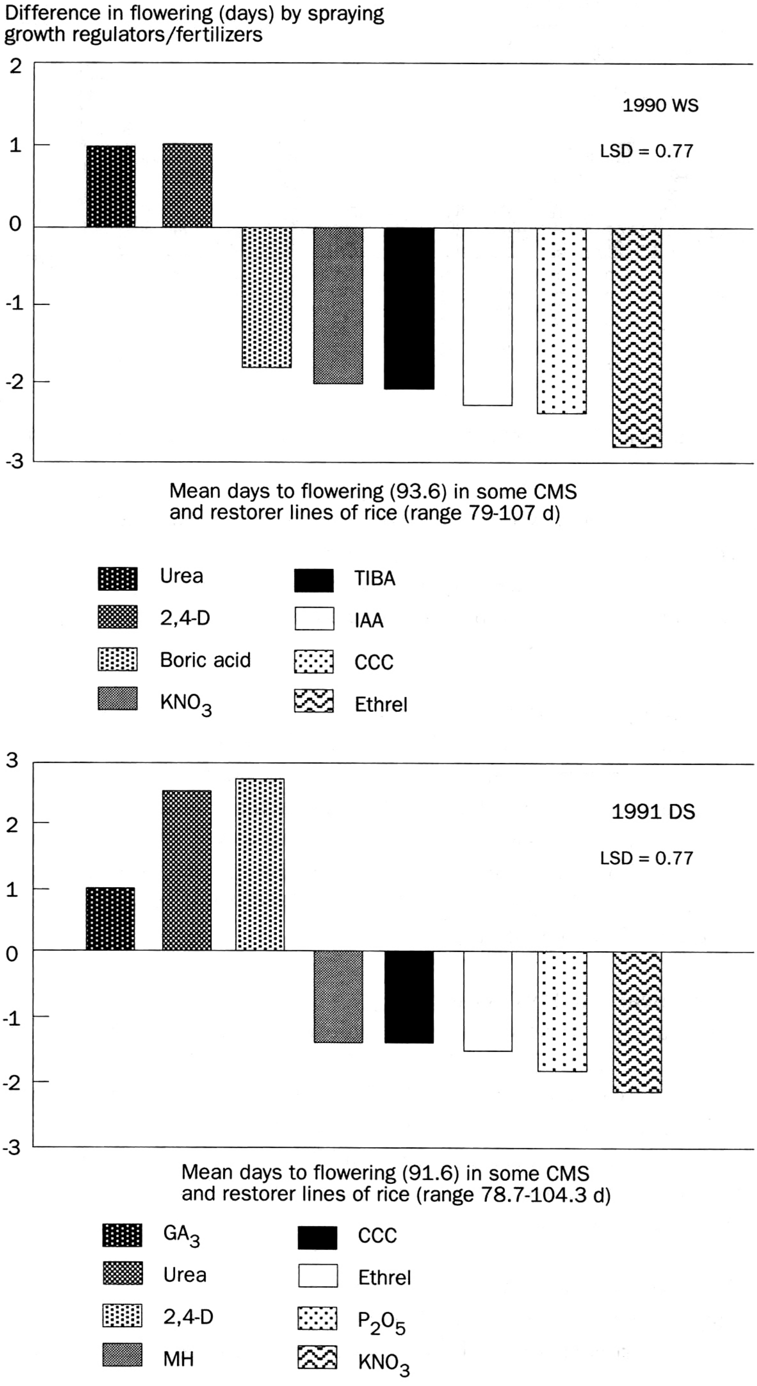
The heading date of a variety can be adjusted according to seedling age at transplanting. Flowering of cytoplasmic male sterile (CMS), maintainer, and restorer lines is affected, irrespective of growth duration. Normal seedling age at transplanting is 21 d. Experiments conducted at IRRI showed that flowering was 2.3-2.8 d earlier on average (range 1.4 - 4.00 d) when 16-d-old seedlings were transplanted (Fig. 2). On the other hand, flowering was delayed by 1.8-2.2 d, and 4.4-4.8 d, when seedlings were transplanted after 26 and 31 d, respectively.

Effect of chemicals on days to flowering

The heading date of a variety can also be adjusted by the application of chemicals. Eleven chemicals (IAA, GA_3, CCC, MH, 2,4-D, Ethrel, boric acid, urea, KNO_3, phosphate, and TIBA) were sprayed at the panicle initiation stage of CMS and restorer lines at IRRI. The chemicals delayed or enhanced flowering in all lines significantly compared with the control treatment. Urea and 2,4-D delayed flowering in almost all lines by 1 d on average, while boric acid, KNO_3, IAA, CCC, and Ethrel enhanced flowering by 1.8-2.8 d (Fig. 3).

Effect of planting density on days to flowering

The heading date could be adjusted by changing planting density or seedling numbers per hill. In an experiment at Tsukuba, the maximum difference in heading date was 2.1 d (Table 1).



3. Delay or advancement of flowering by spraying different growth regulators/fertilizers.

Table 1. Adjustment of heading date by varied transplanting. [a]

Planting density (cm)	Plants/ hill (no.)	Heading date	Variance in heading date
30 × 40	1	27.2	7.50
	3	26.5	7.03
	7	25.1	7.44
30 × 20	1	26.4	6.03
	3	25.3	5.98
	7	25.1	5.55
30 × 10	1	26.1	5.27
	3	25.0	5.39
	7	25.4	5.69

[a] Variety Nekken 2 was transplanted 20 Jun.

Use of exserted stigma

Flowering of CMS lines is sometimes delayed compared with the pollen parent. If the difference in flowering time between a CMS and an R line is more than 1 h, seed set is decreased substantially. Stigmas of some genetic stocks remain outside the lemma and palea after spikelet closure. They are receptive and can accept pollen grains even the next day. The exserted stigma trait is therefore useful for higher seed yield (Virmani and Athwal 1973).

Planting method

Transplanting one male sterile line accompanied by one pollinator line gives a high seed set ratio on the male sterile plants, but does not give a high yield because the total number of male sterile plants is not large enough. If there are very few pollinator lines, then the seed set percent may be so low as to affect yield. The row ratios tested at Lingling were 1:5, 1:8, 1:12, 2:10, 2:12, and 2:18. The results showed that 2:12-18 were better. The growth duration of the R line was longer, and the row ratio was longer.

In the 1970s, both A and R lines were transplanted as single seedlings. In the 1980s, closer transplanting with multiple seedlings was the main way to increase yield. The R line transplanted as single seedlings could not meet the pollen demand of the A line. Similarly, when the A line was transplanted as single seedlings, it was difficult to get enough spikelets for high seed yield. Therefore, Chinese seed growers introduced closer transplanting with multiple seedlings—i.e., 2 or 3 seedlings per hill for R line and 2 seedlings for A line. Transplanting density is 17 × 33.3 cm for R lines and 12 × 13.3 cm for A lines.

Panicle emergence by GA_3

Even if parental lines flower simultaneously, the CMS lines may show poor panicle exsertion, leading to poor outcrossing rate and low seed yields. These problems have been tackled in China by the use of GA_3, which increases panicle exsertion, duration of floret opening, and stigma receptivity (Yuan 1985). Skillful spraying of GA_3 can make the panicles fully exserted and eliminate the pollination barrier. It also effectively adjusts the heading stage of parental lines. Usually, GA_3 is sprayed 2 or 3 times, depending on the growth uniformity of the A line. With a uniform population, spraying twice is better, with concentrations of 200-300 ppm.

The high cost (US$8-20/g) and application rate (at least 45-50 g/ha) make GA_3 too expensive for use in many countries. Ultralow-volume (ULV) sprayers are known to reduce the dosage of insecticides in comparison with knapsack sprayers. Studies were conducted at IRRI on reducing GA_3 use in hybrid rice seed production with ULV sprayers. The sprayer Micro ULVA reduced GA_3 dosage from 45 to 15 g/ha (Table 2).

Supplementary pollination

It has been proved that supplementary pollination is very important for raising the yield. Previously, supplementary pollination was applied from the beginning of anthesis of the A lines to the end of anthesis of the R lines. A large amount of pollen was wasted because the peak time of anther dehiscence was missed, resulting in low out-pollination rates and yield. Studies in Lingling showed that if supplementary pollination was started at the peak time of anther dehiscence, there was a 30% rise in pollination rate of the A line, and the pollen amount was 2.7 times higher on the stigma than with the previous method, giving a significant yield increase.

Disease control

The flowering stage and spikelet opening time of the A lines were much longer than those of conventional varieties, making them susceptible to kernel smut. The infected

Table 2. Comparative plant height, seed set, and yield of two CMS lines sprayed with 45 g GA_3 with knapsack and 15 g GA_3 with ULV sprayers. IRRI, 1991 wet season.[a]

Treatment	IR62829 A			IR58025 A		
	Plant height (cm)	Seed set (%)	Seed yield (t/ha)	Plant height (cm)	Seed set (%)	Seed yield (t/ha)
45 g GA_3/ha (sprayed with knapsack)	87.3b	36.1a	1.0a	96.7b	32.6a	1.1a
15 g GA_3/ha (sprayed with ULV)	89.3a	35.5a	1.0a	99.0a	34.1a	1.1a
Control	79.3c	32.0b	1.0b	85.0c	24.4b	1.0b
CV (%)	1.6	8.0	11.3	1.6	8.0	11.3

[a] In a column, means followed by a common letter are not significantly different at the 5% level by DMRT.

Table 3. Comparison of seed set ratios and yield in alternative planting and mixed planting.[a]

Planting method	Heading date	Culm length (cm)	Seed set (%)	Seed set/ hill (no.)	F_1 seed yield (kg/ha)
Alternative-row planting					
1 CMS:1 pollinator	14.1 (13.6)[a]	82 (100)[a]	16.6	304	68
2 CMS:1 pollinator	13.6 (14.3)	84 (99)	13.8	244	73
Mixed planting					
1 CMS:1 pollinator	13.5 (13.5)	83 (98)	23.9	234	105
2 CMS:1 pollinator	10.8 (11.5)	81 (96)	23.5	269	121

[a] Numbers in parentheses are heading date and culm length of pollinator Tatsumimochi.

seed rate could be 10-20%. Infected parental seeds and soil were shown to be the source of infection. The infection occurred mainly during the flowering stage of the A line. Using sterilized seeds and fungicide controlled kernel smut effectively.

Mixed planting for mechanization

Mechanized seed production is easier if the seeds of both parents are mixed. This method ensures a higher ratio of seed set on the male sterile plants because the pollinators and male sterile flowers are closer than under the alternate-row method (Table 3).

The seeds are harvested as a mixture of pollinator seeds and hybrid seeds. The hybrid seed can be separated from a mixed harvest if the seeds are different in color, size, or other traits. A machine which separates colored and uncolored seeds using a photosensing sorter has been produced. If a female sterile pollinator is available, only hybrid seeds will be harvested. Another possible method for mixed planting is to incorporate a herbicide-sensitive gene in the pollinator, so that it can be eliminated by spraying the particular herbicide just after pollination. In this instance, only hybrid seeds will be harvested.

A hybrid rice line with parents suitable for mixed planting has been developed in Japan (Maruyama et al 1991). The parents have the same heading habits and the pollinator possesses the *Ph* gene for phenol-staining reaction of the hull. The pollinator seeds can be stained with phenol and separated from the F_1 seeds by machine.

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Authors' addresses: Huang Peijin, Lingling Prefecture Seed Company, Hunan China; K. Maruyama, National Agricultural Research Center, Tsukuba 305, Japan; H. L. Sharma and S. S. Virmani, International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.
Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.

Physiological bases of higher yield potential in F_1 hybrids

M.Yamauchi

Heterosis for dry matter accumulation was high at the vegetative and reproductive stages, lower at heading, and partially restored at maturity. Dry matter accumulation was increased by greater leaf area in the vegetative stage. It was controlled by net assimilation rate instead of leaf area at the reproductive and ripening stages. Heterosis in leaf area was associated with more leaves due to high tillering and larger leaves. F_1 hybrids develop roots in association with shoot growth. Although roots of F_1 hybrids had higher total activity and nutrient uptake per plant than those of midparents, the activity and uptake were not much higher when expressed per unit tissue weight. Plant spacing commonly used for transplanting conventional, high-yielding semidwarf varieties seems to be too narrow for F_1 hybrids. Heterosis in grain yield was increased when the spacing was widened. Plant spacing should be optimized to increase growth efficiency through an improved canopy structure and to reduce transplanting labor and hybrid seed requirements.

Heterosis in grain yield is well-demonstrated for rice plants (Virmani and Edwards 1983). Grain yield is the result of many physiological processes. Identifying the process responsible for high grain yield may not only help plant breeders to develop high-yielding cultivars but also help agronomists to establish suitable cultural practices for F_1 hybrids.

Grain yield is the product of dry matter accumulation and harvest index (HI). High dry matter accumulation has been demonstrated in F_1 hybrids. Heterosis for HI has been reported (Blanco et al 1990) but less frequently than for dry matter accumulation. Thus, heterosis in grain yield is due to increased dry matter accumulation. This paper discusses the processes of dry matter accumulation, root growth and nutrient uptake, and the response of plant growth to spacing. The growth of F_1 hybrids was expressed by heterosis (the relative values of the performance of F_1 hybrids to the mean of parental lines) so that the difference in plant growth between F_1 hybrids and parental lines could be understood.

Dry matter accumulation in the shoots

Dry matter production of a crop is analyzed by the equations:

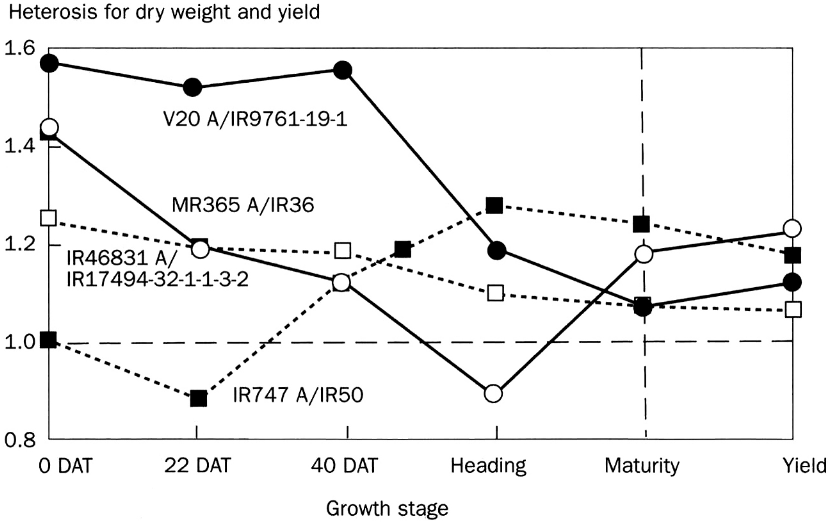
$$CGR = NAR \times LAI \qquad (1)$$

$$RGR = NAR \times LAR \qquad (2)$$

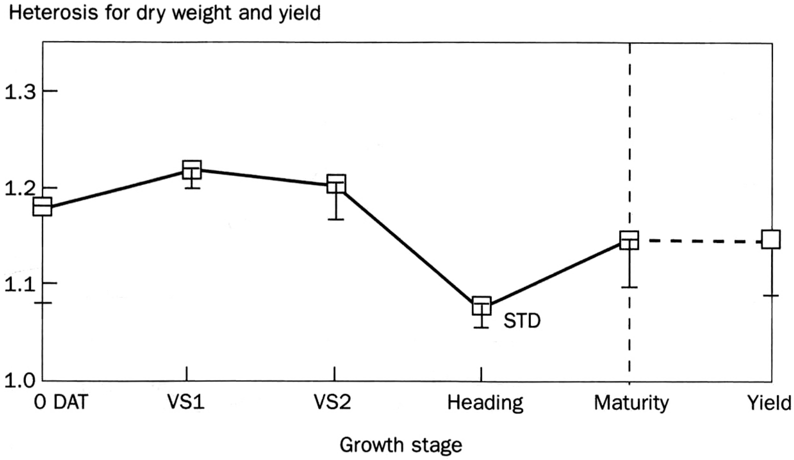
where CGR = crop growth rate, NAR = net assimilation rate, LAI = leaf area index, RGR = relative growth rate, and LAR = leaf area ratio. Equation 1 can be used to analyze canopy crop growth while Equation 2 is more suitable for characterizing the physiological efficiency of dry matter production of individual plants. The high dry matter accumulation of F_1 hybrids implies that they have higher CGR than parental lines.

Net assimilation rate is determined mostly by the balance of carbon between photosynthesis, photorespiration, and respiration. Heterosis for net photosynthetic rate reported by McDonald et al (1971) and Murayama et al (1982) suggested that NAR of F_1 hybrids is higher than that of parental lines. However, Yamauchi and Yoshida (1985) reported little heterosis for net photosynthetic rate, suggesting that rapid leaf area development was the cause of heterosis for dry matter accumulation. Thus, increased CGR of F_1 hybrids has been explained in two ways. This inconsistency for heterosis in CGR can be explained when plant growth stage is taken into account.

Heterosis for dry matter accumulation was expressed differently according to parental combinations and growth stages (Fig. 1). F_1 hybrid V20 A/IR9761-19-1 expressed higher heterosis at seedling (transplanting), vegetative, and reproductive stages than at ripening stage, while IR747 A/IR50 expressed heterosis at the later growth stages with no heterosis at the seedling stage. Heterosis at the seedling stage did not always bring high grain yield. There were also F_1 hybrids which expressed heterosis between the two F_1 hybrids mentioned.



1. Heterosis for shoot dry weight at 0, 22, and 40 d after transplanting (DAT), heading, and maturity and for grain yield. IRRI, 1984, wet season (WS).

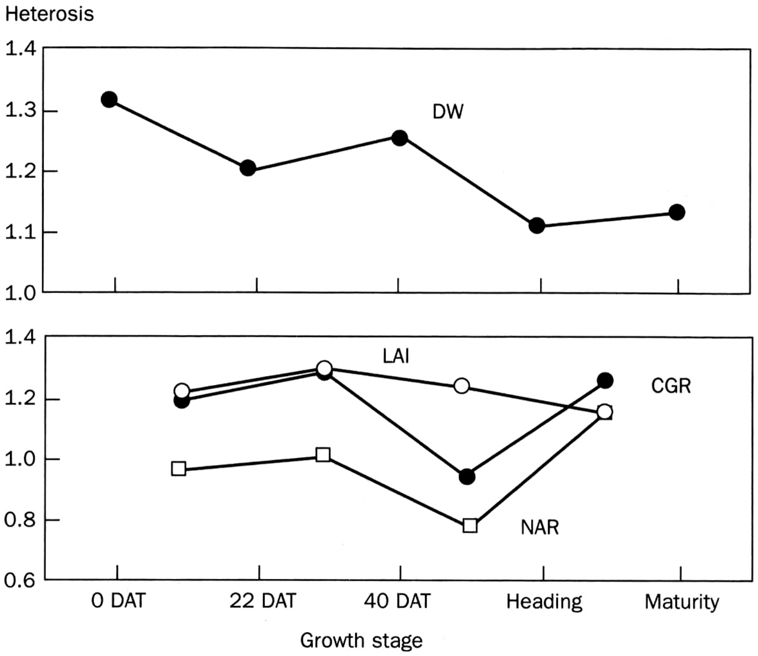


2. Mean heterosis for shoot dry weight (DW) at transplanting (0 DAT), vegetative and reproductive stages (VS1, VS2), heading, and maturity and for grain yield. The values are the means of 4 F_1 hybrids, 1984 WS; 5 F_1 hybrids, 1990 WS; and 5 F_1 hybrids, 1991 DS, IRRI.

Figure 2 shows mean heterosis for dry matter accumulation and grain yield in three crop seasons with 14 F_1 hybrids. Heterosis for dry matter accumulation was highest during the vegetative and reproductive stages and lowest at heading, increasing again during the ripening stage. The lower heterosis at heading decreased the potential heterosis for grain yield. High standard deviation of heterosis at the seedling stage suggests that it varies greatly according to the parental combination. The low standard deviation at the vegetative and reproductive stages and at heading suggests that many F_1 hybrids express high heterosis at vegetative and reproductive stages and lose heterosis at heading. Because heterosis for grain yield is mostly determined by dry matter accumulation, heterosis for grain yield of 1.20 could be obtained if F_1 hybrids did not lose heterosis at heading.

Figure 3 indicates that high CGR at the vegetative stage originates from high LAI and that CGR at reproductive and ripening stages is controlled by NAR. The same was also observed by Haruhara et al (1985) in the cold region of Japan. The depression of heterosis at heading stage is caused by the decrease in NAR. Recovery of heterosis during ripening stage is due to the increase in NAR. Heterosis for photosynthetic rate was reported for F_1 hybrids at the ripening stage (Murayama et al 1982; Murayama 1984, pers. commun.) while heterosis for leaf development and low heterosis for photosynthetic rate were reported for F_1 hybrids at the vegetative stage (Yamauchi and Yoshida 1985). Reports for heterosis in photosynthetic rate imply that there is heterosis in RGR at the ripening stage.

Heterosis in morphological characters indicates that F_1 hybrids can be characterized by bigger single tiller and leaf (Table 1). Leaf area of F_1 hybrids is larger because there are more leaves at the seedling stage, and individual leaves are longer and wider from the seedling stage to ripening. The increase in leaf number may be associated with high tillering at the seedling stage. High tillering of F_1 hybrids was shown by the appearance



3. Mean heterosis for shoot dry weight (DW), crop growth rate (CGR), leaf area index (LAI), and net assimilation rate (NAR) of 4 F_1 hybrids. Same experiment as shown in Figure 1.

Table 1. Mean heterosis in morphological characters of 4 F_1 hybrids. IRRI, 1984 wet season (WS).[a]

Character	Growth stage							
	0 DAT		22 DAT		40 DAT		Heading	
Height	1.13	(0.09)	1.12	(0.06)	1.12	(0.07)	1.04	(0.03)
Tiller number	1.22	(0.38)	0.93	(0.09)	0.95	(0.04)	0.94	(0.08)
Single tiller dry weight[b]	1.16	(0.30)	1.19	(0.11)	1.28	(0.18)	1.17	(0.12)
Leaf area	1.33	(0.21)	1.21	(0.25)	1.39	(0.32)	1.16	(0.13)
Dry matter partition[c]	1.02	(0.09)	1.01	(0.03)	1.02	(0.02)	1.04	(0.07)
SLA[d]	0.95	(0.04)	1.00	(0.04)	1.05	(0.09)	1.00	(0.04)
Leaf number[e]	1.25	(0.29)	0.93	(0.11)	1.02	(0.07)	0.99	(0.11)
Length[f]	1.13	(0.10)	1.12	(0.08)	1.13	(0.06)	1.02	(0.08)
Width[f]	1.11	(0.11)	1.08	(0.02)	1.13	(0.10)	1.10	(0.05)

[a] Same experiment as described in Figure 1. Standard deviation in parenthesis. DAT = days after transplanting. [b] Calculated by dividing shoot dry weight by tiller number. [c] Shoot dry matter partition to leaves. [d] Specific leaf area (cm^2/g dry weight). [e] Leaf number per hill. [f] The length and width of the second leaf from the top (for plants at 0, 22, and 40 d after transplanting) and those of the flag leaf (for plants at heading).

Table 2. Percentage appearance of primary first tiller of F_1 hybrids and their parental lines (Matsuba et al 1986).[a]

Variety/F_1 hybrid	Distance between seeds	
	1 cm	2 cm
Akihikari	0	9.6
Akihikari/Milyang 23	0	71.1
Milyang 23	0	2.6
Akihikari/Shinseiwai 1	10.7	66.2
Shinseiwai 1	0	0
Akihikari/Genpousou	62.1	
Genpouso	1.8	

[a] Distance between the seeds sown were 1 and 2 cm.

of a pri-mary tiller from the axil of the first leaf (Table 2, Matsuba et al 1986), which is normally dormant. F_1 hybrids expressed heterosis for tillering in the pots (Kawano et al 1969), but little in the field (Table 1). This could be due to unfavorable plant spacing in the field.

Heterosis in embryo size was suggested as the primary cause of heterosis for dry matter accumulation. This is called the initial capital theory (Akita et al 1990). The proposal was based on the assumption that there is little heterosis in RGR. However, the presence of heterosis for NAR and net photosynthetic rate suggests that there is heterosis for RGR at the ripening stage. In addition, there are F_1 hybrids which have no seedling vigor but express high heterosis at later growth stages (Fig. 1). These facts suggest that the initial capital theory cannot always explain heterosis in dry matter accumulation.

Understanding the mechanism by which heterosis for dry matter accumulation at heading is depressed (Fig. 2) is important. If the depression is eliminated and the heterosis for dry matter accumulation is maintained at the level of the vegetative stage (about 1.20), heterosis for grain yield could be increased from the present 1.15 to 1.20. The decrease in heterosis in CGR before heading is due to the decrease in heterosis in NAR (Fig. 3). The decrease in NAR might have been caused by a decrease in photosynthetic rate or by an increase in respiration. Jennings (1967) reported that excess vegetative growth of F_1 hybrids lowered the light transmission rate. Mutual shading retards net photosynthetic rate and increases the consumption of stored carbohydrate by respiration, thus lowering NAR. Studies on plant nutritional status and plant canopy structure in terms of spacing might help to explain the decrease in NAR.

Root growth and nutrient uptake

Plant shoots contain nutrients at a certain concentration, so high dry matter accumulation must be associated with high nutrient uptake through the roots. Vigorous root growth has been reported (Lin and Yuan 1980), but little evidence has been provided.

Table 3. Mean heterosis of 16 F_1 hybrids grown in solution culture. IRRI, 1984.

Character	Mean heterosis	Standard deviation
Plant dry weight	1.23	0.11
Root dry weight	1.20	0.10
Dry matter partition to roots	0.98	0.03
Tiller number	1.11	0.08
Root length per plant	1.04	0.04
Root number per plant	1.07	0.07
Oxidation rate per plant[a]	1.15	0.08
Oxidation rate per g root dry weight[a]	0.95	0.05

[a] a -naphthylamine oxidation rate.

Table 4. Mean heterosis of 5 F_1 hybrids.[a] IRRI, 1990 WS.

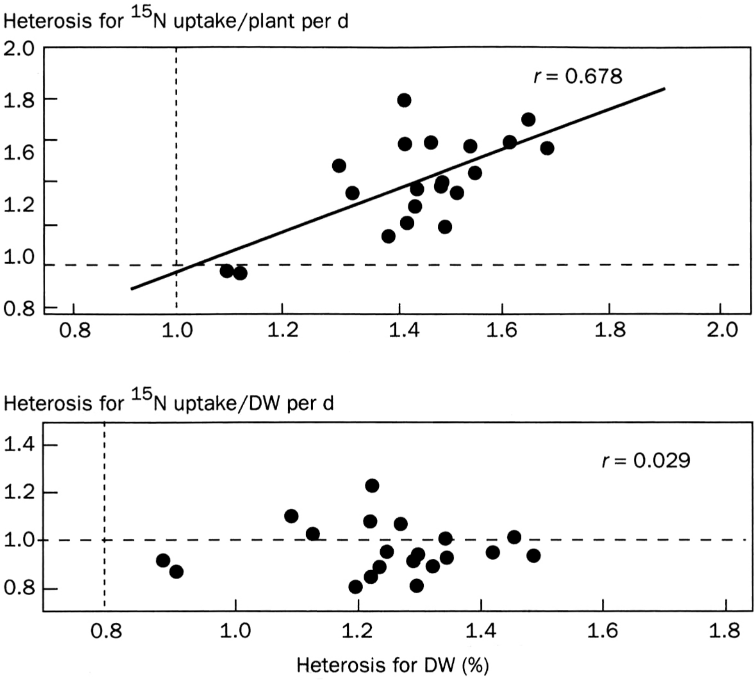
Character	Mean heterosis	Standard deviation
Grain yield	1.23	0.22
Shoot dry weight at maturity	1.22	0.15
Shoot dry weight at heading	1.06	0.20
Root dry weight at heading	1.11	0.22
Dry matter partition to roots	1.05	0.16
Root length at heading	1.03	0.20

[a] Roots were sampled by the use of a block sampler (20 × 20 × 60 cm) up to a depth of 40 cm. Plant spacing was 20 × 20 cm.

Development of leaves and roots and tillering are synchronized for rice plants (Yoshida 1981). F_1 hybrids may have advantage over parental lines in root development, especially in root number, when F_1 hybrids have high tillering activity (Table 3).

Quantitative root analysis of F_1s and their parental lines in the IRRI fields at heading showed that F_1 hybrids tended to partition more dry matter to roots and to have longer roots (Table 4). However, superiority in root characters was not larger than those in grain yield and shoot growth. On the other hand, seedlings of F_1 hybrids grown in culture solution partitioned less dry matter to roots than to shoots (Table 3), which may be advantageous for shoot growth if the nutrient supply does not limit growth. Thus, F_1 hybrids might not have particular superiority over parental lines in morphological characters of roots.

The rate of a -naphthylamine oxidation, which is mediated by peroxidase activity (Matsunaka 1960) and which correlates with respiration rate of the roots (Yamada et al 1961), was greater for F_1 hybrids than for midparents when it was expressed per

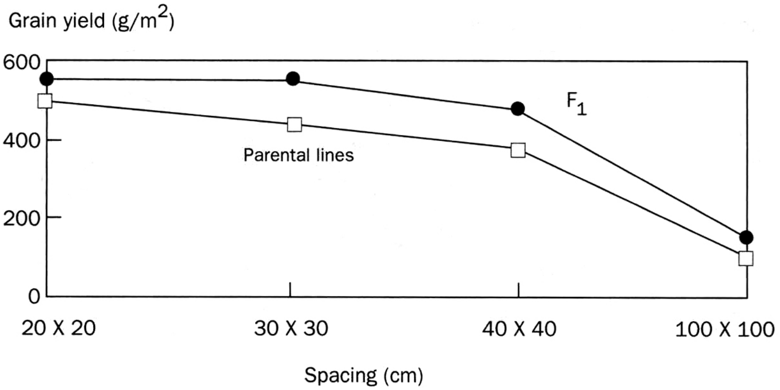


4. Relation between heteroses for shoot dry weight and ^{15}N uptake per plant and per unit dry weight (Suzuki et al 1988).

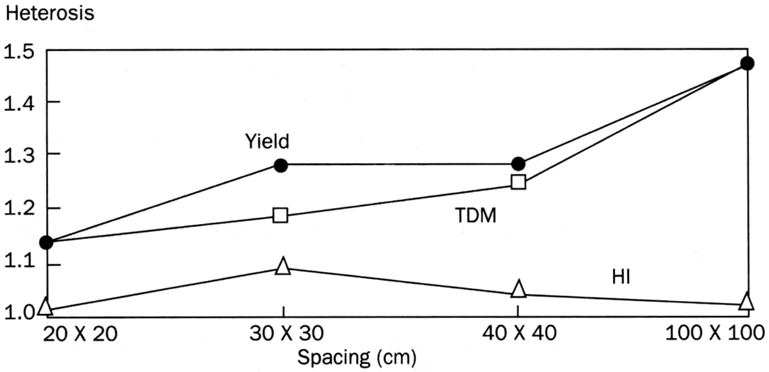
plant, but smaller when expressed per unit tissue weight (Table 3). A similar result was reported for F_1 hybrids and their parental lines grown in the field at heading (Nakayama 1986). Thus, the high root activity of F_1 hybrids might be the character associated with high dry matter accumulation in the shoot.

When F_1 hybrids showed high heterosis for dry matter accumulation, the concentration of N in the tissue was lower than that of parental lines (Kawano et al 1969, Suzuki et al 1986), presumably because of dilution effects. Nitrogen uptake rate of a plant, measured by ^{15}N uptake, was closely correlated with shoot dry matter accumulation (Fig. 4, Suzuki et al 1988). When the uptake was expressed as per unit tissue weight, it did not correlate with shoot dry matter accumulation and was lower than that of the midparent. Thus, it seems that F_1 hybrids do not have particular superiority over parental lines in root activity.

F_1 hybrids may require highly fertile soil or intensive fertilizer application where soil fertility is low because they might not have superiority in morphology and activity of nutrient uptake over parental lines. Sinha and Khanna (1975) also suggested little heterosis for nutrient uptake for other crops. It is generally accepted that photosynthetic rate correlates with N concentration in leaves (Tsuno 1975). The lower concentration of N in F_1 hybrids which showed high dry matter accumulation (Kawano et al 1969) suggests that N limits the growth of F_1 hybrids. The depression of heterosis in dry



5. Mean grain yield of 4 F_1 hybrids and their parental lines at various plant spacings. IRRI, 1984 WS.



6. Mean heterosis for grain yield, shoot dry matter accumulation (TDM), and harvest index (HI) of 4 F_1 hybrids. IRRI, 1984 WS. Same experiments as shown in Figure 5.

matter accumulation at heading (Fig. 2), where ordinary fertilizer management was practiced, might have been caused partly by lack of N fertilizer application. The mean heterosis for N concentration in the shoots of 4 F_1 hybrids shown in Figure 1 was 0.97. F_1 hybrids would require more intensive N fertilizer application before heading than parental lines.

Plant spacing

Optimizing plant spacing is important for crop production. Spacing determines not only the intensity of intravarietal competition for light and nutrients but also the dry matter partition between the organs (Kuroiwa 1975). Spacing changes the canopy structure of a crop, controlling CGR and HI. Wide spacing makes more nutrients available for a plant than narrow spacing. Optimum spacing between the hills for a transplanted conventional, high-yielding, semidwarf variety at IRRI is 20 × 20 cm. F_1 hybrids grown at IRRI with 20- × 20-cm spacing have the following features: big plant size (leaf, tiller, and height), depressed heterosis for dry matter accumulation at heading, and no heterosis for panicle number and tillering after seedling stage (Table 1, Fig. 2). F_1 hybrids might reach maximum LAI earlier than parental lines because of vegetative vigor.

Grain yield decreased more for parental lines than for F_1 hybrids when spacing was increased from 20 × 20 cm (25 hills/m^2) to 30 × 30 cm (11.1 hills/m^2) and 40 × 40 cm (6.3 hills/m^2) (Fig. 5). Heterosis for yield and shoot dry matter accumulation increased at wider spacing (Fig. 6). Heterosis for HI was maximum at 30 × 30 cm. F_1 hybrid IR747 A/IR50, which had the highest grain yield among four F_1 hybrids tested during the 1984 wet season, achieved highest yields at 30- × 30-cm spacing due to the heterosis expressed for spikelet number per panicle and percentage of filled spikelets. Davis and Rutger (1976) also reported higher heterosis for 30- × 30- and 30- × 45-cm spacing than for 15 × 15 cm.

Using wider spacing for F_1 hybrid cultivation reduces hybrid seed requirements and transplanting labor remarkably. Transplanting at wide spacing was adopted in Japan not only to reduce labor requirements when transplanting machines were not available but also to utilize soil fertility efficiently (Noubunkyo 1975). When plant spacing is widened from 20 × 20 cm to 30 × 30 or 40 × 40 cm, 56 and 75% fewer seeds are required, respectively, and transplanting is much faster. Another advantage of wide spacing is the prevention of lodging. Lodging is one of the most serious problems of high-yielding plants and is, therefore, an important concern in hybrid rice production.

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Author's address: M. Yamauchi, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

A conceptual framework for nitrogen management of irrigated rice in high-yield environments

K. G. Cassman, M. J. Kropff, and Yan Zhen-De

Differences in yield potential of rice genotypes cannot be fully expressed under resource-limited growth conditions. For irrigated rice without water limitations, high yields are possible only when plant N uptake is sufficient to maintain dry matter accumulation and sink formation throughout the growth cycle. Depending on solar radiation and temperature regime, there is a minimum quantity of N accumulation at each growth stage that is just sufficient to achieve a specified yield level. We define this quantity of N accumulation as the minimum N uptake requirement (MNUR) for the specified yield target and propose a quantitative approach for management strategies to meet the MNUR in diverse environments. The strategy requires prediction of three variables which define the "N supply environment," namely, 1) the N demand, or MNUR, determined by crop growth rate, which in turn depends on temperature, solar radiation, and genotype; 2) the N supply parameters, which include the seasonal pattern of N supply from indigenous soil resources, which is governed by the quantity and quality of organic matter, biological N_2 fixation by microorganisms in soil and floodwater, and soil-floodwater temperature; and 3) the N uptake efficiency from fertilizer, which depends on the quantity, placement, and timing of application. Together, these components determine the N status of the rice crop at any point in the cropping season. Despite its importance, our ability to predict plant N status in different environments is poor, regardless of whether such predictions are based on existing simulation models or on empirical soil test indices. The knowledge required to attain this predictive capability is the subject of this paper. Information about the N requirements of hybrid rice in China and results from recent studies at IRRI will be used to demonstrate the need for, and the merits of, such an approach to N management in varietal selection trials, and ultimately, by the rice farmers of Asia.

Present N management strategies employed by researchers and breeders and recommendations made to farmers do not account for the dynamic nature of the N supply and N demand balance in the flooded rice ecosystem. At the IRRI research farm, for instance, a total N rate of 150 kg N/ha is recommended in the dry season (DS), with a standard split of 2/3 incorporated before transplanting and 1/3 broadcast into shallow floodwater 5-7 d before panicle initiation (PI). Rigid prescriptions for N inputs, however, are inconsistent with the fact that year-to-year variation in yield is considerable due to differences in solar radiation, temperature, planting dates, etc. Similarly, the long period between recommended split applications does not account for the difficulty of maintaining an adequate N supply in the soil-floodwater system.

In breeding trials at IRRI, yields of check varieties such as IR72 may range from 5.4 to 7.0 t/ha in the DS. Grain yield is closely correlated with total N accumulation in aboveground biomass. For IR72, an increase in total N uptake of approximately 40 kg N/ha is required for a yield difference of 1.6 t/ha. With an N uptake efficiency from applied fertilizer of 40%, a 7.0 t rice crop/ha would require 100 kg/ha more applied N than a rice crop yielding 5.4 t/ha. Therefore, a flexible strategy of N management is required to avoid excessive N input in years with relatively low yields, which can lead to increased disease and lodging, or too little N in years with relatively high yields. Excessive N supply or N-limited growth conditions do not provide an appropriate environment for selecting new plant types or hybrid lines with greater yield potential.

As geneticists and plant breeders develop improved rice varieties and hybrids with greater yield potential, increased precision and efficiency of N management will become even more important because of the greater N uptake requirements of the improved genotypes. This will be true for researchers as well as for farmers who will someday utilize these new cultivars. In this paper, we will develop a conceptual framework for improving N management and emphasize the need for predicting and quantifying the N supply environment as the basis for N management of field tests of improved germplasm in high-yield environments.

The N supply environment

Yield potential for irrigated rice in a given environment is determined by the genotype and climate when water, nutrients, and pests do not limit crop growth. Assuming appropriate pest management, N supply is the most limiting resource. At each stage of growth, plant N status is determined by the balance of crop N demand and the N supply. The N demand is governed by the rate of dry matter accumulation, which in turn is determined by the amount of incident solar radiation and temperature regime. Plant N supply is controlled by availability of N from indigenous soil resources and from applied inputs and the ability of the root system to take up N from the available pool. A change in any one of the components of the N demand-supply balance results in a different N supply environment.

The factors that define the N supply environment are extremely variable in time and space. Climate varies each year. Soil N-supplying capacity depends on the previous cropping history, residue incorporation, tillage, water regime, and temperature

(Broadbent 1979, Dei and Yamasaki 1979). The efficiency of fertilizer N recovery is also extremely variable due to the potential for rapid and large losses of applied N through volatilization and denitrification, both very sensitive to environmental conditions at the time of N application (Fillery and Vlek 1986, De Datta and Buresh 1989). Much less is known about the factors that govern the efficiency with which the rice root system acquires N from the soil and floodwater system, although efficiency is likely to vary with regard to root age and temperature.

Because all the factors that determine the N supply environment vary each cropping season, it is no wonder that rice response to a standard N management regime is typified by tremendous variation, even when monitored in the same field in different years. Results summarized by Bouldin (1986) from hundreds of field experiments with labeled ^{15}N fertilizers are indicative of the unpredictable nature of rice response to standard N management treatments. Our inability to predict response to applied fertilizer N results partly from a lack of research in a framework that integrates the key elements of N supply and demand in the irrigated rice ecosystem. An integrative framework is needed to predict the demand-supply balance, and quantification of the N supply environment is a prerequisite for such integration.

Components of the N supply environment are defined in the following sections and approaches for their quantification are discussed. Our focus here is on the irrigated rice ecosystem, and in the discussion we assume that water, pests, and factors other than N and solar radiation do not limit yield potential.

The minimum N uptake requirement

Crop dry matter accumulation is driven by light interception and conversion of captured energy to photosynthate. Recent improvements in existing crop simulation models now allow accurate prediction of biomass and leaf area index throughout a crop growth cycle, given data inputs of solar radiation, mean daily temperature, and the N concentration of the leaf canopy (Kropff et al 1993). Leaf N status is a pivotal parameter because the rate of photosynthate production in a leaf under light-saturated conditions is a linear function of leaf N concentration (Cook and Evans 1983, van Keulen and Seligman 1987).

If we specify the incident solar radiation, temperature regime, and an achievable yield target, there is a minimum leaf N concentration at each point in the crop growth cycle that supports sufficient leaf area development and photosynthesis to achieve this yield goal. Crop N accumulation below this minimum threshold for even brief periods results in a yield that is less than the target, while N uptake greater than the threshold is not needed and represents luxurious consumption. Along with the quantity of N required in other organs such as stems, and later in panicles, we can define a minimum N uptake requirement (MNUR) at each growth stage for a given genotype and yield target when solar radiation and temperature are specified.

Accurate estimation of the MNUR is crucial for creating the appropriate N supply environment to select high-yielding plant types and hybrids that are efficient in their N utilization. For example, we know that rice yields in the DS at IRRI were 9 t/ha and wet-season (WS) yields were 6-7 t/ha in the late 1960s and early 1970s, based on data

Table 1. Effect of N input and timing on flag leaf N content 7 d after anthesis (AN) and yield of IR72 (early-maturing) and IR58109-113-3-3-2 (medium-maturing) rice. IRRI, 1991 WS.[a]

N input and timing (kg N/ha)						
Transplanting to 5 d before PI	AN	Total	Variety	Grain filling (d)	Flag leaf N concentration 7 d after AN (%)	Grain yield (t/ha)
0	0	0	IR72	25	2.05 a	3.79 a
80	0	80	IR72	28	2.34 b	4.81 b
80	30	110	IR72	28	2.63 c	5.32 c
0	0	0	IR58109-113-3-32	23	1.99 a	4.07 a
80	0	80	IR58109-113-3-3-2	26	2.19 b	5.18 b
80	30	110	IR58109-113-3-3-2	29	2.63 c	6.07 c

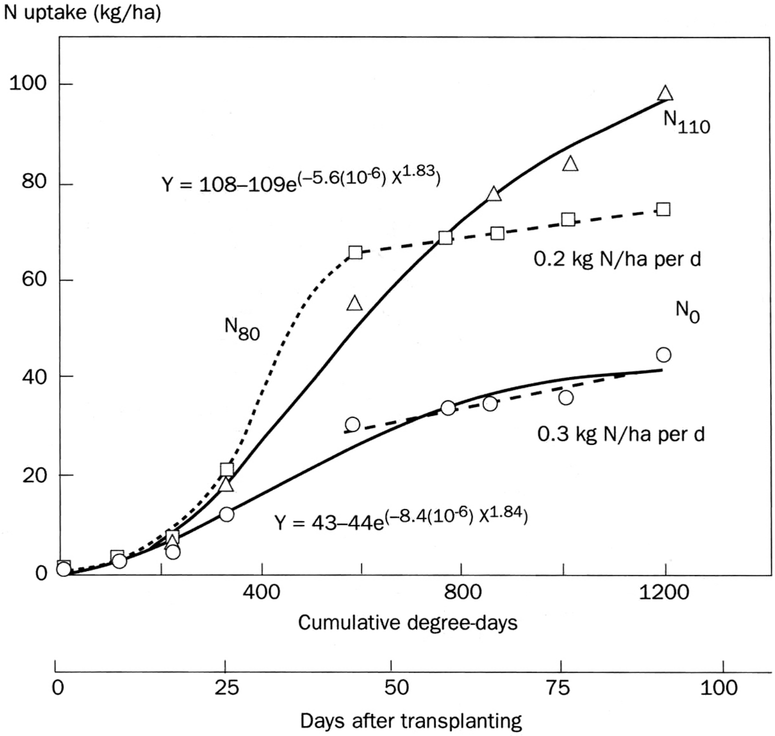
[a] For each variety, means followed by a different letter are significantly different at the 5% level by DMRT.

from the long-term continuous cropping experiments (Flinn and De Datta 1984). Today, with the same rate and timing of N inputs, DS yields rarely exceed 6.5 t/ha, while WS yields have fallen to 4-5 t/ha. Recently, plant N status was monitored in these long-term experiments and in several breeding trials. The results indicated that flag leaf N concentrations at anthesis were well below 3%, even in treatments that received the recommended rate and timing of N inputs. In China, N management for hybrid rice seeks to maintain leaf N at or above 3% at flowering.

To test the hypothesis that an inadequate late-season N supply limits grain yield, an experiment was conducted in the 1991 WS at IRRI to compare N uptake, leaf N, green leaf area duration, and yield of several cultivars in three N regime treatments, a control (N0), 80 kg N/ha applied in two splits before PI (N80), and a treatment with 110 kg N/ha that included an extra 30 kg N/ha broadcast at anthesis (N110). Late-season N application resulted in greater flag leaf N concentration and a yield increase of 0.5-0.9 t/ha depending on the cultivar (Table 1). Seasonal patterns of N accumulation indicated that the N applied at flowering was efficiently absorbed (Fig. 1).

Although we do not yet have sufficient knowledge of plant N utilization and partitioning in relation to the seasonal pattern of N supply, plant density, or climate to make accurate predictions of the MNUR, simulation models will be developed to estimate the MNUR as discussed by Kropff et al (1994). For the present discussion, we shall assume that the pattern of N uptake in the N110 treatment provides a reasonable estimate of the MNUR for the yield levels attained. A Weibull function was fitted to the N uptake data based on degree-day accumulation (15 °C threshold to match predictions of soil N mineralization in the next section) and was found to accurately predict the observed N accumulation of both cultivars in the N110 treatment ($r^2=0.98$ for IR72, Fig. 1). For each cultivar, these functions predict the MNUR at each point in the crop growth cycle at the observed yield levels of 5-6 t/ha (Fig. 2).

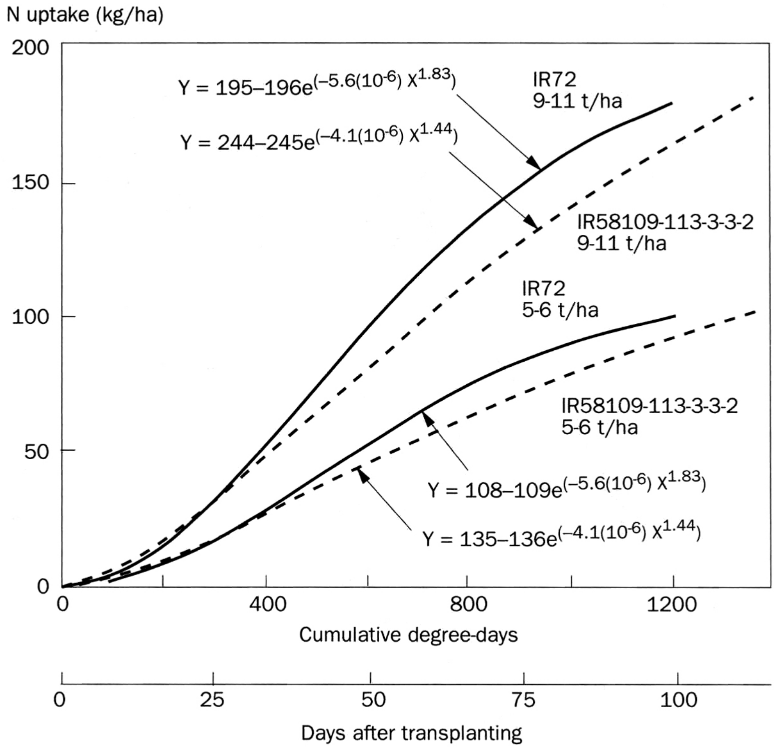
To estimate the MNUR for these two cultivars at yield levels of 9-11 t/ha (an 80% yield increase above observed yields in N110 treatments), the Weibull asymptote values for N uptake based on actual observations were multiplied by 1.8 while retaining the same curvature coefficients (Fig. 2). The resulting equations predict the increase



1. Seasonal N accumulation of IR72 in the 1991 WS at IRRI without N fertilizer inputs (NO), with a total of 80 kg N/ha applied in two splits at transplanting and before PI (N80), or with a multisplit strategy that includes 80 kg N/ha in three splits before PI plus an additional 30 kg N/ha at anthesis. Fitted N uptake functions for the NO and N110 treatments are based on cumulative degree-days with a 15 °C minimum threshold. Dashed lines are linear uptake rates per day after PI in NO and N80 treatments.

in the rate of N accumulation required for the high-yield situation and an 80% increase in the MNUR at each growth stage. At maturity, total N uptake must reach 180 kg N/ha for 9-11 t/ha vs 100 kg N/ha at yield levels of 5-6 t/ha. The proportional increase in leaf and stem dry matter at the high-yield level will be less than for N because the yield increase will include greater late-season assimilate production due to higher N content of the upper leaf canopy and a longer green leaf area duration and grain-filling period.

The issues for breeders at IRRI and elsewhere who seek to select germplasm with high yield potential are whether N input recommendations provide sufficient N to meet the expected MNUR under existing soil conditions and whether to avoid applying excessive N, well above the MNUR. When 9-10 t/ha yields were achieved with varieties (such as IR8) 20-25 yr ago, total N accumulation must have approached the levels predicted in Figure 2 at similar yields. In the long-term continuous cropping experiments, mean N accumulation of four cultivars, including IR72, was only 110-115 kg N/ha in the 1991 DS, with 150 kg N/ha applied in the standard 2/3 basal, 1/3

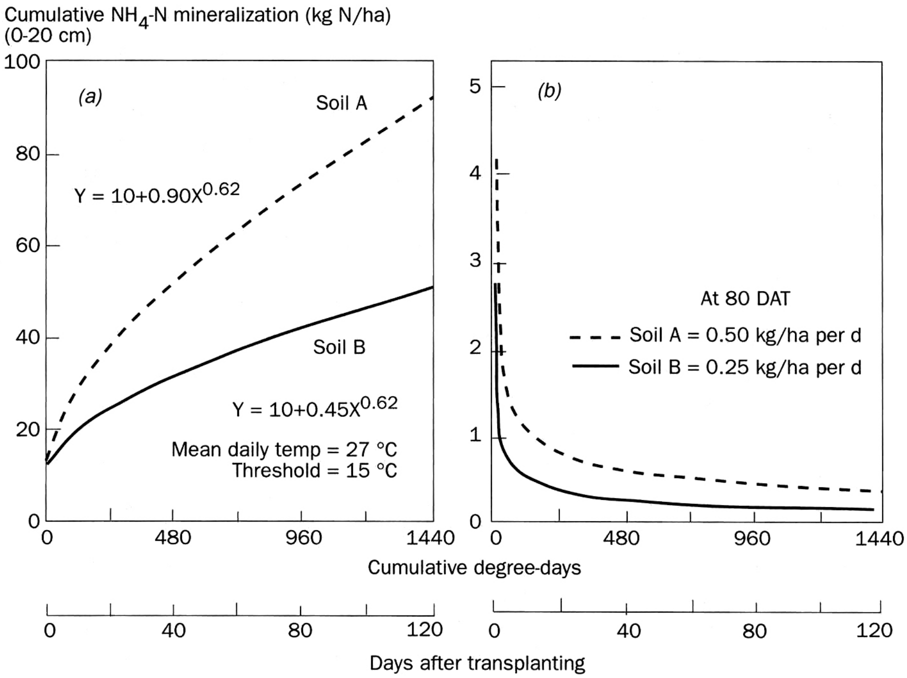


2. Weibull functions of N uptake vs cumulative degree-days (15 °C threshold) fitted to direct measurements of N uptake for the two varieties with yields of 5-6 t/ha in the 1991 WS at IRRI, and hypothetical N uptake functions for targeted yields of 9-11 t/ha based on asymptote values that are 1.8 times larger than the predicted asymptotes for the 5-6 t/ha yield levels.

PI split. Mean yield was 5.7 t/ha. Clearly, greater N uptake will be required to achieve higher yields. To determine if increased inputs of N fertilizer are needed and to know the proper timing of these inputs, one must understand the seasonal pattern of the MNUR, the soil N supply, and the expected plant recovery of applied N, which is governed by root absorption efficiency and the rate of gaseous N losses from the soil-floodwater system.

Seasonal pattern and quantity of soil N supply

The N supply that becomes available for uptake by the rice crop from soil in the flooded rice ecosystem is derived from two main sources. One is the N mineralized from organic matter, such as incorporated crop and weed residues, including rice straw, leguminous green manures, azolla, and applied animal manures. The second N source is biological N_2 fixation (BNF) in soil and floodwater, primarily from blue-green algae in floodwater and on the soil surface, and from heterotrophic bacteria that decompose rice straw and colonize the rhizosphere of the rice root system (Roger and Watanabe 1986).



3. Seasonal pattern of N mineralization of two hypothetical soils, one relatively high (soil A) and the other relatively low in native soil N-supplying capacity, under flooded conditions based on a minimum threshold of 15 °C (as proposed by Dei and Yamasaki [1979]) and a mean daily temperature of 27 °C.

Taking the simplest approach, it is the difference between the quantity and seasonal pattern of soil N supply and the MNUR that determines when additional inputs of N must be applied. To our knowledge, however, prediction of the N uptake of rice on diverse soils without inputs of fertilizer N is not a component of present N management strategies. Indeed, we are unaware of reports that document such a predictive capability. By contrast, laboratory incubation studies under anaerobic conditions indicate that the kinetics of N mineralization follow predictable patterns. When temperature differences are considered, the cumulative release of N by a given soil (Y) can be described by an exponential function of the form:

$$Y = AX^n \tag{1}$$

where A is a measure of the mineralization potential, X is the time expressed as cumulative degree-days with a minimum threshold of 15 °C, and n is a constant that fits the pattern of anaerobic N mineralization (Dei and Yamasaki 1979) (Fig. 3). Such a pattern is not likely to occur when large quantities of straw, manure, or leguminous materials are incorporated at puddling, but in most intensive rice systems and on most research stations, only small quantities of organic residues are incorporated, mainly straw stubble and weeds.

Based on this generic function of cumulative N mineralization, it is possible to make predictions of N uptake by rice when mineralized N is the primary Source of N supply. In pot studies, such predictions appear to be quite accurate (Dei and Yamasaki 1979), but extension to field situations is less certain. Some of this discrepancy between pot and field may reflect the N supply from BNF under field conditions. Little BNF would occur in laboratory incubations. In the tropics, estimates of N inputs from BNF range from 15 to 50 kg N/ha per crop, based on N balances constructed from long-term experiments, and it is clear that BNF helps to maintain and stabilize the N economy of irrigated rice systems (Koyama and App 1979). However, the actual quantity of N in a rice crop derived from current BNF appears to be quite small (Eskew et al 198l), and it is possible that in vitro estimates of N mineralization fail to predict N uptake under field conditions due to artifacts of the incubation method itself rather than from the exclusion of BNF inputs.

There is strong evidence, however, that it is difficult to replace the yield benefits of high native soil N fertility and, by implication, greater N mineralization with increased inputs of fertilizer N. Based on yields of hybrid rice on two soils in China, application of 245 kg N/ha to a soil of low native N fertility resulted in a yield that was 2.2 t/ha less than when only 54 kg N/ha was applied to a soil with high organic carbon and total N content (Table 2). Likewise, the pattern of N mineralization in two hypothetical soils predicted by Equation 1 indicates that N supply from mineralization is greatest immediately after puddling and extremely low after the midseason, about 50 DAT (Fig. 3). For example, total N mineralization is only 12 kg N/ha in soil A and 6 kg N/ha in soil B during a 25-d grain-filling period from anthesis to physiological maturity, 80-105 DAT for short-season varieties. Based on the measured increase in N uptake in the 1991 WS at IRRI, N uptake from soil in the N0 and N80 treatments was similar to the predicted daily N mineralization of hypothetical soil B. This quantity of N supply is not sufficient to achieve maximum yield when leaf N status is marginally deficient at flowering (Table 1).

If the N supply from soil resources is greatest during the first few weeks after puddling and planting, as predicted by the generic N mineralization function of Equation 1 (Fig. 3), we would expect little benefit from an early-season N application on soils with relatively high native N fertility. This expectation is consistent with results from a field study with hybrid rice on a soil that supported a yield of nearly 7 t/ha without fertilizer N inputs (Table 3).

In summary, although we do not yet have the capacity to predict the seasonal N supply to the rice crop in a flooded ricefield, results from studies that monitor N uptake indicate a pattern of N acquisition that agrees with the prediction of extremely low N mineralization after the midseason, based on in vitro incubation studies. At IRRI, we will attempt to improve the method for predicting N mineralization by including a cation resin “sink” in the anaerobic incubation procedure, as suggested by Keeney and Sahrawat (1986). The ability to predict soil N supply is fundamental to defining the N supply environment and to developing more efficient strategies of N management.

Table 2. Effects of native soil fertility and rate of fertilizer nutrient inputs on yield of hybrid rice in Xuzhou, China.

Field	Soil nutrients			Nutrient inputs(kg/ha)			Grain yield (t/ha)
	Total N (g/kg)	Available P (mg/kg)	Organic C (g/kg)	N	P	K	
A	0.86	43	13.2	245	32	35	10.7
B	4.10	92	23.7	54	16	25	12.9

Table 3. Effect of a single N application of 120 kg/ha at different growth stages on components of hybrid rice yield in a relatively fertile soil, Xuzhou, China.

Time of application	Spikelets/m^2 (no.)	Spikelets per panicle		Grain/m^2 (X10^4)	Grain yield (t/ha)
		Total	% filled		
Control (0 N)	226	150	82	2.78	6.75
Tillering	246	157	78	2.99	6.86
Panicle initiation	267	167	72	3.19	7.65
Anthesis	249	177	79	3.44	7.97
Mid-grain filling	251	155	81	2.92	6.75

N supply from applied N fertilizer

Judging from the amount of scientific literature on rice response to N fertilizer, this subject has received considerable attention. In much of this work, however, direct measures of N uptake in relation to amount of applied N are lacking, or, if measured, the relationship is not presented or discussed. This relationship is a prerequisite for interpreting N response data because grain yield depends on the quantity of N accumulated by the rice plant under N-limited conditions. With regard to studies of fertilizer N use efficiency, lack of N output/input data can lead to a focus on relative N losses from fertilizer, rather than on the influence of fertilizer N application on grain yield. In fact, artifacts that result from use of microplot techniques with ^{15}N-labeled fertilizer often indicate large differences in N losses from different fertilizer application methods that have no effect on rice yield (Table 4).

To design an efficient N fertilization strategy to meet the MNUR for a given yield level requires a reasonable prediction of N uptake from applied N. There is a general consensus that N fertilizer uptake efficiency of irrigated rice is relatively poor compared with that of upland cereals such as maize or wheat. This perception is based mostly on microplot data of ^{15}N-labeled fertilizer recovery in numerous field experiments conducted both on research stations and in farmers' fields. However, the recovery of ^{15}N from labeled fertilizer is consistently much lower than the actual difference in N uptake that results from N application (Bouldin 1986). Plant recovery of ^{15}N from applied fertilizer is influenced by "added N interactions" that confound interpretation (Jenkinson et al 1985). In contrast, the net benefit derived from N inputs

Table 4. Grain yield vs N losses from ^{15}N-labeled fertilizer applied to microplots In two field experiments on irrigated rice.

Site, year, and season	Treatment	Total N applied (kg N/ha)	^{15}N losses (% of applied)		Grain yield (t/ha)	Reference
			From basal	Total (B+PI)		
Mabitac, Laguna[a]	Control	0	-	-	3.9 a[b]	De Datta
1985 DS	Farmer's split	80	60	42	5.4 b	et al
	Researcher's split	80	33	17	5.6 b	1989
Muñoz, Nueva Ecija	Control	0	-	-	3.3 a	Schnier
1987 DS	Researcher's split	87	45	36	7.6 b	et al
	Urea supergranules	87	4	4	7.8 b	1990a

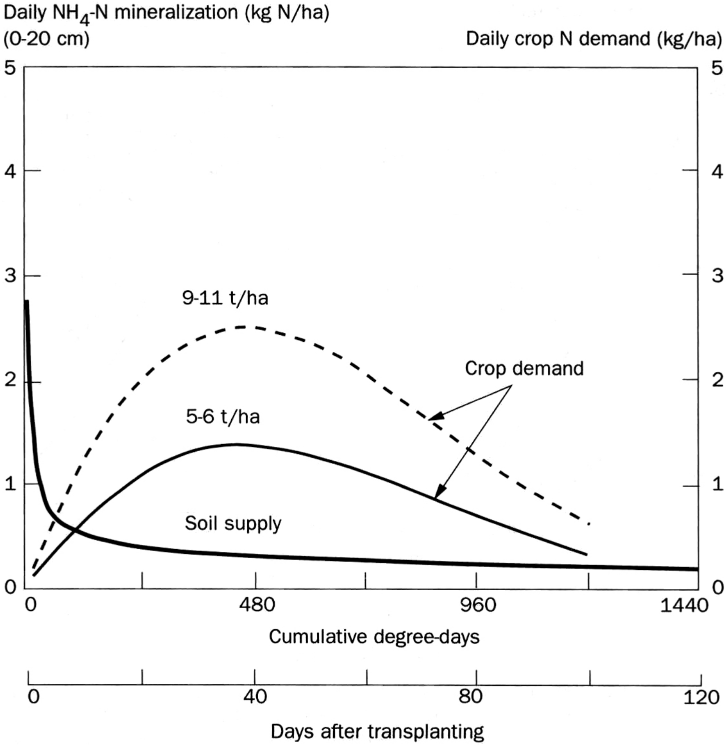
[a] Experiment conducted in a farmer's field. [b] Means for each experiment followed by the same letter do not differ at $P < 0.05$.

Table 5. N uptake efficiency from prilled urea of transplanted, irrigated rice, estimated by the difference In actual plant N uptake from fertilizer N application, or by recovery of ^{15}N from labeled fertilizer from microplots in the same treatment plots.

Site, year, and season	Application timing[a]	N rate (kg/ha)	Plant uptake efficiency (% of applied)		Reference (variety)
			N difference	^{15}N uptake	
Muñoz, Nueva Ecija					
1985 DS	2/3 BI, 1/3 PI	87	34	37	De Datta et al 1988
1986 DS	2/3 BI, 1/3 PI	87	59	38	(IR60, 1985) (IR64, 1986)
Muñoz, Nueva Ecija	All BI	58	-	27	Schnier et al
1987 DS	2/3 BI, 1/3 PI	87	64	38	1990a (IR64)
Muñoz, Nueva Ecija 1987 DS	1/3 BI, 2/3 PI	150	98	-	Schnier et al 1990b (IR64)
IRRI, Laguna	2/3 BI, 1/3 PI	40	58	-	Castillo et al 1992
2-yr means	2/3 BI, 1/3 PI	80	54	-	
1989,1990 WS					(IR72)
Victoria, Laguna[b]					
19902/3 BI, 1/3 PI	80	57	37		De Datta, IRRI,
unpubl. data					
1991	All BI	87	45	27	(IR72)

[a] BI = basal incorporated. PI = 5 d before panicle initiation. [b] Experiments conducted in farmers' field.

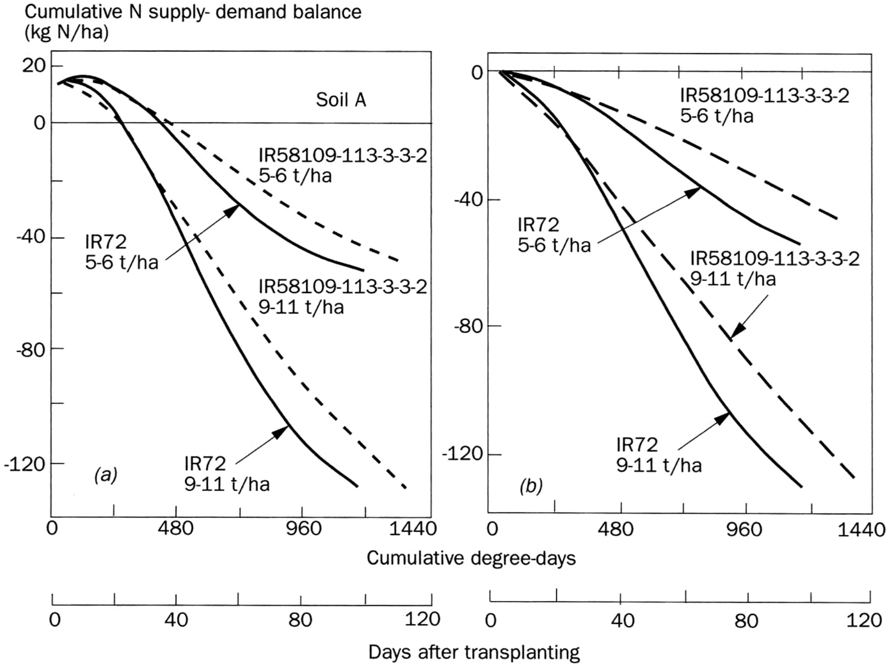
to an N-limited system is directly quantified by the influence of applied N on N uptake. In many cases, the fertilizer N uptake efficiency based on the difference in N uptake by rice from plots with and without applied N indicates an "effective efficiency" between 45 and 60% (Table 5), which is closer to values reported for upland cereals.



4. Comparison of the daily N uptake demand of IR72 at two yield levels and daily N mineralization of soil B of Figure 3b. Crop N demand is predicted by the Weibull functions for IR72 in Figure 2.

Even higher values of effective efficiency seem feasible. The 45-60% range shown in Table 5 (excluding the lowest and highest values) was obtained using standard application strategies, either all basal or a 2/3 basal, 1/3 at PI split. These strategies provide most of the N inputs early in the season, when there is little crop demand and the root system is not well-established. Furthermore, soil N supply is greatest during the early season (Fig. 4), so this application strategy supplements soil N supply with fertilizer N. Applied N does not remain long in the soil-floodwater system, usually 15-20 d for the basal application and less than 7 d for N broadcast into floodwater (De Datta 1986), due to crop uptake and rapid losses through volatilization and denitrification.

Given the behavior of N in the irrigated rice system, an application strategy with 4-5 splits to make up the difference between plant demand and soil N supply may improve N uptake efficiency. A multisplit strategy would match N demand better. It would also reduce the proportion of fertilizer N lost through volatilization and denitrification because the rate of crop N uptake is relatively constant over periods of several days, while the rate of gaseous losses follows first-order kinetics and increases directly in proportion to increasing N in the system. Consistent with this, a fertilizer N uptake efficiency of 57-83% was indicated from an application of 30 kg N/ha at flowering in



5. Cumulative N supply-demand balance for two cultivars at different targeted yield levels based on (a) the cumulative difference in the predicted N uptake in Figure 2 and predicted N mineralization of soil B in Figure 3a, and (b) the cumulative difference in the predicted N uptake in Figure 2 and the predicted N uptake of the N0 treatments for each cultivar as shown for IR72 in Figure 1.

the 1991 WS at IRRI. The agronomic efficiency of this applied N was also high (Table 6). A multisplit strategy that reduces the risk of N losses and improves uptake efficiency from each application would reduce uncertainty concerning the efficacy of N fertilization and facilitate more accurate prediction of N application timing in relation to the expected MNUR and the soil N supply.

Integrating the components of the N supply environment

Although we cannot yet predict each of the components of the N supply environment, we are optimistic that this will be possible in the near future. To illustrate the importance of quantifying the components of the N supply environment for developing an appropriate N management strategy, we shall examine the N supply-demand balance as predicted for IR72 at two targeted yield levels (Fig. 2), when grown on a soil with N supply characteristics of hypothetical soil B in Figure 3.

The derivative (slope) of the N uptake functions for IR72 represent the crop N demand per degree-day. Assuming a constant mean daily temperature of 27 °C, which is the mean DS and WS temperature at IRRI, the derivative can be converted to a daily

Table 6. Late-season N application at anthesis, 1991 WS. [a]

Variety	N applied at anthesis (kg/ha)	Total N accumulation (kg/ha)		Post-anthesis N Uptake (kg/ha)	N fertilizer efficiency	
		Anthesis	Physiological maturity		Uptake[b] (%)	Agronomic[c] (kg rice/kg N)
IR72	0	71	76	5	-	-
	30	78	100[d]	22	57	17
IR58109-113-3-3-2	0	72	69	−3	-	-
	30	73	98[d]	25	83	30

[a] Both treatments received a total of 80 kg N/ha in split applications during the early season (from transplanting to panicle initiation) as shown in Table 1. [b] Uptake efficiency of IR72 estimated as the difference in post-anthesis N uptake with and without N applied at anthesis divided by the rate of N application, expressed as a percentage. Uptake efficiency of IR58109-113-3-3-2 was based on the total post-anthesis N uptake divided by the N rate, expressed as a percentage, due to a decrease in measured N content from anthesis to maturity without the anthesis N application. [c] The increase in rice yield per kg N applied at anthesis. [d] Indicates a significant difference in N accumulation between treatments with and without N applied at flowering ($P < 0.001$).

N demand. When daily N demand is compared with daily N supply from mineralization in soil B, the greatest imbalance occurs about 40 DAT (Fig. 4), which is about 5-10 d before PI for IR72. Although the greatest N deficit occurs before the reproductive growth stage begins at PI, a significant deficit continues until maturity. Throughout crop growth, the daily shortfall in N supply is magnified at higher yield targets. The rate of N mineralization exceeds uptake only for a very brief period after transplanting.

Based on the difference between daily N demand and supply, the cumulative N supply-demand balance can be estimated (Fig. 5a). This balance assumes that all of the mineralized N is acquired by the rice crop. An N supply surplus is indicated until 20-35 DAT, depending on the yield target. In the field, however, the actual difference between measured N accumulation of IR72 in the N110 and N0 treatments of the 1991 WS experiment (Fig. 1) indicates a deficient N supply within a few days after transplanting (Fig. 5b, 5-6 t/ha yield). Although soil B is a hypothetical example, the seasonal mineralization pattern of a flooded field soil would be similar to that shown in Figure 3b, and the rate of late-season N mineralization for soil B is similar to measured rates of N accumulation of IR72 in the N0 and N80 treatments after midseason (Fig. 1). Likewise, the initial available N at transplanting in the N0 treatment was 16 kg N/ha, measured in the surface soil (to a depth of 20 cm), which is similar to the initial 10 kg available N/ha assigned to soil B as the Y intercept in Figure 3a. Therefore, it appears that not all available N is acquired by the rice crop in the first 5-10 d after transplanting, possibly due to N losses through volatilization, denitrification, or immobilization.

The greatest uncertainty about the N supply-demand balance based on predictions of MNUR and soil N mineralization will probably concern the first weeks after transplanting. This uncertainty reflects interactions between puddling method, the quality of incorporated crop and weed residues as substrates for mineralization, seedling vigor, and transplanting shock. Fortunately, crop N demand during this period is very low, so the amount of applied N needed to avoid an early-season deficit would be relatively small.

There seems to be good reason to avoid large basal applications because N losses are greater and uptake efficiency is lower from basally applied N than from applications made later in the season (De Datta et al 1989, Schnier et al 1990a). Another option is to increase plant density, either by closer hill spacing in transplanted rice or by direct seeding. Even without basal N application, N uptake from soil can more than double with closer hill spacing, and a threefold increase in the effective uptake efficiency from basal fertilizer N has been recorded at higher plant densities (Wada and Sta. Cruz 1990).

Subsequent applications would meet the predicted N deficit and be split to reduce the proportional loss from each dose. This would also assure a steady supply of N by taking into account the short residence time of added N. Although the rate of basal N application must be based on predictions of the early-season MNUR and soil N supply, later applications could be adjusted in response to simulation of dry matter production and updated predictions of the cumulative N demand-supply balance based on direct measurements of actual solar radiation and temperature. The timing of split N applications should avoid booting stage (stem elongation) to reduce the risk of lodging, but applications at PI and again at early heading should suffice.

Another tool to help researchers and breeders manage the N supply-demand balance in high-yield environments is the chlorophyll meter, which provides a rapid, nondestructive measure of leaf N status (Takebe and Yoneyama 1989). By standardizing the relationship between the meter reading and leaf N concentration for a few standard varieties and taking leaf thickness into account (S. Peng, IRRI, 1992, pers. commun.), it is possible to determine when leaf N status falls below thresholds predicted to be necessary for a given yield target and MNUR by simulation. Split N applications could then be scheduled as indicated by the chlorophyll readings.

Discussion and conclusions

It is extremely difficult to maintain adequate N nutrition throughout the cropping season in the irrigated rice ecosystem by making only one or two N applications. Even with a larger number of split applications, breeders must select their germplasm in an appropriate N supply environment, and this requires some quantification of the components that define the N supply environment. At IRRI, for example, the extremely low N supply characteristics of the soil after PI may lead to unintended selection pressure for genotypes that perform well in this environment, especially with a standard N management strategy that applies most N early in the season. Genotypes selected in this N supply environment may not have the traits required for achieving a new yield frontier. Indeed, selection where all N applications are made before PI and N supply in the late season is low, would place mid- and late-maturing lines at a disadvantage, since their longer growth period allows greater dry matter accumulation against an extended period of reliance on a deficient soil N supply. It is noteworthy that mean yield levels from early-, mid-, and late-maturing lines in selection nurseries are similar at IRRI and in the multilocation testing program of the Philippine Seed Board.

It is also important to avoid excessive N inputs, even when this N is applied in a multisplit strategy. Too much N often causes lodging and promotes infections by several diseases. Moreover, selection for high yield potential in an N-rich environment would mask genotypic differences in N use efficiency.

As achievable yield levels increase above 9 t/ha, the MNUR will exceed 200 kg N/ha. Typical soil N supply in most of tropical Asia ranges from 40 to 60 kg N/ha, and this level is relatively constant in most irrigated rice systems. It is crucial to select high-yield genotypes with N use efficiency equal to or better than present cultivars, because N inputs will probably cost more by the time the new plant types and tropical hybrids are available to the rice farmers of Asia.

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Notes

Authors' addresses: K. G. Cassman and M. J. Kropff, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines; and Yan Zhen-De, Xu-Zhou Prefecture, Agricultural Institute, Xu-Zhou City, Jiangsu Province 221000, People's Republic of China.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Quantitative understanding of the irrigated rice ecosystem and yield potential

M. J. Kropff, K. G. Cassman, and H. H. van Laar

A systems simulation approach is used to evaluate the physiological basis and crop management requirements for achieving rice yields higher than present yield frontiers in tropical environments. A general crop simulation model is parameterized for rice and used to evaluate yield differences between varieties grown with different N management and in different environments to understand the physiological basis of the system. The model explains accurately variations in productivity on the basis of differences in radiation, temperature, leaf N content, and leaf area index (LAI) throughout the growing season. The model predicts that higher N inputs could raise dry season yields from the current 7 t/ha to more than 9 t/ha. The simulations suggest that the yield potential of current short-duration varieties is similar to the yield potential of the first semidwarf variety, IR8. For yields above 10 t/ha, a simplified yield formation model predicts that leaf senescence must be delayed, the grain-filling period must be longer, and there must be more grains per m^2. Theoretically, 15 t/ha could be obtained in a tropical environment with a growth duration of 134 d, a grain-filling period of about 40 d, high LAI, and high leaf N concentration. The simulation model confirms these figures. F_1 hybrids show advantages in several physiological traits that are required for raising yield potential. Optimum crop management is crucial for realizing higher yield potentials. A rice crop would need at least 300 kg of N in aboveground biomass for a 15 t/ha yield with normal N concentration in the grains. Much of this N has to be taken up late in the growing season to meet the N requirements of a larger sink and a longer grain-filling period and to support the extended active leaf area duration due to delayed senescence.

One of IRRI's major objectives is to develop varieties with a yield potential of 15 t/ha in a tropical environment. This requires major genetic changes in the rice plant and improved management. Current breeding programs aim to improve the plant characteristics that are thought necessary for improved yield potential. Ecophysiological models have been used to design these plant types (Dingkuhn et al 1991, Penning de Vries 1991).

Rice breeding programs that focus on raising yield potential above 10 t/ha have problems when experiments cannot be conducted under optimum conditions. A simulation model for rice growth was developed to understand these conditions. Its performance was assessed using data from different environments and N management treatments. The model was used to determine the management requirements that would allow current varieties to express their full yield potential.

An ecophysiological model was used to determine more detailed physiological traits and crop management requirements that could lead to a major increase in yield potential, based on indications of the genetic variability of these traits. The possible role of hybrid rice in achieving increased yield potential is discussed.

Increasing the yield potential of rice: a simple concept

Yield potential can be defined as the yield of a crop when growth is not limited by shortages of water and nutrients, pests, diseases, or weeds. The determinants of potential growth and production are light, temperature, and varietal characteristics. Thus, yield potential must be defined for a specific environment.

Recent efforts have focused on obtaining a yield potential of 15 t/ha by improving the rice plant type (IRRI 1989). Several plant traits that improve yield potential have been identified. Penning de Vries (1991) analyzed the possibility of genetic improvement for a wide range of processes and concluded that there was some scope for increased assimilate production and that the grain-filling duration had to be lengthened. He emphasized that N uptake after flowering was important to maintain growth for a longer period. Dingkuhn et al (1991) emphasized a modified partitioning of assimilates between leaves and stems. However, the plant they modeled would not produce leaves after panicle initiation (PI), which would require major genetic changes and result in leaf area duration problems. This section discusses a simple framework of yield potential in rice, largely based on the work of Yoshida (1981), and insights obtained from systems approaches in agriculture.

The driving forces in crop yield formation are well-known. In the first place, both a source of carbohydrates are needed for yield formation. The source is formed by chlorophyll-containing tissue, mainly in the leaves. Stems, leaf sheaths, and the panicle contribute a small amount to canopy photosynthesis. The amount of dry matter stored in the grains comes from allocated stem reserves produced in the vegetative phase and from assimilates produced in the grain-filling period. Grain production is therefore 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 (or growth rate duration).

Climate and N supply environment largely determine these components. Temperature affects the length of the vegetative period, thereby influencing the amount of stem reserves that can be translocated to the panicles, and the length of the grain-filling period. Radiation determines the growth rate of the crop. The growth rate at a given radiation level depends on the leaf area index (LAI) of the crop and the leaf N concentration. Based on this analysis, a very simple model for grain yield can be defined.

$$Y = S + G \times D$$

where Y is grain yield, S is the net amount of stem reserves allocated, G is the average growth rate per day during the grain-filling period, and D is the length of the grain-filling period. Yoshida (1981) concluded that the contribution of stem reserves could account for about 2-2.5 t grains/ha. The rest must come from growth during the grain-filling period. For 10 t/ha, achieved in the 1960s with IR8 at IRRI, the grain-filling duration was 30 d, of which 25 d comprised 'effective' or linear-phase grain filling. These numbers give an estimated growth rate of (10000 - 2000) × 0.86 (14% moisture) /10 = 230 kg/ha per d, or 275 kg/ha per d during the linear grain-filling period. This is a reasonable estimate; rice in tropical environments with a high LAI and a high leaf N content can produce 300-350 kg dry matter/ha per d.

This simple model for yield formation indicates that yields above 10 t/ha should come from increased allocation of stem reserves, a longer grain-filling period, or from an increased growth rate during grain filling. Increasing stem reserves beyond 2.5 t dry matter/ha is not realistic if we want to keep the vegetative period as short as possible, and because a sturdy stem and a high LAI are needed. For a grain yield of 15 t/ha, about 13 t dry matter/ha is needed. Assuming an average growth rate of 275 kg/ha per d during effective grain filling and an allocation of 2.5 t/ha dry matter grain from stem reserves, 38 d of effective grain filling and 43 d of total grain filling would be needed to produce the remaining 10.5 t/ha. Basically, this indicates that a variety that performs in tropical environments the same way current varieties perform at higher latitudes (where temperatures are lower) must be developed.

To achieve such yields, a proper sink is required. With a 1000-grain weight of 28 g, about 360 panicles/m^2, and 100 grains/panicle, a yield of 10 t/ha was obtained with IR8 in the 1960s (Yoshida 1981). A 15 t/ha yield requires about 150 grains/panicle with the same number of panicles/m^2, or 60,000 spikelets/m^2 with a normal number of unfilled spikelets.

Yield potential of current varieties

The yield potentials of rice varieties released in the past few decades have not been compared directly due to disease problems and declining yields at several experimental stations. The decline in yield on the IRRI experimental farm was first reported by Evans and De Datta (1979). Recent analysis of long-term experiments clearly shows a continuous decline in yield of fertilized and nonfertilized crops. Yields at IRRI in the 1960s reached 10 t/ha with 120 kg of N from fertilizer. Nowadays, top yields are 5-7 t/ha in the dry season (DS). In the minus-N plots (control), DS yield has declined from 6 to 3-4 t/ha.

It is hypothesized that this yield decline is partly due to a change in the N supply environment, which reduces growth rates in the vegetative and grain-filling periods, through early leaf senescence and low photosynthesis rates. The rate of leaf photosynthesis at light saturation is linearly related to leaf N concentration (Van Keulen and

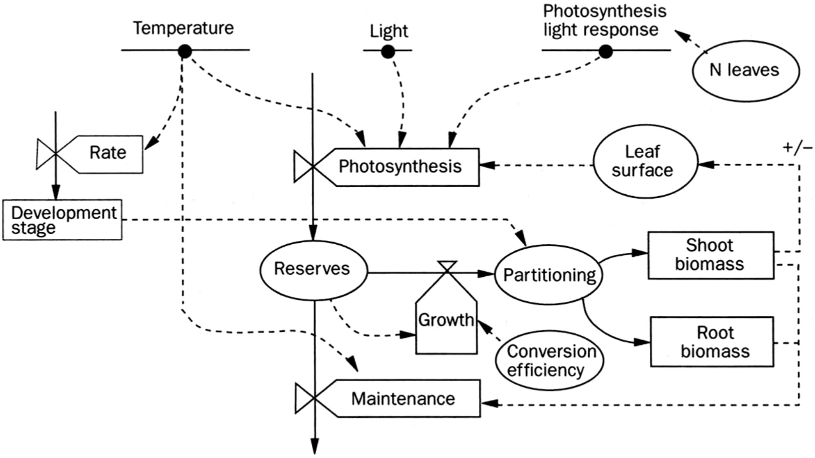
Seligman 1987), so the lower leaf N concentration could explain the reduction in growth rate. However, ecophysiological models and detailed data are needed to analyze the effect of different leaf N concentrations on yield.

To analyze the yield potential of varieties released by IRRI in the past 28 yr, a field experiment was conducted in the 1991 wet season (WS) with different N regimes, including a late N treatment. All the relevant growth parameters were carefully measured to allow data analysis with a simulation model.

The monoculture version of the model for crop-weed interactions, INTERCOM, was used (Kropff and Spitters 1992, Kropff and van Laar 1993). INTERCOM is based on the model SUCROS (Spitters et al 1989). (The MACROS module for potential rice production [Penning de Vries et al 1989] was not used because it greatly overestimated LAI and was calibrated to current yield levels by photosynthesis parameters.) Experimental data were first analyzed with LAI as input, since the carbon balance of the model is well-developed and validated (Kropff 1990, Spitters et al 1989, Kropff and Goudriaan 1989), so inaccuracy in the simulation of leaf area development could not confound conclusions made in the first analysis.

The ecophysiological model

The general structure of the model is presented in Figure 1. Under favorable growth conditions, crop growth rate is determined mainly by light and temperature. From the LAI of the species and the vertical distribution of leaf area, the light profile within the canopy is calculated. On the basis of single leaf photosynthesis, which depends on N concentration, the photosynthesis profile for the full canopy is obtained from the light and N profiles in the canopy. Integration over the height of the canopy and over the day gives the daily assimilation rate. After subtracting respiration requirements and accounting for losses due to conversion of carbohydrates into structural dry matter, the



1. A schematic representation of the model. Boxes are state variables, valves are rate variables, circles are intermediate variables. Solid lines are flows of material, dotted lines are flows of information.

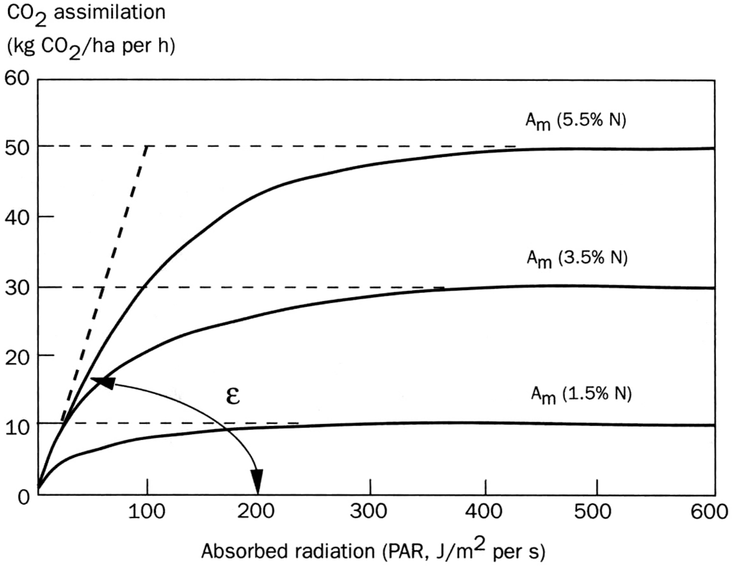
net daily growth rate in kg/ha per d is obtained. The dry matter produced is partitioned among the various plant organs. The development rate is tracked in the model as a function of ambient mean daily air temperature.

Before the canopy closes, leaf area development is calculated from mean daily temperature. The LAI can be simulated or experimental values can be used in the model. When the canopy closes, the increase in leaf area is obtained from the increase in leaf weight. Calculation of the net daily growth rates combines the increase in dry weight of leaves, stems, and grains, based on a partitioning coefficient that depends on the stage of development.

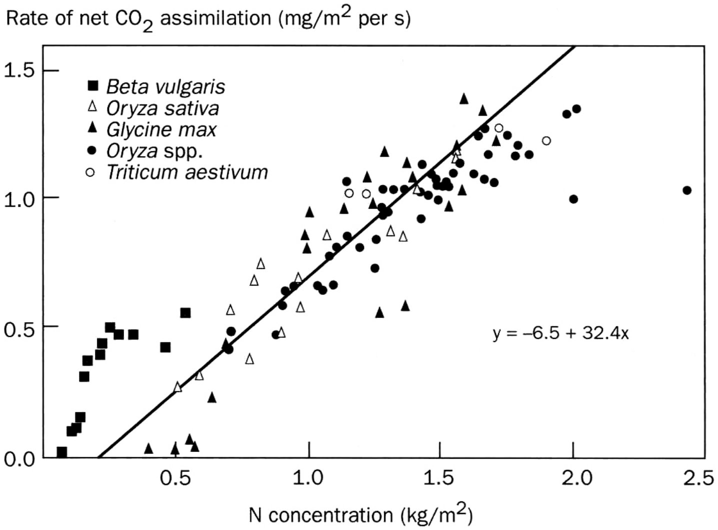
The model requires the following information: geographical latitude, standard daily weather data, plant density, date of crop emergence or transplanting, and parameter values that describe the morphological and physiological characteristics of the plant species. The time step of integration is 1 d.

The maximum rate of CO_2 assimilation at high radiation levels (the asymptote, A_m) depends on leaf N concentration (Fig. 2). The relationship between A_m and leaf N concentration is linear and shows little variation across environments and species (Van Keulen and Seligman 1987, Cook and Evans 1983, Fig. 3). The relationship given in Figure 3 was used in the model. It is important to note that N concentration is expressed on a per leaf area basis and not as a percentage of dry weight. This is because the maximum rate of CO_2 assimilation is expressed on a per area basis and depends on the amount of chlorophyll per unit of leaf area instead of weight. The total daily rate of CO_2 assimilation of the species is obtained by integrating the instantaneous rates of CO_2 assimilation over the LAI and over the day.

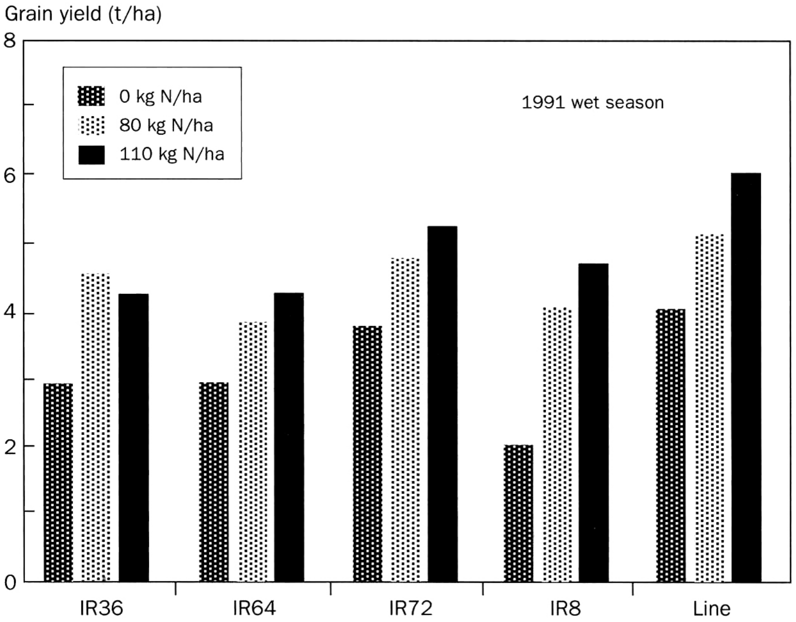
The effect of the profile of N concentration in the leaf canopy was taken into account.



2. The CO_2 assimilation-light response curve of single leaves calculated for three N concentrations.



3. The relation between the maximum rate of CO_2 assimilation of single leaves and the leaf N concentration on a per area basis (kg/m^2) (Redrawn after van Keulen and Seligman 1987)



4. Grain yields of five rice varieties at three N application levels in the 1991 wet season (WS) at IRRI, Los Baños, Philippines.

Experimental design

Four improved, semidwarf indica rice varieties released since 1964—IR8, IR36, IR64, and IR72—and IR58109-113-3-3-2 (a new line) were grown on the IRRI experimental farm during 1991 WS. All varieties were transplanted on 13 Jul. Three N management treatments were applied: 0 N, the standard recommendation (80 kg N/ha in two splits before PI), and an alternative N management treatment with 110 kg N (80 kg N in two splits before PI and 30 kg N at flowering). Treatments were laid out in four replicates in a split-plot design, with N treatments as the main plots and varieties as subplots. Samples were taken from 14 hills at intervals, and LAI and organ dry weights were measured.

Experimental results

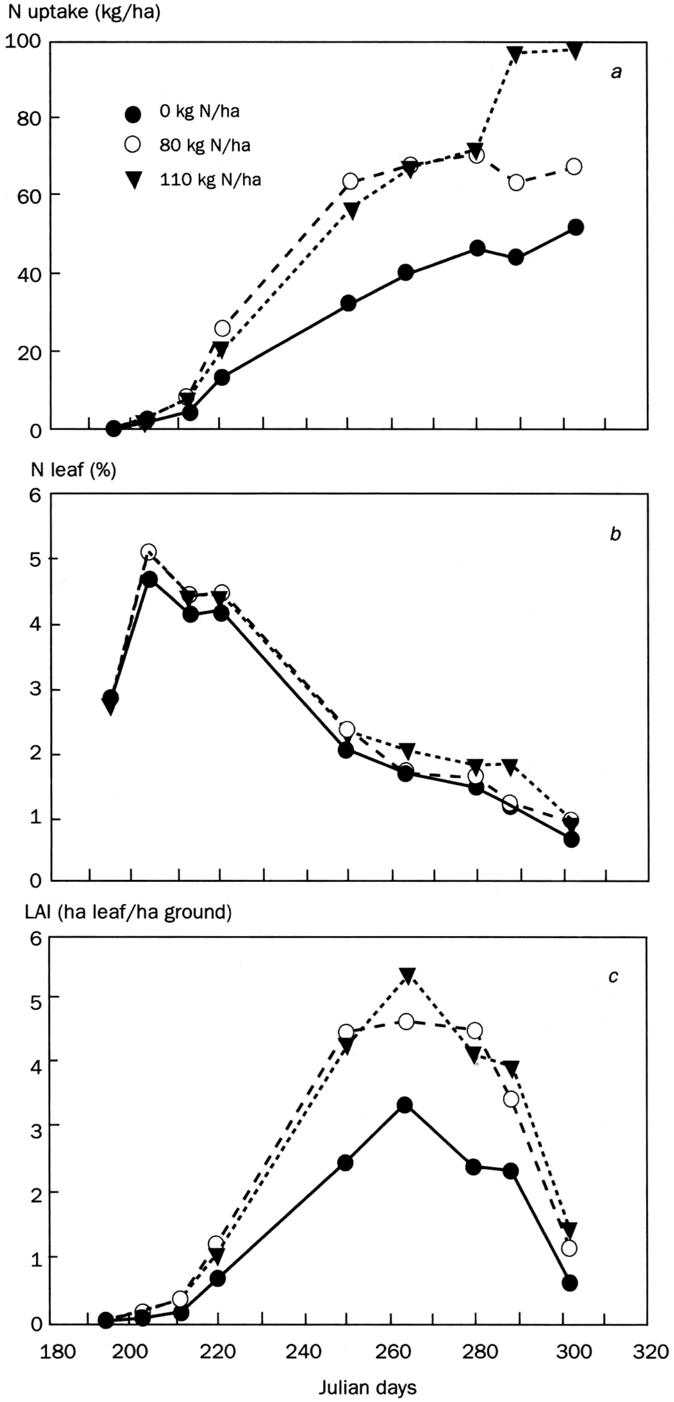
For all varieties, applying N increased yield (Fig. 4). The extra, late-season N application (30 kg N) raised yields in most varieties, with a maximum increase of 0.9 t/ha. The data for IR8 and IR36 are confounded because disease infections occurred in some treatments. At 110 kg of N, senescence was delayed by several days in the new line, and N concentration was higher during the grain-filling period (Fig. 5). In the 80 kg N treatment, total plant N decreased after flowering, indicating that soil N supply was deficient during grain filling.

Several important effects of late N application are evident in the three-quadrant analysis of the N response (Fig. 6). The recovery, or the slope, of the relation between N uptake and N supply increased greatly with late N, indicating that the additional 30 kg of N at flowering was taken up at a very high efficiency. This contrasts with conclusions from previous experimental and simulation studies which showed that no N could be taken up after flowering and that no benefit was to be expected at these yield levels (Penning de Vries et al 1990).

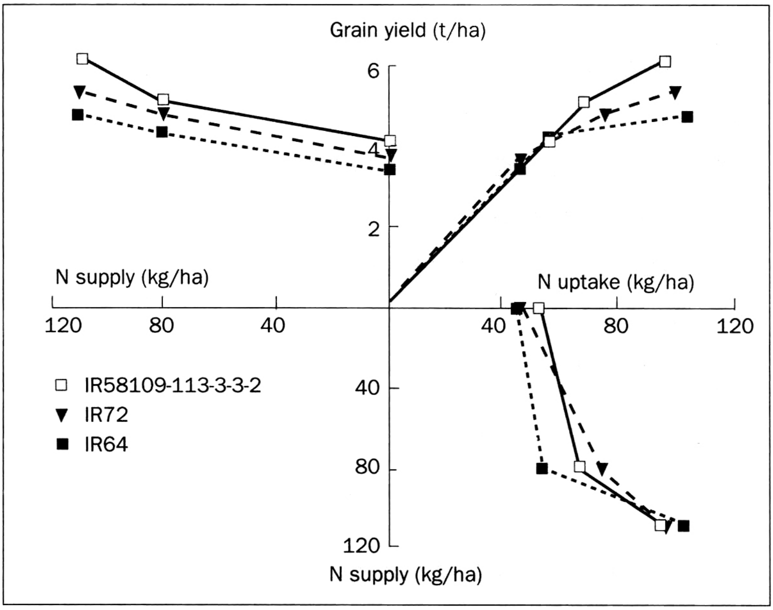
For all varieties, yield increased with higher N uptake, but the response curves indicate that the maximum yield level was not attained. Furthermore, the response curves suggest that the use of N for dry matter production is much more efficient in the new line, indicating a higher yield potential. The yield obtained with the new line was comparable with the best WS yields of IR8 in the 1960s. IR72 yielded somewhat below the new line, probably because of its small flag leaf and lower LAI. The distribution of LAI and N concentration in the leaf over height of the canopy shows that late N application mainly increased the N concentration in the flag leaf (Fig. 7).

Interpretation of experimental results using the ecophysiological model

The simulation model was used to analyze the data from the 1991 WS experiment. Leaf area index and measured leaf N concentration were put into the model. The simulation results were compared with the observed data (Fig. 8). Total biomass and panicle dry matter were simulated accurately by the model. The simulation predicted accurately



5. Measured results for IR58103-113-3-3-2 with three N treatments—0 kg N, 80 kg N, and 110 kg N—at IRRI, Los Baños, in the 1991 WS. (a) Time course of total N up take, (b) Time course of average leaf N content, and (c) Time course of LAI.



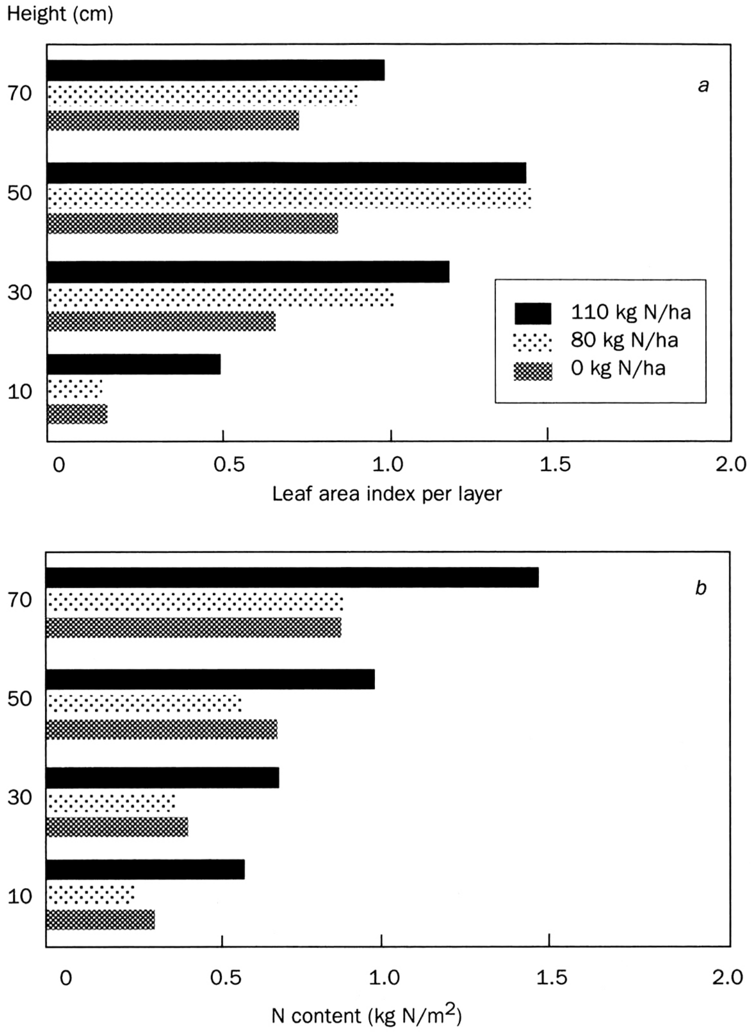
6. Three-quadrant relationships between grain yield, N uptake, and N supply for rice varieties IR58103-113-3-3-2, IR72, and IR64.

the enhanced growth rate of the crop during grain filling as a result of a higher leaf N content and LAI. Thus, the effects of late N application can be fully understood on the basis of differences in LAI and leaf N concentration.

To test the model further, the relation between simulated and measured total biomass and yield was examined. The data used were from the 1991 WS experiment (as above), a 1988 experiment at IRRI with IR64, and experiments with IR64 and five N rate treatments in 1988 DS in Muñoz, Nueva Ecija, Philippines (Dingkuhn et al 1991) (Fig. 9). The results indicate that the model explains differences in biomass production and yield across N treatments, varieties, and environments.

Predicting DS yield potential of current varieties

The model was used to study the attainable yield of IR72 and the new line under DS conditions at IRRI (Table 1). Weather data from 1987 DS were used. With similar N concentrations in the leaves, yields of 7.0 and 8.2 t/ha were simulated. Yields of up to 9.3 t/ha were simulated by assuming a 20% higher N concentration in the leaves. These results indicate that the DS yield potential of current varieties is similar to that of IR8, and that present yields at IRRI are lower than this potential because of insufficient N uptake by the crop.



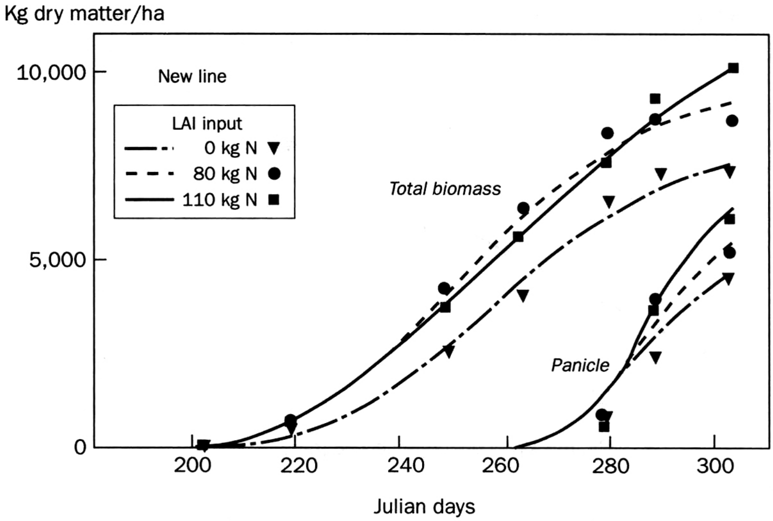
7. Distribution of LAI (a) and leaf N concentration (b) over height of the canopy of IR58103-113 3-3-2 in the 1991 WS at three treatments, 0 N, 80 kg N/ha before PI, and 110 kg N/ha given as 80 kg in two splits before PI and 30 kg at flowering.

Increased yield potential

This section analyzes the three key processes of yield formation using the ecophysiological simulation model.

Increasing the amount of stem reserves and their allocation

Dingkuhn et al (1991) proposed raising stem reserves by increasing partitioning of assimilates from leaves to stems. They changed the dry matter allocation pattern in their



8. Simulated (lines) and observed (symbols) time course of total dry matter production and panicle dry weight for IR58103-113-3-3-2 in the 1991 WS.

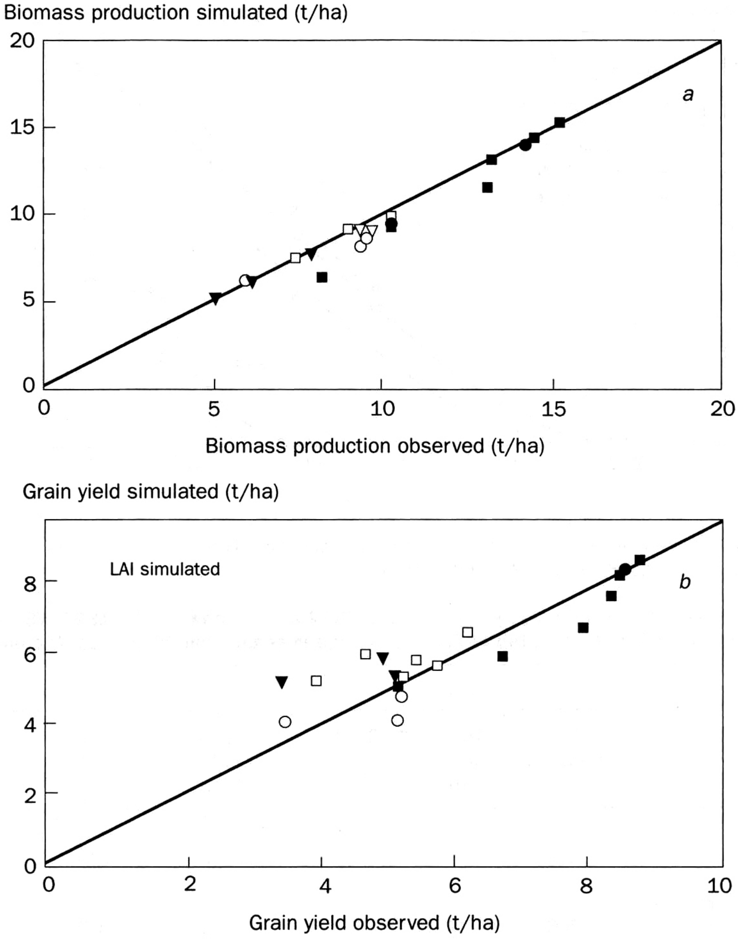
Table 1. Observed and simulated yields (t/ha) of IR72 and the new line for 1991 WS (IRRI, Los Baños, Philippines) and simulated effect of a change in season and higher leaf N content.

	IR72			New line		
	Yield duration (t/ha)	Total filling (d)	Grain (d)	Yield duration (t/ha)	Total filling (d)	Grain (d)
Observed						
1991 WS	5.7	94	28	6.1	108	23
Simulation results						
1. 1991 WS	5.6	94	28	6.3	109	23
2. 1987 DS	7.0	100	30	8.2	118	24
3. As 2 + N conc. 20% higher	7.9	100	30	9.3	118	24

simulation model and found that a yield increase of 25% was possible. However, in their model, the allocation of dry matter to leaf tissue stopped at PI, which is not realistic as several leaves, including the flag leaf, must still emerge and expand. Increasing the amount of stem reserves and efficiency of their allocation to the grain would probably have major consequences for lodging resistance.

Increasing the rate of dry matter production during grain filling

The superiority of higher yielding varieties only becomes apparent toward the end of the growing season. The maximum growth rate of closed canopies does not differ that much among C_3 crop species (Evans 1990). The maximum growth rate of hybrid rice is the same as that of inbred parents (Akita 1988).



9. Observed vs simulated total biomass (a) and yield (b) of five varieties at three N application levels in the 1991WS and IR64 in the 1988 dry season (DS) (Akita, unpubl. data) at IRRI's farm (Los Baños, Philippines) and IR64 in Muñoz (Philippines) in the 1988 DS.

In many crops, increased 'stay green' has been a major achievement of breeders over the past few decades (Evans 1990). The crops still had green leaves at maturity (C. T. de Wit and H. van Keulen, pers. commun.). For wheat, yield increases were based on lengthening the duration of photosynthetic activity by splitting N applications and improving crop protection (Spiertz and Vos 1985). Unfornately, no detailed complete data sets from that time are available. However, the effect of late N application in the 1991 WS experiments shows that late N can have the same effect in rice as it has in wheat.

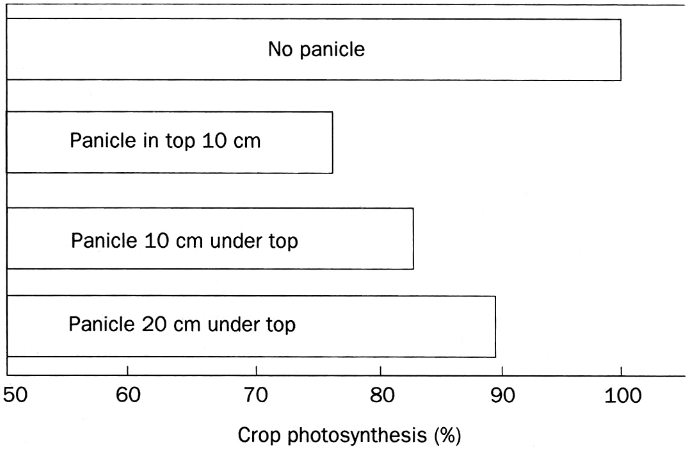
Penning de Vries (1991) discussed the possibility of increasing yield potential by improving physiological processes—for instance, by suppressing photorespiration and reducing maintenance respiration. So far, there are no indications that photorespiration can be suppressed in C_3 plants. Indications that genetic variation in maintenance respiration is related to variation in yield were found by Spitters, de Visser, and Penning de Vries (Centre for Agrobiological Research, Wageningen, The Netherlands, pers. commun.), although the size of the effect was very small. An interesting option mentioned by Penning de Vries is the increase of CO_2 flow from the soil through the root aerenchyma to the leaves, providing extra CO_2 for photosynthesis. However, sound evidence that this mechanism contributes to photosynthesis has not yet been documented.

Dingkuhn et al (1991) suggested increasing the N gradient in the canopy. This fits very well with the conclusions of our study and the results of the 1991 experiment. However, leaf N concentration in the top of the canopy is more important than the gradient itself. Dingkuhn et al (1991) simulated yields of 11.5-13.5 t/ha with 48 d of grain filling, which is much longer than what we found, based on both the simple approach and the simulation study.

We observed that the position of the panicles in the canopy varies strongly between varieties. The effect of panicle position on light absorption by the leaves was studied with a detailed model for interplant competition for light capture (Kropff and Spitters 1992). In 1991 WS, the panicle area index (PAI) reached 0.6-0.9 m^2 panicle/m^2 ground. The model showed that panicles in the top 10 cm of the canopy reduced canopy photosynthesis (LAI=4) by 25%, whereas panicles 20 cm below the top reduced canopy photosynthesis by only 10% (Fig. 10). There is large genetic variability in panicle height and flag leaf size in the canopy. These traits may provide promising characteristic for modification by breeders.

Lengthening the grain-filing period with long green leaf area duration

The ecophysiological simulation model was used to evaluate the outcome of the simple calculations. The starting point was the simulated yield of 9.3 t/ha of the new line with



10. Simulated reduction in leaf canopy photosynthesis as a result of shading by panicles at different positions in the canopy.

Table 2. Simulated effect of a change in grain-filling duration in the new line using 1987 DS weather data, Los Baños, Philippines.

	Yield (t/ha)	Total duration (d)	Grain filling (d)
1. 1987 DS	8.2	118	24
2. As 1 + N conc. 20% higher	9.3	118	24
3. As 2. Grain-filling duration from 24 to 31 d	11.7	125	31
4. As 2. Grain-filling duration of 40 d	14.7	134	40

Los Baños weather data from 1987 DS, with 20% higher leaf N concentrations than was observed in the 1991 WS experiment (Table 1). The effect of a longer grain-filling duration was examined, based on the outcome of the simple conceptual analysis previously presented.

Lengthening the grain-filling period from 24 to 31 d increased panicle dry matter to 11.7 t/ha. A grain-filling duration of 40 d and a harvest index of 0.6 gave 14.7 t/ha (Table 2). This is very close to the 43 d calculated with the simple concept of grain filling and illustrates the relatively simple structure of the system. However, in these simulations, a substantial amount of green leaf area remained active for a long period. This requires thick, large, and green leaves (due to high N concentrations), that senesce slowly. Japonica varieties have these characteristics, and a hybrid developed recently between a tropical japonica and an indica variety shows similar visual characteristics (S.S. Virmani, IRRI, pers commun.). The question that remains to be answered is: What is the genetic variability in the length of the grain-filling period? Senadhira and Li (1989) studied the length of the grain-filling period of 21 rice cultivars at IRRI's experimental farm during the 1987 DS. The duration of grain filling ranged from 16 to 40 d. However, rate of grain filling was low in the long-duration varieties, giving lower panicle weights. Interpreting this data is hindered by the agronomic practices used in the study, one plant per hill at 30- × 20-cm spacing, and only 60 kg of N given as a basal application. Experiments to evaluate the length of the grain-filling duration in relation to growth and production of some of these lines at optimum N levels are now in progress.

Implications for crop management

Increasing yield potential from 10 to 15 t/ha will have major implications for crop management. Based on normal N concentrations in the plant organs, it was calculated that about 200 kg of N must be taken up by a crop yielding 10 t/ha, and 300 kg of N is required for 15 t/ha. Reducing the grain N content could be an option, but that would reduce grain quality and protein content. Normal rice soils can supply the crop with about 60 kg N/ha, so a substantial amount of N must be added to achieve potential yields. At a recovery of 50%, which is high for existing flooded rice ecosystems, large amounts of N fertilizer will be needed. Of course, the economical and environmental implications of such high inputs have to be studied in detail. Better N management, including a multisplit application strategy that maintains adequate N supply throughout the season while minimizing N losses, is likely to be a prerequisite. At the foundation of such a strategy is the prediction and in-season reestimation of the minimum N uptake requirement (MNUR) (Cassman et al 1994). The simulation model could be helpful in estimating the MNUR throughout the growing season. However, processes related to N translocation and their relationship to the N status of the plant must be quantified accurately. A first setup for such a model is being developed.

Increasing yield potential and hybrid vigor

It is extremely important to analyze the physiological background of the so-called hybrid vigor, as it may be possible to obtain similar traits in conventionally bred lines.

One physiological trait cited in hybrids was vigorous seedling growth, resulting in earlier canopy closure and better sink formation (Akita 1988). However, as soon as the canopy closed, no differences in photosynthesis, respiration, and growth rate were observed (Akita 1988, Yan Zhen De 1988). This fast early growth and leaf area development may help to produce high yield in short-duration varieties, but similar effects may be obtained by narrower spacing of the hills. An important advantage is improved partitioning of photosynthates to the grains, which may be due to the different lengths of the generative and vegetative phases. A better canopy structure was also reported by Yan Zhen De (1988) and Akita (1988). However, detailed physical information was not given.

Conclusions

Systems approaches at different levels of detail can help in the process of designing and testing varieties for specific environments. Simple approaches as discussed in this paper help to identify the most promising options. Detailed ecophysiological models can help in analyzing the physiological processes and predicting crop management requirements, such as the MNUR (Cassman et al 1994). These models can be used to analyze genotype-environment interactions and to interpret the results of multilocation trials (Dua et al 1990). However, one should be careful in using the detailed simulation models to define the effect of physiological traits, as compensation effects may confound conclusions. For example, in the model used in this study, the effect of shading by panicles was not included. The competition model showed that canopy photosynthesis was reduced by more than 15%. It may well be that the simplified way that the effect of a vertical N profile in the canopy was introduced compensated for this. It is important, therefore, that the components of these detailed models are tested with experimental data.

Leaf area development and dry matter partitioning are not simulated satisfactorily by the existing models. Empirical functions that cannot explain different allocation patterns across N treatments are used (de Wit and Penning de Vries 1985, Evans 1990, Thiyagarajan et al 1991).

A combination of longer grain-filling duration, more spikelets/m^2, and longer green leaf area duration are needed to obtain grain yields beyond 10 t/ha in tropical environments. Multilocation trials, where a range of varieties is grown under optimum management and where the crop is sampled in detail, are needed to obtain further insights into the feasibility of raising the yield frontier in rice.

Acknowledgments

The authors kindly acknowledge the help of R. Torres and S. Liboon in conducting the experiments in the 1991 WS. They are grateful to C. T. de Wit for discussions that initiated this work.

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Authors' addresses: M. J. Kropff and K. G. Cassman, International Rice Research institute, P.O. Box 933,1099 Manila, Philippines; and H. H. van Laar, Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Managing diseases and insect pests of hybrid rice in China

Tian Ji-Rong and Li Xuan-Keng

Diseases and insect pests which occur in hybrid rice in China are similar to those which occur in inbred rice. Major diseases and insect pests are blast (*Pyricularia oryzae*), sheath blight (*Thanatephorus cucumeris* [*Rhizoctonia solani*]), bacterial blight (*Xanthomonas oryzae*), stem borer, rice planthopper, and leaffolder (*Cnaphalocrocis medinalis*). As the characteristics and cultural practices of hybrid rice are different from those of inbred rice, the occurrence of diseases and insect pests in hybrid rice has its own distinguishing features. In southern China, were high-yielding hybrid rice is the major crop, the strategy for disease and insect control involves integrated pest management (IPM) as the main method and artificial regulation as the subordinate one. The key technical measures include the develop ment of resistant varieties, cultural control, protection and use of natural enemies, and rational use of chemicals. In 1986-90, the above measures were undertaken in six provinces (Sichuan, Jiangsu, Zhejiang, Hubei, Hunan, and Guangdong), the area of ricefields where IPM was practiced reached 6.60 million ha, and the economic, social, and ecological benefits obtained were very significant. The direct economic benefit was worth US$0.1-0.2 billion.

Hybrid rice in China is grown mainly along the middle and lower reaches of the Yangtse River and in southwest and south China. These regions are in the subtropical zone, with mild climate, abundant rainfall, and a great variety of rice diseases and insect pests. It is known that there are 252 rice insects and 72 rice diseases including 20 insects and 10 diseases that cause damage in epidemic proportions (Xiao et al 1988).

The diseases and insect pests which occur in hybrid rice are basically similar to those which occur in inbred rice. Major diseases are blast (Bl), sheath blight (ShB), and bacterial blight (BB); major insect pests are stem borers (SB), planthoppers (BPH), and leaffolders (LF). However, as the characters and cultural practices of hybrid rice are different from those of inbred rice, the disease and insect occurrence in hybrid rice has its own distinguishing features,

Diseases

Yellow stunt was prevalent in Hunan in the mid- and late 1970s. This had a negative influence on the extension of hybrid rice in the rice-growing regions along the Tongding Lake. In 1976, rice hybrids Nan-You 2 and Nan-You 3 in Hunan were damaged by BB. Plants showed kresek, and the affected area covered more than 30,000 ha. In 1990, bacterial leaf streak was severe and greatly affected hybrid rice. Sheath blight has become a major disease of hybrid rice grown in fields with sufficient fertilizer and water. In Changde, Yiyang, and other counties, the loss caused by ShB comprised more than 60% of the total losses caused by rice diseases and insect pests. Variation is easily seen in B1 organisms. When a hybrid combination is commercially grown in a place for several years, its original resistance to B1 is lost as the physiological races of the B1 fungus change. For instance, B1-resistant Wei-You 6 has now lost its resistance in western and southern parts of Hunan.

Some diseases, such as kernel smut (*Tilletia barclayana*), false smut (*Ustilaginoidea virens*), and sheath rot (*Acrocylindrium oryzae*), which were not considered important for inbred rice and which required no specific control measures in the past, have become major problems in hybrid rice during its later growth stages. In hybrid seed production and male sterile line multiplication fields, the percentage of diseased grains caused by kernel smut was generally 5-20% and, when it was serious, 40-60%, even 100%.

Insect pests

Since the hybrid rice area expanded, the population density of rice striped borer (*Chilo suppressalis*) has increased very rapidly, resulting in severe damage to hybrid rice. According to observations made in Changsha region, Hunan, the density of adults in each generation was 20-35% greater in hybrid rice than that in ordinary rice, and the density of egg masses in the former was 2.1-3.7 times greater than in the latter. The larvae of rice striped borer cause deadhearts in hybrid rice during tillering and injured plants, dead booting, and whiteheads are common during the reproductive stage. Wei-You 35 grown in Liling, Hunan, was damaged by striped borers of the second generation. The percentage of injured plants in the most severely damaged fields was as high as 98%.

In Sichuan Province, a farming system of rice - wheat (rape) is practiced, and a single-cropping hybrid rice is grown mainly in the system (more than 85%). In recent years, with the rapid expansion of the area of ratooning hybrid rice, damage due to yellow stem borer (YSB) (*Tryporyza incertulas*) became more serious each year. In the less-damaged fields, yield was reduced by 10-20%, and in severely damaged field, by 50%. This was because the peak of the third-generation YSB moth coincided with the booting and heading stages of ratooning hybrid rice, optimal conditions for ovipositing. Furthermore, after harvesting ratooned hybrid rice, many overwintering insect sources remain in the field, increasing the base population for the following year (NPPS 1992).

Rice planthoppers are major insect pests of rice grown in the Yangtse Valley. The population density of BPH in hybrid rice is higher than in ordinary rice. Whitebacked planthopper (WBPH) has also become a major insect pest in hybrid rice. In the fields, more WBPH appear on hybrid rice than on inbred rice. This is because hybrid rice leaves are dark green, and dry matter in hybrid rice is 29.3-53.5% more than in ordinary rice. The average number of eggs laid by a female WBPH in each generation on Wei-You 35 is 23.3% more than in Guang-Lu-Ai 4 (inbred) (Li et al 1988). Thus, the density of the insect populations in fields planted to hybrid rice is greater than in those planted to inbred rice. With the expansion of hybrid rice area, damage by BPH has become more serious each year. In recent years, the area affected by BPH was more than 1.3 million ha. Outbreaks occurred in 1987 and the affected area throughout the country was 1.8 million ha. Outbreaks also occurred in 1991 (NPPS 1992).

Use of IPM in hybrid rice

Integrated management of a single disease or a single insect pest in the rice-growing regions in south China has changed to integrated management of multiple diseases and insect pests. Keeping in view the characteristics of various ecological regions and the high yield potential of rice hybrids, emphasis is on three major areas—B1, SB, and LF. The key techniques involve natural control as the main method and artificial regulation as the subordinate one. The overall aim is to obtain high yields, control diseases and insect pests, protect the environment, reduce inputs, and increase benefits to farmers.

Evaluation and utilization of multiresistant varieties

The objective of resistant variety breeding has changed from monoresistance to multiresistance and from disease resistance alone to disease and insect resistance. In the last 5 yr, more than 90,000 entries were screened and 25 high-yielding varieties and hybrid combinations were bred, which were planted in at least 20,000 ha in south China. Hybrids with multiple resistance included Wei-You 64, Shui-Yuan 290, Xiang-Zao-Xian 7, Qi-Gui-Zao 25, Gan-You 64, D-You 63, Shan-You 63, Shu-Feng 106, and Lian-Jing 1. In China, the area planted to these varieties and hybrid combinations amounted to 10.6 million ha (Table 1) (Du and Wang 1990).

To give direction to the breeding program for varietal resistance and to make rational use and distribution of resistant varieties, extensive cooperation has been secured in China. The differentiation of the pathogenicity of Bl and BB organisms has been basically verified and of BPH biotypes have been monitored.

The pathogenicity of BB organisms in China has its own distinguishing features. It is different from six races in the Philippines and types in Japan. According to five principal differential varieties (Jin-Gang 30, Tetep, Nan-Jing 15, Java 15, and IR26), seven pathogenic types in China may be identified. In the japonica-growing regions in north China, types I and II are the main ones; in the Yangtse Valley, types I1 and IV are common (Gui and Xu 1991).

As to races of Bl fungus, in the indica-growing regions in Guangdong, Fujian, Hunan, Sichuan, Hubei, and south Zhejiang, races of groups B and C have become

Table 1. Varieties and hybrids with multiple disease and insect resistance.

Variety/hybrid	Type	Locality	Resistance[a]			
			Blast[b]	Bacterial blight	Sheath blight	Brown planthopper
Wei-You 64[c]	Hybrid	Hunan	MR	MR		MR
Shan You 63	Hybrid	Jaingsu, Sichuan	MR-R	MR	MR	
D-You 63	Hybrid	Hunan, Sichuan	MR	MR	MR	
Gan-You 63	Hybrid	Sichuan	R	MR	MR	
Xi-You 56	Hybrid	Guangdong	R	R	R	
Wei-You 35	Hybrid	Hunan	MR			T
D-You 10	Hybrid	Sichuan	R	MR	MR	
Qi-Gui-Zhao 25	Early indica	Guangdong	MR	R		MR
San-Huang-Tian	Early indica	Guangdong	R	MR		R
Te-Qing	Early indica	Guangdong	MR	R		
Zhe 852[d]	Early indica	Zhejiang	R	MR		
E-Zhao 6	Early indica	Hubei	MR	MR		
Xiang-Zhao-Xian 7	Early indica	Hunan	MR	MR		R
Yang-Dao 3	Medium indica	Jiangsu	R	R	MR	T
Nan-Jing 14[e]	Medium indica	Jiangsu	R	R		T
Chuan-Zhi 3	Medium indica	Sichuan	R	MR		
Shu Zi 106	Medium indica	Sichuan	R	MR		T
Xiu-Shui 620[f]	Late japonica	Zhejiang	MR			R
Xiu-Shui 664	Late japonica	Zhejiang	R	MR		R
Wu-Yu-Jing	Late japonica	Jiangsu	R	R		
Lian-Jing 1[g]	Late japonica	Jiangsu		MR		
Xiang-Wan-Xian 1	Late indica	Hunan	MR	MR		
Qing-Hua-Ai	Late indica	Guangdong	MR	R		
Qing-Ye-Qing-Feng	Late indica	Guangdong	MR	R		
Shui-Yuan 290[h]	Late glutinous	Jiangsu, Hunan	R	R		R

[a] MR = moderately resistant, HR = highly resistant, R = resistant, T = tolerant. [b] Refers to resistance to a certain dominant race of blast at the observation site. [c] Wei-You 64 = HR to RTYV. [d] Zhe 852 = tolerant of WBPH. [e] Nan-Jing 14 = MR to WBPH. [f] Xiu-Shui 620 = R to WBPH. [g] Lian-Jing 1 = MR to striped borer. [h] Shui-Yuan 290 = R to RTYV.

dominant. Races of group B have reached 39% and 50-64.5% in the rice-growing regions in West Sichuan and along Tongding Lake, respectively, and are seriously affecting Shan-You 63. In the rice-growing region along Tai Lake in north Zhejiang, races of groups D and E have markedly increased and races of group E have become dominant (Jin 1991).

Brown planthoppers in the ricefields in Guangdong, Hunan, Zhejiang, and Jiangsu belong to biotype I. The survival rate of BPH on IR26 reached more than 40% in Hainan Island (as damage rating was more than 3), which was close to that of biotype II.

Cultural control

In China, cultural practices have always been one of the principal measures for controlling insects and diseases. After experiencing the instability of the crop phase in ricefields, the easy transformation of disease and insect resistance, and the importance of ecological control, attention has switched to cultural control. The following strategies are used.

Adjusting planting time and ratio of varieties. Varieties are planted so that the time they are most susceptible to diseases and insects does not coincide with the period when the diseases and insects are most damaging to rice. For instance, in the rice-growing region along Tongding Lake, the proportion of early-, medium-, and late-maturing varieties grown as early rice was adjusted from 1:2:7 to 1:8:1, and full heading of early rice was completed before 20 Jun. This was not only favorable for harvesting early rice and transplanting late rice, but also made 90% of early rice escape damage from second-generation striped borers and YSB. The damage rate was reduced from 5-6% to below 0.5%. In general, chemical control was not needed.

Healthy cultivation. This involves techniques that realize both high yields and disease and insect control. The following specific measures are taken in the rice-growing region along the Tongding Lake.

- Sparse seeding is practiced to raise vigorous seedlings. The seeding rate in the early rice nursery is 600-700 kg/ha, and the nursery is covered with plastic film. The maturity stage may be 2-3 d earlier, and the damage caused by borers during heading can be avoided or reduced. The seeding rate in the late rice nursery is 225-300 kg/ha for hybrid rice and 375-450 kg/ha for late indica. The seeding date, seedling stage, and transplanting stage are adjusted so that full heading is completed before 15 Sep. In this way, it is possible to ensure stable and high yields of late rice and escape the damage caused by fourth-generation SB and fifth-generation BPH.
- Lower plant populations per unit area are established. This means that the leaves do not cover the rows between plants too early, so air and sunlight may penetrate. This promotes vigorous plant growth, increases stress resistance, and improves the microclimate in ricefields. As a result, damage from diseases and insects is reduced.
- Fertilizer and water are carefully managed. Organic manure is used as the main fertilizer. Nitrogen fertilizer application is minimized. The ratio of NPK is generally 2:1:1. Early rice requires 120 kg N/ha, and late rice requires 150 kg N/ha. This quantity ensures high yields and reduces damage from ShB and BPH. Intermittent irrigation is practiced. When the number of tillers is sufficient, the field is sun-dried. Late rice should not be dehydrated too early (Jin 1991).

Mixed planting of various varieties. At the Sichuan Academy of Agricultural Sciences, several rice varieties which were similar to each other in agronomic characters and maturity stage but had different resistances to diseases and insects were planted. The results obtained in a 3-yr experiment showed that B1 was reduced by 74.23%, and the criteria for B1 were decreased by 85.30%. Sheath blight and BB were also reduced. In addition, the rice yield in mixed planting was 11.85% higher than for single planting, and the rice yield in mixed planting of hybrid rice and ordinary rice was increased by 10%. The photosynthetic rate and rooting ability of a susceptible variety were higher in mixed planting than in single planting (Wang and He 1991).

Biological control

The natural enemies in the ricefields in Changde region belong to 380 species, 74 families, and 11 orders. Those in Yiyang belong to 180 species, 20 families, and 6 orders. There are 29 dominant natural enemies of rice insects. According to recent investigations by the Hunan Plant Protection Institute in the rice-growing region along the Tongding Lake, the parasitic rate of natural enemies such as rice planthopper red dryinid wasp (*Haplogonatopus japonicus*) and nematode (*Agamermis* sp.) was 51.7-55.5%. The ratio of predatory spider and green bug (*Cyrtorhinus lividipennis*): rice planthopper was about 1:1. The population density of rice planthopper was always below the control threshold.

The measures taken to protect and use natural enemies are to plant resistant varieties, use favorable ratios of varieties, extend soybean planting on the bunds between fields, and to apply chemicals with high efficiency but low toxicity (Luo et al 1990).

Chemical control

Chemical use in the rice-growing region along the Tongding Lake is based on rice disease and insect forecasts, the growth stage of the rice, resistant varieties grown, and control thresholds (Luo et al 1990).

Timing and objectives in chemical control. First-generation rice striped borer is the main insect that must be controlled during the active tillering stage of early rice. Sheath blight is the main disease during the booting stage of early rice. Second-generation rice striped borer, LF, and BPH are the main pests to be controlled, and emphasis is placed on late-maturing early rice. Third-generation rice striped borer is the main pest for control during the active tillering stage of late rice, and LF, BPH, and rice leafhopper are pests for concurrent control. Sheath blight is the main disease for control during the booting stage of late rice, and LF and BPH are pests for concurrent control. Fifth-generation BPH is the main pest for control during the heading stage of susceptible varieties.

Control threshold. The control thresholds of single diseases or insects are as follows:

Rice striped borer—3-5% plants with withered sheath during tillering and 1.8-2.0% during heading.

YSB—600-750 egg masses/ha.

LF—60-65 larvae in 2d-3d instars/l00 hills during the tillering stage of ordinary rice, 35-40 larvae/100 hills during the booting stage of ordinary rice, 85-95 larvae/100 hills during the tillering stage of hybrid rice, and 60-70 larvae/100 hills during the booting stage of hybrid rice.

BPH—l,000-1,500 nymphs/100 hills during the heading stage of late inbred rice, and 2,000-2,500 nymphs/100 hills during the heading stage of hybrid rice.

ShB—30-35% diseased hills.

Bi-control threshold. In the rice-growing region along Tongding Lake, BPH and ShB often occur simultaneously. A model of yield losses caused by compound damage from BPH and ShB was set up. Based on local rice production levels, the bi-control threshold of BPH and ShB for hybrid rice is 930-1,430 BPH/100 hills of rice from late tillering stage to booting stage, and the percentage of diseased hills by ShB is 12.5-18.5% (when a great quantity of BPH occurs, choose its upper limit and the lower limit of ShB; if sheath blight is serious, choose its upper limit and the lower limit of BPH). Application of Aplaud plus Validamycin A is an effective method for controlling both BPH and ShB. In 1991, BPH and ShB outbreaks were reported. Good results were obtained when the above method was used over large areas.

Summary

The Government of the People's Republic of China pays great attention to research on integrated management of rice diseases and insect pests. It was listed as a key problem in the National Science and Technology Development Program included in the sixth, seventh, and eighth five-year plans. The efforts made in 1986-90 resulted in the establishment of a China-type technological system of IPM and setting up of IPM models for six rice-growing regions distributed in the Chuanxi Plain, the Zhujiang Delta, along the Yangtse-Huai Rivers, the Tai Lake, the Yangtse-Han Rivers, and the Tongding Lake. IPM has been practiced 6.6 million ha. There has not been any BHC residue which was applied in the fields before. The direct economic benefits were worth US$0.l-0.2 billion. This indicates that the economic, social, and ecological benefits are very significant (Du et al 1991).

In China, disease and insect forecasting stations at all levels (state-province-district-county) have been set up, thus forming a network. These stations do long-, medium-, and short-term forecasting of occurrence of a pest, population trends, damage ratings, and suggest control methods accordingly. The township level has an agricultural technology station with 2-3 persons, and in the village, an agrotechnician is assigned to advise farmers on plant protection.

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Authors' address: Tian Ji-Rong and Li Xuan-Keng, Hunan Academy of Agricultural Sciences, Changsha 410125, China.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Grain quality consideration in hybrid rice

Ish Kumar, K. Maruyama, and H. P. Moon

Grain size, shape, and weight are determined by maternal genotype. However, the ultimate economic product of hybrid rice is basically a bulk of segregating endosperms of the F_2 generation. This makes hybrid rice breeding complicated. In most cases, hybrid rice grain size and shape are intermediate between those of the parents. But some long slender-grained varieties, like IR58025 A, maintain their shape in most F_1 combinations. Heterosis in grain weight differs according to cross combination. Endosperm appearance is primarily decided by the amylose content. It varies from waxy to dull to translucent as amylose content increases. If one parent has waxy or dull endosperm and the other has translucent, the grains on the hybrid plant show a segregation of 3 translucent and 1 waxy or dull endosperm. Waxy, dull, and translucent are controlled by different alleles and genes of different loci. There fore, segregations of 1:2:1 or even 1:1:1:1 may be observed. Parents with the same genotype for endosperm opacity should be selected because consumers do not like the segregation in endosperm appearance. Amylose content is also highly related to cooking and eating quality. Hybrid rice grains have different cooking and eating qualities from the parents because of the segregation in amylose content. Generally, cooking and eating qualities are intermediate. However, in some cases, the influence of the high-amylose parent remains strong. Gelatinization temperature may also be related to cooking quality but does not affect it severely and, therefore, may not influence the acceptability of hybrid rice. Gel consistency (GC) in rice determines softness/hardness of cooked rice on cooling. In single-grain analysis of F_2 grains, segregation could be observed and hard or intermediate GC was found to be dominant over intermediate or low. Aromatic rices are preferred in many parts of the world. The aroma of Basmati rices was observed to be recessive in F_1 seed tests. A ratio of 13 nonaromatic:3 aromatic seeds was observed in the F_2 grains from a cross of aromatic and nonaromatic varieties. When cooked, such samples emitted a mild aroma compared with the aromatic variety. If aromatic rice is preferred, it is suggested that both parents of hybrids should be aromatic.

Breeders aim to increase productivity per unit area. Diverse genotypes are crossed to achieve high genetic gains. Heterotic hybrids yield about 15-20% higher than popular conventional varieties and are accepted by the farmers. However, grain and cooking quality affect the acceptability of hybrid rices to consumers. Cooking quality is important because rice is consumed whole after cooking, unlike other cereals like maize, sorghum, and pearl millet, where primarily the flour is used. From the consumers' point of view, endosperm appearance, size, shape, and cooking and eating characteristics of grains harvested from F_1 plants are of great concern.

The economic product of rice hybrids is the seed borne on F_1 plants. These are F_2 seeds, and they show genetic segregation for endosperm traits in the grain due to genetic differences between the parents. The product that reaches the consumer is therefore basically a bulk of grains segregating for endosperm traits.

Endosperm appearance

Rice endosperm may appear waxy, dull, or translucent. Waxy rices are opaque and cook glossy and sticky, as do dull and hazy grains. Among the translucent or nonwaxy rices, the cooking quality varies mainly according to amylose content.

Each grain category in a mixture of waxy, dull, and translucent grains cannot be identified individually after cooking, but still consumers do not like the variation in endosperm appearance. We have observed that if one parent in a hybrid has waxy or dull endosperm and the other has translucent, the grains on the hybrid plant showed a segregation of 3 translucent: 1 waxy or dull endosperm. Depending on the differences in endosperm opacity and amylose content of the parents, ratios of 1 waxy:1 hazy:2 translucent or 1 dull: 1 hazy:2 translucent were obtained among the grains of a single panicle, thus lowering the market acceptability of the hybrid. When both parents had either translucent or waxy/dull endosperm, no segregation for endosperm appearance was observed. Therefore, in areas where translucent grains are preferred, both parents must have translucent grains. Similarly, in areas where waxy or dull grains are preferred, both parents should have either waxy or dull endosperm. However, in crosses between waxy and dull parents, the F_2 seeds could not be categorized according to physical appearance.

Segregation patterns for seeds obtained from hybrids with parents of different endosperm appearance are summarized in Table 1. The results suggest that parents with similar endosperm appearance should be chosen to avoid segregation for physical appearance among the grains.

All the currently available cytoplasmic male sterile (CMS) lines for indica rices have translucent endosperm, as do almost all the restorer lines, except for IR29, which has waxy endosperm. For areas which prefer waxy grains, the right genetic background must be developed. Waxy endosperm is a recessive trait and therefore very easily transferred to the required genetic background for developing hybrids with waxy endosperm.

Table 1. Physical appearance of kernels borne on rice hybrids.

Cross combination of different endosperm appearance	Segregation pattern for endosperm opacity
Translucent (T) (×) translucent	No visible segregation
Waxy (W) (×) translucent	1W:3T 1W:1H:2T
Dull (D) (×) translucent	1D:3T 1D:1H[a]: 2T
Waxy (×) dull	No visible segregation
Waxy (×) waxy	No visible segregation

[a] H = hazy.

Grain size, shape, and weight

The grain size of any hybrid is highly uniform, irrespective of the size and shape of grain in the parents. Grain size and shape are determined by the size of lemma and palea, determined in turn by the genetic composition of the female parent, i.e., the F_1 plant. No genetic segregation is expected or observed within the panicle.

Grain length, which is a primary factor in marketing, has been reported to be under single, two, three or polygenic control (Ramiah et al 1931, Bollich 1957, Ramiah and Parthasarathy 1933, Mitra 1962, Chang 1974, Somrith et al 1979). Similarly, grain width and weight have been reported to be under polygenic control (Ramiah and Parthasarathy 1933, Nakatat and Jackson 1973, Chang 1974, Lin 1978). Some maternal effects for these characters have also been observed (Kumar, unpubl.).

Seed borne on hybrid plants is normally expected to be between the two parents, but in crosses between a long slender-grained CMS line, IR58025 A, and a set of restorers, most of the hybrids had long slender grains as in the CMS line V20 A. The seeds on the F_1 plants were either coarse or medium. These results suggest that as far as possible both parents should have the desirable grain size. Where grain size differs, the female parent should have the desirable grain size and shape if possible. There is, however, a general feeling among breeders that CMS lines with short grains have higher outpollination potential. However, we have observed outpollination to be equally high in CMS line IR58025 A. Outpollination seems to depend more on stigma exsertion and angle and time of opening of lemma and palea rather than on grain size. Therefore, it is suggested that in order to produce long slender-grained hybrids, CMS lines with long-grained genetic backgrounds should be developed.

Heterosis in grain weight differs according to cross combinations. Grain weight is highly correlated to grain size. Grain size is a product of grain length and grain width. Grain length and grain width inherit independently, which might explain the variation in F_1 grain weights.

Grain appearance

Grain appearance of brown or milled rice is a complex agronomic trait in which many characters are involved, e.g., endosperm type, grain size, shape, and weight. The characters which influence grain quality are seed coat color, depth of groove, dorsal white, core white, and chalkiness. Akita (1990) reported that embryos of indica hybrids are larger than those of the parents. This may be disadvantageous for hybrid rice. But embryo size of indica/japonica hybrids is not always bigger than the parents (Akita, pers. commun.). Thus, grain appearance involves many characters under both dominant and recessive genetic control. Grain appearance is often graded in between the parents.

Cooking and eating qualities

Cooking and eating qualities are of great significance in consumer acceptance of a hybrid. Of the endosperm characteristics, it is primarily amylose content that affects eating quality. Rices with high amylose content cook fluffy but become dry on cooling. Intermediate-amylose rices cook fluffy and remain soft on cooling. The low-amylose rices cook sticky and soft. Very low-amylose and waxy rices cook glossy, very sticky, and soft. This character has been reported to show both dosage and maternal effects and has been reported to be monogenic in inheritance (Kumar and Khush 1986,1987,1988; Kumar et al 1987).

Grains harvested from hybrid plants are basically a mixture of kernels with different chemical compositions, since the seeds borne on F_1 plants are F_2 seeds and thus show segregation for amylose content within the same panicle. There is no problem with eating quality if both parents have the same amylose content, as there will be no segregation. However, if the parents vary in their amylose content, hybrids of desirable quality can still be bred by selecting the parents carefully. For example, if the preferred amylose content in the hybrid is intermediate, then either both parents should have intermediate amylose content, or one parent should have high and the other low amylose content. By selecting parents with low and high amylose contents, genetic segregation and dosage effects resulted in F_2 grains of parental and intermediate categories for amylose content in the ratio of 1:1:1:1. The cooking quality was similar to intermediate-amylose rices. However, in crosses involving a waxy/very low-amylose parent and a high-amylose parent, very low dosage effects were observed. On account of this, F_2 seeds showed a segregation of 3 high amylose: 1 very low/waxy amylose content. Thus there were fewer sticky grains than even low-amylose rices. The selection of parents, therefore, should be done according to the specific cooking/eating qualities required (Table 2).

In temperate Asia, sticky and soft rice is preferable. Rice vendors often mix in a small amount (less than 5%) of their old (stale) rice to improve stickiness and softness. A typical indica/japonica hybrid rice produces segregating grains of different amylose contents. An experiment was done to simulate this. Addition of waxy rice improved cooking quality to some extent, but did not change the fundamental level (Table 3).

Table 2. Suggested parents for producing nearly desirable amylose content in rice hybrids.

Preferred amylose level	Suggested parents for hybrids	Quality characteristics of hybrids
High	High x high High x intermediate	High amylose, fluffy, hard upon cooling
Intermediate	Intermediate x intermediate Intermediate x low High x low	Intermediate, fluffy, soft upon cooling
Low	Low x low Intermediate x very low	Low amylose, sticky, soft upon cooling
Very low	Very low x very low Very low x waxy	Very low amylose, sticky, glossy, soft upon cooling
Waxy	Waxy x waxy	No amylose, very sticky, glossy, soft upon cooling

Table 3. Cooking quality of rice mixtures with different amylose contents.[a]

Content	Cooking quality	Appear-ance	Aroma	Taste	Sticki-ness	Soft-ness
High-amylose rice (100%)	-3.66	-2.22	-0.66	-3.15	-4.04	-3.54
High-amylose rice (95%) + waxy rice (5%)	-3.62	-1.40	-0.09	-3.12	4.08	-3.16
High-amylose rice (90%) + waxy rice (10%)	-3.42	-1.32	-0.29	-2.92	-3.71	-2.88
High-amylose rice (80%) + waxy rice (20%)	-2.72	-1.14	-0.14	-2.16	-2.79	-2.62
Low-amylose rice (100%)	-0.63	-0.52	+0.03	-0.57	+0.61	-0.04
Low-amylose rice (95%) + waxy rice (5%)	-0.58	-0.56	-0.08	-0.34	+1.00	+0.11
Low-amylose rice (90%) + waxy rice (10%)	-0.37	-0.64	-0.03	-0.39	+1.05	+0.20
Low-amylose rice (80%) + waxy rice (20%) -	-0.20	-0.99	-0.10	-0.26	+2.15	+0.82
Akihikari (check)	+0.66	+1.27	+0.35	+0.26	+0.77	+0.36
Koshihikari (check)	+1.85	+1.44	+0.13	+1.45	+1.83	+0.79

[a] High-amylose indica rice = Guichao 2, low-amylose indica rice = Milyang 23, waxy rice = Fukei Mochi 119. Each 400g of milled rice was cooked in an electric pot. Data were av of 3 replications with 17-22 panel tasters. Cooking quality is evaluated as an integration of these 5 factors–appearance, aroma, taste, stickiness, and softness. For cooking quality, appearance, aroma, and taste, 5 = good and 6 =bad; for stickiness, 5 = sticky and -5 = not sticky; for softness, 5 = soft and -5 = hard.

This suggests that factors other than amylose content may be involved. One possibility may be the softness when cooked rice cools to room temperature. Japonica varieties remain soft after they cool. Koshihikari, the leading rice variety in Japan, comprising

Table 4. Quality of indica/japonica F_1s using wide compatibility line, Norin PL 9.

Cross combination	Heading date	Culm length (cm)	Yield[a] (t/ha)	Grain[b] appearance	Grain[b] weight (mg)	Cooking[c] quality
Norin PL9/Milyang 23	16 Aug	113	8.78	4.5	25.0	-0.32
Norin PL9/IR26	14 Aug	101	8.94	5.5	23.1	-1.92**[d]
Norin PL9/IR36	21 Aug	113	8.78	6.0	23.3	-1.65**
Norin PL9/Guichao 2	17 Aug	120	9.63	7.0	24.6	-2.00**
Milyang 23/Guichao 2	23 Aug	95	8.63	6.5	25.2	-1.63**
IR26/Guichao 2	23 Aug	84	8.44	7.0	22.8	-2.16**
IR36/Guichao 2	19 Aug	89	8.71	7.0	21.8	-2.32**
Norin PL9	7 Aug	84	7.77	5.0	23.3	-0.24
Milyang 23	22 Aug	82	8.11	6.5	24.3	-0.42
Guichao 2	24 Aug	91	7.71	7.0	23.6	-2.47**
Akihikari (Check)	12 Aug	87	6.71	4.5	22.3	-0.15
Nipponbare (Check)	26 Aug	87	6.55	3.0	23.2	0 (ck)

Transplanted 9 Jun, one plant per hill. Forty plants of the center 2 rows out of 4 rows were examined. Randomized block design of 2 replications. [a]unhulled grain; 1 = best, 9 =worst. [b]Brown rice. [c]Cooking quality as per 25 panel tasters; 3=good, -3=worst. [d]**= Significantly low compared with check variety at 1% level. Each 400 g of milled rice was boiled in one electric pot.

Norin PL 9 : Japonica wide compatibility line selected from Ketan Nangka (bulu variety)/Nihonmasari/Akihikari
Milyang 23 : Korean indica variety with intermediate amylose content
Guichao 2 : Chinese indica variety with high amylose content
IR26 Indica variety with high amylose content
IR36 Indica variety with high amylose content
Akihikari : Japanese variety with bad cooking quality
Nipponbare : Japanese variety with medium cooking quality

The eating quality of IR26 and IR36 was not tested in this experiment, but their scores were below -2.5 in other experiments.

almost 30% of production, is characterized by low yields and susceptibility to diseases, but its grains remain soft when it cools.

Some indica/japonica F_1s were tested for yield and cooking quality. Japonica sticky rice was preferred by the Japanese panel. Milyang 23, the medium-amylose indica variety was second. The high-amylose indica varieties were not popular. The eating quality of indica/japonica hybrids compared with that of their indica parents could be improved (Table 4).

Gelatinization temperature

Gelatinization temperature (GT), the temperature at which the starch granules begin to swell irreversibly in hot water, is known to affect the cooking quality of rice. Rices with high GT are reported to take longer to cook than those with low GT. In our indica breeding program, almost all restorer and maintainer lines identified possessed either intermediate or low GT. The seed harvested from hybrids with low- and intermediate-GT parents showed genetic segregation for alkali digestion value within the same panicle but did not show any difference in cooking and eating characteristics to bulk grain harvested from F_1 plants. This is probably because the rice is left covered in the cooking pan for some time after cooking, and the heat released by the fully cooked rice completes cooking of the partly cooked grains. The differences in GT of the parents are thus unlikely to affect acceptability of hybrid rice, as no differences could be detected in high- and low-GT grains after cooking.

Gel consistency

Gel consistency (GC) in rice determines softness or hardness of cooked rice after cooling. In indica rices, it varies from hard, through medium to soft, whereas in japonica rices, it is mostly soft. In our study between crosses of parents possessing hard, intermediate, and soft GC, hard GC was found to be dominant over intermediate or soft. Similarly, intermediate GC was found to be dominant over soft GC in analysis of F_1 seeds. In single-grain analysis of F_2 grains, laboratory tests indicated segregation for GC. However, no difference in cooking or eating quality could be observed between seeds from hybrids involving soft-, hard-, and intermediate-GC parents. The release of starch and other chemicals in the boiling gruel probably results in their uniform distribution and coating on the grains.

In indica rices, intermediate GC is preferred. Hybrids with desirable softness can be developed by selecting suitable parents, e.g., with intermediate/intermediate or intermediate/soft GC. When parents with hard and soft GC were involved, the seeds were less soft than intermediate GC grains.

Aroma

Aromatic rices, which emit a pleasant aroma on cooking, are preferred in many parts of the world. Basmati rices, which are aromatic, are sold at 4-5 times premium. Aroma was observed to be recessive in F_1 seed tests with crosses involving basmati rices. In F_2 seeds of aromatic × nonaromatic crosses, a ratio of 13 nonaromatic:3 aromatic seeds was observed within a panicle. When cooked, such samples emitted a mild aroma due to the low frequency of aromatic seeds. If aromatic rices are preferred, both parents should be aromatic. For nonaromatic rices, neither of the parents should be aromatic.

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Notes

Authors' addresses: Ish Kumar, PROAGRO Seed Co. Ltd., 8-1-39 Touchowki, Hyderabad, India; K. Maruyama, National Agriculture Research Center, Kannondai, Tsukuba, 305 Japan; and H. P. Moon, Crop Experimental Station, Rural Development Administration, Suweon 440-707, Korea.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Economic assessment of the potential for hybrid rice in tropical Asia: lessons from the Chinese experience

Justin Yifu Lin and P. L. Pingali

About 30% of China's rice hectarage is devoted to hybrid rice. Rigorous household-level studies have found that the yield advantage of hybrid rice over conventional semidwarf varieties is about 15%, without major differences in material costs and labor requirements. However, several problems were faced in the diffusion of hybrid rice: 1) the range of hybrid varieties available was small; 2) a complicated seed production and distribution system had to be established; 3) cash requirements for seed purchase each season were high; and 4) the duration of the hybrid crop was longer, making it difficult to include hybrids in a two-crop system. This paper reviews evidence on farmer adoption behavior before and after the household responsibility system was introduced. Policies for hybrid rice research and seed production for other Asian countries are derived from the Chinese experience.

The introduction and rapid spread of high-yielding rice varieties throughout Asia in the late 1960s and early 1970s resulted in strong output growth. Aggregate rice output growth for Asia increased from 2.1% per annum during 1955-64 to 3.3% per annum during 1964-81. Rapid yield growth from 1964 to 1981 was the primary contributor to output growth. In the past decade, however, the growth in aggregate rice output declined to 1.5% per annum due to a sharp decline in yield growth. For the first time since the Green Revolution, rice output growth in South and Southeast Asia is in danger of not matching population growth rates.

China managed to sustain its output growth through the 1980s by switching from conventional modern varieties to hybrid rice. In the irrigated ricelands of China, hybrid rice was rapidly adopted and resulted in 15-20% higher yield. China's success with hybrid rice technology has generated interest in other Asian countries. However, hybrid rice varieties from China cannot be easily transferred to the rest of tropical Asia. Under tropical conditions, these varieties tend to be more susceptible to insect and disease damage. The duplication of China's success in hybrid rice for the rest of Asia would require intensive research efforts to generate varieties suitable for tropical conditions.

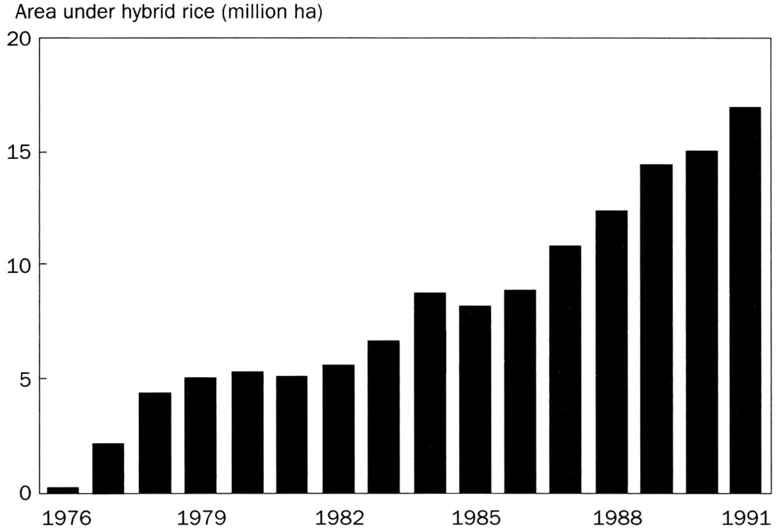
In considering the prospects for hybrid rice in Asia, there are valuable lessons to be learned from the Chinese experience. On the demand side, it is important to understand the conditions under which hybrid rice would be profitable relative to conventional modern varieties. On the supply side, it is important to understand the constraints associated with technology generation and seed production and distribution. This paper describes the Chinese experience and draws implications for the rest of Asia.

Hybrid rice in China

Rice is the most important crop in China. In 1986, 22% of the total sown hectarage (or 29% of total grain hectarage) was devoted to rice production (Ministry of Agriculture 1989). Since the socialist takeover in 1949, rice technology has been evolving continuously, and China has kept ahead of other countries in rice research. In the 1950s, emphasis was given to the selection and promotion of the best local varieties, and the main improvement was the shift from single to double cropping. Between 1952 and 1957, the multiple cropping index rose from 167 to 187% in the South China rice-growing region. During the same period in Taiwan, the index rose from 174 to 179% (Barker and Herdt 1985). A major breakthrough in rice breeding occurred in 1964, when China began full-scale distribution of fertilizer-responsive, lodging-resistant dwarf rice varieties with high yield potential, 2 yr before the release of IR8, the variety which launched the Green Revolution in other parts of Asia. Semidwarf varieties were grown on 80% of China's rice acreage by the late 1970s (Ministry of Agriculture 1989). The commercial distribution of F_1 hybrid rice seeds in 1976 marked the start of a third stage of rice breeding and extension in China. It must be noted that 93% of the total rice area in China is irrigated (IRRI 1991), and this is the land on which modern rice technology is used.

The successful development of hybrid maize in the 1930s in the United States provided an important impetus for breeders of other crops. Suggestions that heterosis be commercially exploited by developing F_1 hybrid rice were made from time to time. However, unlike maize and sorghum, rice is a self-pollinating plant with tiny florets, and it is thus impossible to produce hybrid seed in bulk by hand emasculation. The most effective way is through exploiting the phenomenon of cytoplasmic male sterility. The commercial production of F_1 hybrid rice seed involves a complicated three-line method: 1) locating a cytoplasmic male sterile parent plant; 2) crossing it with a maintainer line to produce offspring with sterility but with desirable genetic characteristics; and 3) crossing these seeds with a restorer line to produce F_1 seeds with normal self-fertilizing power (Yuan 1985). Because of the difficulties of hybrid seed production, most researchers were discouraged from continuing their research. Breeders in China were exceptions (Virmani and Edwards 1983).

China's hybrid rice research, under the initiative and leadership of Professor Yuan Long-Ping, started in Hunan Province in 1964. A breakthrough was made when Yuan and his assistant found a male sterile rice in 1970. In 1971, the search for maintainer



1. Areas under hybrid rice in China, 1976-91.

and restorer lines became a concerted nationwide program involving more than 20 research institutes in several provinces. The first maintainer variety was discovered by Yuan and another researcher in Jiangxi Province in 1972, and the first restorer variety was discovered by a breeder in Guangxi Province in 1973. A hybrid combination with marked heterosis was developed in 1974. Regional production tests were conducted simultaneously in hundreds of counties in 1975. In 1976, hybrid rice began to be commercially released to farmers (Zhu Rong 1988).

By 1991, more than 50% of China's rice hectarage was devoted to F_1 hybrid rice (Fig. 1). Rigorous household-level studies have found that the yield advantage of hybrid rice over the conventional semidwarf varieties is about 15%, without major differences in material costs and labor requirements (He et al 1984, 1987). He and coworkers compared hybrid rice growing with conventional method of growing modern rice varieties in Jiangsu Province during the 1984 crop season. They found hybrid rice yields to be at least a ton higher than conventional varieties, which were around 6.5 t/ha (Table 1). Returns to labor were higher for hybrid rice, but returns to nonlabor inputs and total costs were similar to conventional varieties.

These results were substantiated by a survey of 500 farm households in Hunan Province for the 1988 crop season by Lin (1990). While the mean yields of hybrids were significantly higher than conventional varieties for middle- and late-season rice, the difference was not statistically significant for early-season rice (Table 2). The yield advantages of hybrid rice were found to be partly offset by added requirements for chemical inputs and more expenditures for seeds. Therefore, the advantage of growing hybrids compared with conventional varieties depends largely on the prices of chemical inputs and seed, even for middle- and late-season rice. However, hybrid rice does not require more labor inputs than does conventional rice.

Table 1. Comparison of yields and resource use of hybrid rice and japonica (conventional) rice (He et al 1987).

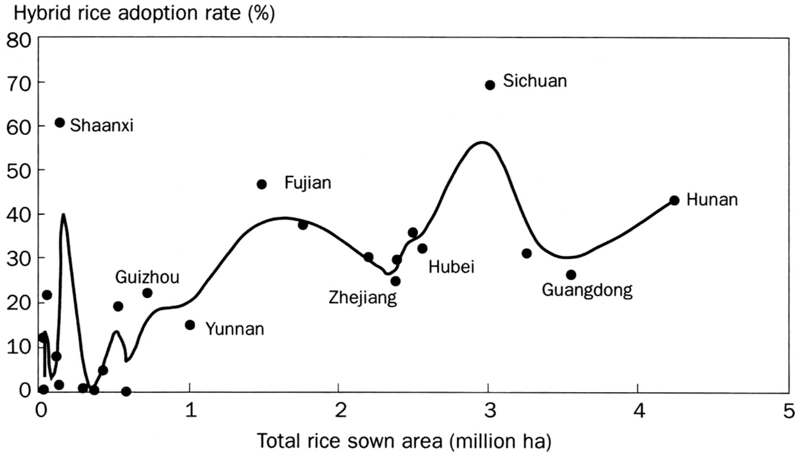
	Hybrid rice	Japonica rice	Difference	
			Quantity[a]	Percent
Mean yield (t/ha)	7.8	6.8	1.0	15
Seed (kg/ha)	21	96	-75*	-78
Pesticide (kg/ha)	39	22	17	77
N from organic and inorganic fertilizer (kg/ha)	260	285	-25 ns	-9
Total labor inputs (labor-days/ha)	273	297	-25*	-8
Irrigation expenses (US$/ha)	26	26	0 ns	0

[a]* = significant at the 5% level, ns = not significant.

Table 2. Means and standard deviation of inputs and outputs for hybrid and conventional rice (Lin 1990).

	Early-season rice		Mid-season Rice		Late-season rice	
	Conventional (n=392)	Hybrid (n=13)	Conventional (n=34)	Hybrid (n=116)	Conventional (n=213)	Hybrid (n=308)
Seed (kg/ha)	173.13 (3.7)	46.27 (2.2) ***	102.99 (3.1)	29.85 (0.9) ***	92.54 (3.3)	29.85 (1.1) ***
Fertilizer cost (Yuan/ha)	313.43 (9.4)	410.45 (7.9) *	222.39 (7.9)	282.09 (10.4) *	338.81 (13.2)	368.66 (10.7) *
Pesticide cost (Yuan/ha)	76.12 (4.7)	108.96 (2.7)	61.19 (3.5)	92.54 (4.1) *	85.07 (3.9)	108.96 (5.4) ***
Labor (days/ha)	228.36 (6.4)	253.73 (3.8)	332.84 (13.6)	302.99 (7.4)	207.46 (5.8)	214.93 (5.4)
Draft animals (days/ha)	22.39 (1.1)	28.36 (1.0)	44.78 (3.0)	55.22 (2.1)	16.42 (1.1)	16.42 (0.7)
Machine (days/ha)	7.46 (0.8)	19.40 (1.4) **	20.90 (6.9)	0.90 (0.31)*	8.96 (0.8)	8.96 (0.9)
Rice output (kg/ha)	5264.18 (97.3)	5752.24 (172.1)	4029.85 (117.8)	6455.22 (124.2) ***	4829.85 (90.2)	5770.15 (85.3) ***
Straw (kg/ha)	3088.06 (109.9)	4374.63 (57.4) **	3162.69 (92.4)	4416.42 (89.6) ***	3594.03 (95.7)	4419.40 (98.1)

[a]*, **, *** = significantly different at the 10, 5, and 1% levels of confidence, respectively. Figures in parentheses are standard deviations.



2. Hybrid rice adoption rate and total rice area, China, 1987.

Regional differences in hybrid rice adoption

National statistics on the rapid rise in hybrid rice production tend to mask dramatic geographic differences. The adoption rates in Sichuan and Hunan provinces were more than 50% in 1987, while the adoption rate in Heilongjiang and eight other provinces was zero in the same year (Fig. 2). Lin (1990) attributes the regional differences to differences in agricultural research infrastructure, adaptive research investments, and the share of rice in provincial agricultural output.

Agricultural research infrastructure tends to be concentrated mostly in the provinces with high population densities. Agricultural research in these provinces tends to concentrate on innovations that increase yield per unit of land, i.e., land-saving innovations. Provinces with high labor-land ratios also have high levels of irrigation infrastructure and have high levels of modern variety adoption. In provinces with high population densities and proportionately large rice area, the provincial academy's allocation of scientists and funds to research of both conventional and hybrid rice tends to be high. Therefore, the supply of yield-increasing rice technologies tends to be positively associated with labor-land ratios.

Like other types of improved seed, the F_1 hybrids proved to be sensitive to local ecological conditions. To obtain the yield potential, each region had to develop its own hybrids or screen hybrids developed in other regions to suit specific local conditions.

Adaptive research on hybrid rice is conducted in provincial and lower level research institutes in each rice-producing province. With any given yield advantage, the marginal returns to the innovation of a new rice variety are a positive function of the size of the rice-producing area and the price of rice. Therefore, the larger the rice area or the higher the rice price in a region, the more resources research institutes in that region will allocate to rice research, including research for F_1 hybrids. Consequently, the larger the rice area or the higher the rice price in a region, the more F_1 hybrid varieties will be available in that region. Since the availability of adaptable F_1 hybrids is a positive function of the size of rice area and the price of rice in a region, the adoption rate of F_1 hybrids will also be a positive function of the size of rice area and the price of rice in that region.

In a centrally planned economy such as China's, prices are regulated by the state. Regional rice price variation, if it exists at all, is negligible. Therefore, rice price cannot become a factor in determining regional discrepancies in the availability and adoption rate of hybrids. However, there are significant regional variations in rice-producing area. The resources devoted to hybrid rice research, the availability of hybrid varieties, and the adoption of hybrid rice in a region will thus depend on the rice-producing area in that region.

Because the allocation of manpower and expenditure to both hybrid and conventional rice research in a provincial academy depends on the rice-producing area in that province, a positive significant relation exists between the number of new varieties of hybrid rice and conventional rice developed by a provincial academy and the area devoted to rice in that province.

The proportion of rice area to total cultivated area in a province is also an important determinant of profitable hybrid seed production. The higher the proportion of rice area, the lower the marketing costs for seed companies, and therefore, the higher the availability of hybrids.

The profitability of hybrid rice production is higher in provinces with a larger rice area. This is due to the greater availability of hybrid rice varieties and lower seed costs. The returns to farmers' time and other investments for adopting hybrid rice are higher.

Economics of hybrid seed production

As farmers could not use their harvest as seed for the next crop, a complicated seed production and distribution system was necessary for large-scale dissemination of hybrid rice. A sophisticated three-tier seed system—province, prefecture, and county—was set up in major rice-growing provinces. In general, a provincial seed company was responsible for the purification and rejuvenation of male sterile seeds and the distribution of seeds to the prefectural seed companies. The prefectural seed companies were responsible for the multiplication of male sterile seeds. They distributed the male sterile seed and provided technical guidance to registered male sterile seed producers, and then bought seed back from the producers, checked its quality, and resold it to county seed companies in their respective prefectures. The county seed companies in turn arranged the multiplication, quality control, and sale of F_1 hybrid seeds to farmers, in a way similar to a prefectural company. In addition, a four-level research-extension network—county, commune, brigade, and production team—provided a mechanism for rapid evaluation and selection of adopted seed and diffusion of information about hybrids.

An economic evaluation of hybrid seed production is provided by He et al (1987) for Jiangsu Province. Detailed information was collected from 180 farms and 29 commercial seed producers in Jiangsu Province in 1984. Typical seed yields were 1.4 t/ha for male sterile A lines and 1.7 t/ha for F_1 hybrids (Table 3). Labor input for A line

Table 3.Yield of male sterile A line seed multiplication and F_1 hybrid seed production trials. Jiangsu, China (He et al 1987).

	Seed produced (t/ha)	
A line multiplication	A line	B line
Av yield	1.4	1.2
Minimum value	0.9	0.6
Maximum value	2.0	1.5
F_1 hybrid seed	F_1 seed	R line
Av yield	1.7	1.8
Minimum value	1.4	0.4
Maximum value	2.3	2.9

multiplication was nearly 400 d/ha, more than 100 d higher than for hybrid rice production. Total N (organic and inorganic) applied exceeded 250 kg N/ha. At 1984 prices, the net return from A line multiplication averaged $1,264/ha, more than 60% higher than that for hybrid rice production. For F_1 seed production, labor input was around 75 d/ha more than that for hybrid rice production, and net returns averaged $1,765/ha. Other inputs and operations were similar to A line production.

In considering the economics of hybrid seed production, further attention ought to be given to labor and land requirements. The largest labor inputs are for transplanting, special activities, harvesting, and threshing. Male parents are often transplanted two or three times to ensure that the flowering of the male and female parents is synchronized. Special activities are undertaken to ensure a good seed set. In addition to spraying gibberellic acid (GA_3, a growth stimulant), most farmers clip flag leaves, which increases panicle exposure to pollen, and drag a rope across the field to mechanically encourage pollen transfer. This is usually done five or six times a day during flowering of the female parent (He et al 1987). The quality of labor and supervision are as important as the quantity of labor in hybrid seed production. Seed producers must have a good grasp of seed production techniques and must take great care to retain the purity of the A lines and the hybrid seed.

Implications for tropical Asia

The demand for yield improvements associated with hybrid rice technology would generally come from the irrigated lowlands rather than from rainfed lowland and upland rice environments. In China, hybrid rice is grown exclusively in irrigated areas, where the switch from conventional high-yielding varieties to hybrid rice, from a farmer’s point of view, involves a change in variety only. Meanwhile, a change from current practice to hybrid rice in the uplands and rainfed lowlands would involve changes in variety, input use, and cultivation practices. In other words, in the latter cases, it involves an entire switch in the farming system. For example, it is unlikely that a rainfed lowland farmer cultivating a traditional rice crop with almost no purchased inputs would find high-input hybrid rice production profitable.

In the irrigated lowlands, yield improvements associated with hybrid rice would be demanded only after yield gains associated with conventional high-yielding varieties have been exhausted. On the technology supply side, the probability of success in breeding hybrids for the irrigated environments is substantially higher than for the less favorable rice environments.

The proportion of irrigated riceland in a country is therefore an important determinant of the potential of hybrid rice. The potential for hybrid rice may be higher in countries with a high proportion of irrigated rice, such as India and Indonesia, relative to countries with lower proportions of irrigated area, such as Bangladesh and Myanmar.

The relative profitability of hybrid rice over conventional rice is determined by the ratio of rice price to hybrid seed price. Given the high labor requirements in seed production, one can anticipate that seed prices will be relatively lower in lower wage countries. Since agricultural wages are determined by labor-land ratio, among other factors, the relative profitability of hybrid rice production is directly related to the labor-land ratio.

Potential demand for hybrid rice technology can be identified by cross-classifying countries in terms of the proportion of irrigated area and labor-land ratio (Table 4). Countries with high labor-land ratio and high proportion of irrigated area are likely to have the highest potential demand for hybrid rice technology. In tropical Asia, these are India, Indonesia, Philippines, Sri Lanka, and Vietnam. Countries with a high proportion of irrigated area but low labor-land ratio would not find hybrid rice production profitable, since agricultural wages would be relatively higher in these countries. Malaysia and Pakistan are examples. Countries with a low proportion of irrigation infrastracture—e.g., Bangladesh, Nepal, Myanmar, and Thailand—would have low potential demand for hybrid rice technology, irrespective of wage rates. Under nonirrigated conditions, yield improvement and output growth can be achieved through means other than hybrid rice technology.

In evaluating the potential supply of hybrid rice technology, we need to assess the absolute magnitude of the irrigated rice area and labor endowments by country. The

Table 4. Classification of countries by labor-land ratio and irrigated ricelands.

Proportion of irrigated riceland	Labor-land ratio	
	Low	High
High	Malaysia Pakistan Sri Lanka Vietnam	Philippines Indonesia India
Low	Myanmar Thailand	Bangladesh Nepal

returns to investment in hybrid rice research and the development of hybrid seed industry depend on the absolute size of the irrigated rice area in the country. Of the total irrigated area in tropical Asia, 31% is in India and 13% is in Indonesia (Table 5). These two countries would potentially be the most important suppliers of hybrid rice technology. Given the size of the market, seed producers in these countries would benefit from substantial economies of scale. Scale economies would accrue in the provision of hybrid seed adapted to specific ecological regions, input supplies, especially GA_3, and technical skills.

The Chinese hybrid rice experience has shown that the yield potential of hybrid rice can only be achieved if each ecoregion develops its own hybrids or screens hybrids developed in other regions to meet specific local conditions. In countries such as India and Indonesia, it is economically feasible to set up a regional research and seed production infrastructure. Region-specific technical skills could be enhanced under such a system. Region-specific institutions would not be cost-effective in countries with smaller irrigated areas. In the Philippines, for example, a hybrid research and seed production system would not be economical for all the major ecoregions, with the possible exception of Central Luzon. In the case of input supplies, GA_3 is uniquely required for hybrid seed production; the unit costs of this input would decrease with an increase in the scale of production.

Countries with smaller rice areas, rather than set up their own hybrid rice research and seed infrastructure, could possibly benefit from spillovers from their neighbor's efforts. Sri Lanka, for instance, could benefit from technological spillovers from hybrid rice research conducted in southern India. Similarly, Malaysia could benefit from the efforts in West Java, Indonesia. The costs of developing region-specific hybrid rice technology for tropical Asia would be substantially lower if regional cooperation based on ecological similarities were fostered.

Before making a large-scale commitment to hybrid rice-related infrastructure, a detailed assessment of the land and labor requirements ought to be made. Table 6 provides an estimate of land and labor requirements for hybrid seed production for

Table 5. Distribution of irrigated rice area in South and Southeast Asia.

Country	Area ('000 ha)	% of all South and Southeast Asia
Bangladesh	1717	2.95
India	18082	31.15
Indonesia	7769	13.38
Malaysia	340	0.58
Myanmar	826	1.4
Nepal	302	0.5
Pakistan	2066	3.56
Philippines	1837	3.16
Sri Lanka	524	0.9
Thailand	2387	4.1
Vietnam	2539	4.4

Table 6. Net increase in land and labor requirements for hybrid seed production.

	Irrigated area (million ha)	Hybrid seed production	
		Land (million) ha	Labor (million mandays)
China (current)	10	0.15	15.0
India[a]	6	0.09	9.0
Indonesia[a]	2.7	0.04	4.0
Philippines[a]	0.67	0.009	1.0
Thailand[a]	0.67	0.009	1.0
Vietnam[a]	0.83	0.012	1.25

[a] Estimated on the assumption that one-third of the irrigated area is grown to hybrid rice.

selected Asian countries. In each case, estimates are based on the assumption that 30% of the irrigated area will be under hybrid rice. For instance, if 30% of the irrigated area in India were under hybrid rice, that would be 6 million ha. Seed production required for servicing this area would involve 90,000 ha of land and 9 million additional person-days. What are the opportunity costs of diverting these resources to hybrid rice production? In India's case, given the low wage rates and high price of rice, it may make sense to pursue this technology. In the case of Thailand, with high and increasing wage rates and the high opportunity cost of irrigated land for growing high-value crops for export, hybrid rice may not be the best option. Such questions have to be answered on a country by country basis before major investments on research and infrastructure are made.

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Authors' addresses: Justin Yifu Lin, Department of Rural Economic Development, Xihuangchenggen Nanjie No. 9, Beijing, China; and P. L. Pingali, Agricultural Economist/ Leader, Irrigated Rice Ecosystem Program, International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in China

L. P. Yuan, Z. Y. Yang, and J. B. Yang

Hybrid rice helped China to increase rice production by 200 million t from 1976 to 1991. It has been proved practically on a large scale that hybrid rice has a yield advantage of more than 30% over conventional pureline varieties. Current research in China indicates that the yield potential of hybrid rice can be increased by improving breeding methodology and increasing the degree of heterosis. Existing hybrid rice varieties used commercially in China are intervarietal hybrids produced by the cytoplasmic genetic male sterility (CMS) system. A series of elite CMS and restorer lines have been bred and show potential not only in quantity but also in quality. The CMS system is the most effective genetic tool in hybrid rice breeding. However, some constraints and problems remain to be solved. Chinese rice scientists have been exploring new technological approaches. Photoperiod-sensitive genic male sterile lines and thermosensitive genic male sterile lines have been developed successfully. Exploiting these lines to develop two-line hybrids has many advantages over the classical three line hybrids. Several improved intervarietal and intersubspecific hybrids produced by the two-line system have been under regional and farmer's field trials since 1989. The results are promising. Some of them outyielded the best existing hybrids by 10-30%. A one-line method to develop true-breeding rice hybrids through apomixis is also under investigation in China. Hybrid seed production practices in China are well-developed and give average seed yields of 2.3 t/ha. The field area ratio between A line multiplication, hybrid seed production, and F_1 commercial cultivation is 1:50:5000. However, seed yield, and therefore profitability of seed companies, is greatly influenced by the weather conditions during flowering time. Government intervention likewise plays an important role. Prospects for hybrid rice in China are considered to be bright, and the development of hybrid rices with higher degree of heterosis using new methodology is of strategic significance in rice production.

Table 1. Yield of hybrid rice compared with that of conventional rice. 1981-90, China.

Year	Yield		
	Conventional (t/ha)	Hybrid (t/ha)	Hybrid over conventional (%)
1981	4.1	5.3	29.3
1982	4.5	5.9	31.9
1983	4.8	6.4	33.5
1984	5.0	6.4	28.8
1985	4.8	6.5	34.4
1986	4.9	6.6	35.9
1987	4.8	6.6	38.4
1988	4.5	6.6	45.4
1989	4.5	6.6	45.9
1990	4.6	6.6	41.4

Research on hybrid rice in China began in 1964 (Yuan 1966, Lin and Yuan 1980). The genetic tools essential for producing F_1 hybrids, cytoplasmic male sterile (CMS), maintainer, and restorer lines, were developed in 1973, and hybrid seed production techniques were basically established in 1975. In 1976, hybrid rice was released commercially and was planted on 140,000 ha. Since then, the area planted to hybrid rice has increased each year. The area under hybrid rice increased to 17.6 million ha in 1991, 55% of China's rice area, and contributed 66% of total rice production (Fig. 1).

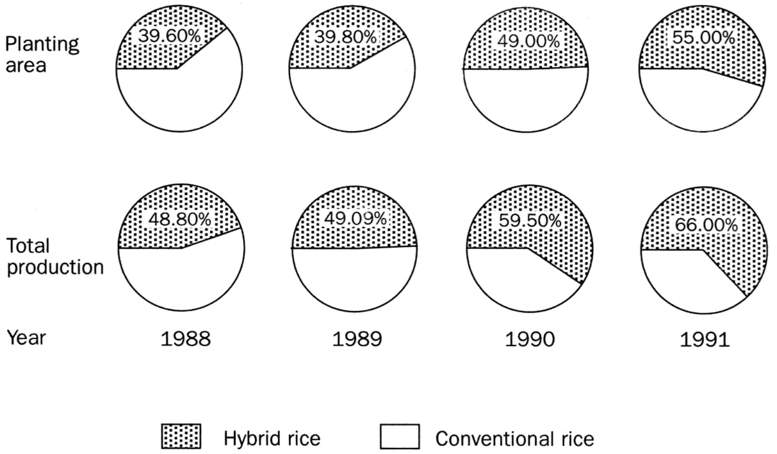
Hybrid rice varieties used commercially in China are intervarietal hybrids produced by the CMS system. This kind of hybrid has helped China to increase rice production by nearly 200 million t. Hybrid rice has been shown to yield 30% more than conventional pureline varieties (Table 1).

This paper summarizes the status of hybrid rice breeding, seed production techniques, and commercial production in China and discusses prospects and problems.

Development of hybrid rice in China

Hybrid rice development in China occurred in four phases.

- 1975-79—experiment, demonstration, and extension phase. Hybrid rice varieties, such as Er-Jiu-Nan A/IR24, Zhen Shan 97 A/IR24, and V41 A/IR24 were developed and released. These hybrids outyielded conventional pureline varieties by 20%. In 1979, the area planted to hybrid rice was 4.97 million ha, with an average yield of 4.7 t/ha.
- 1980-81—adjustment phase. The area under hybrid rice was stagnating at around 4.8 million ha and yield increased slowly to around 5.3 t/ha. The old hybrid varieties could not be extended further because of their susceptibility to diseases and insects. However, some promising hybrid varieties with multiple resistance were developed during this period.



1. Percentages of planting area and total production of hybrid rice compared with conventional rice for 1988-91.

- 1982-85—continuous development phase. In 1984, the area of hybrid rice increased to 8.85 million ha and yielded 5.9-6.5 t/ha. Zhen Shan 97 A/Min-Hui 63 and V20 A/Ce 64 were the two most popular hybrids, with a cultivated area of nearly 10 million ha each year.
- 1986-present—rapid and steady development phase. The area under hybrid rice doubled to 17.6 million ha by 1991. A series of new hybrids, including early-maturing ones, have been developed. They show advantages not only in maturity but also in yield and pest resistance.

The maximum recorded yield from a single crop of a japonica hybrid variety was 15.7 t/ha in AKSU, Xinjiang Province, for 10120 A/Hoi 73-28. The record yield of indica hybrid Zhen Shan 97 A/Min-Hui 63 in Yunnan Province was 15.3 tiha. In Sichuan Province, where hybrid rice was cultivated on 2.83 million ha, average yield was 7.2 t/ha in 1991. There were a further 0.36 million ha of ratooning rice, so the average yield was 8.8 t/ha including the ratoon crop.

Ratooning hybrid rice has been used widely in cooler areas recently. In Fujian Province, the farmers usually produce 2.0-2.5 t/ha on their ratoon crop. In 1991, the farmers in Youxi County planted Zhen Shan 97 A/Min-Hui 63 and averaged 9.8 t/ha on the first crop and 6.2 t/ha on the ratoon crop. The highest recorded first crop was 11.5 t/ha; for the ratoon crop, it was 8.0 t/ha (135 ha). A great deal of work has been done on ratooning hybrid rice and the area will spread quickly (Si 1991).

Hybrid seed production

Hybrid seed production based on the three-line method involves two steps—multiplication of CMS lines in A/B seed production plots and production of F_1 hybrid seed in A/R plots. The current field area ratio between A line multiplication, F_1 hybrid seed production, and F_1 commercial cultivation is 1:50:5000. The hybrid seed production system has been well-established. The high seed yield obtained in 1990 enabled China to grow 17.6 million ha of hybrid rice during 1991, with extra hybrid seed for use in 1992. Floods in 1991 reduced the total seed production area to 134,000 ha, which produced 310,000 t of hybrid seed, averaging 2.3 t/ha. Recent yields of CMS line multiplication are around 1.9 t/ha. The yield of a CMS line with high outcrossing potential, You 1 A, has increased to 5.4 t/ha in Dayong, Hunan Province (Qin and He 1992). As for large-scale hybrid seed production, a total of 43 ha in Zhinxin City, Hunan Province, averaged 4.2 t/ha in 1991. The highest yield ever reported was 6.3 t/ha (He and Chao 1992).

Enhancing hybrid seed production has two important aspects. The first is the development of CMS lines with higher outcrossing potential, such as Luon Tepu A and You 1 A. Seed yield using these CMS lines is commonly 3-4 t/a. The second is the improvement of seed production techniques, which include:

- — shortening the flag leaves of parents instead of leaf cutting.
- — increasing gibberellic acid (GA_3) dosage (to around 100 g/ha) to promote panicle exsertion and stigma elongation. (Some biochemical products, such as Tiaohualin, were found to be more effective than GA_3.)
- — widening row ratio between A and R lines.
- — intensifying supplementary pollination at the appropriate time.

Constraints and prospects

In spite of the great success in developing hybrid rice through the three-line method in China, some constraints and problems remain to be solved.

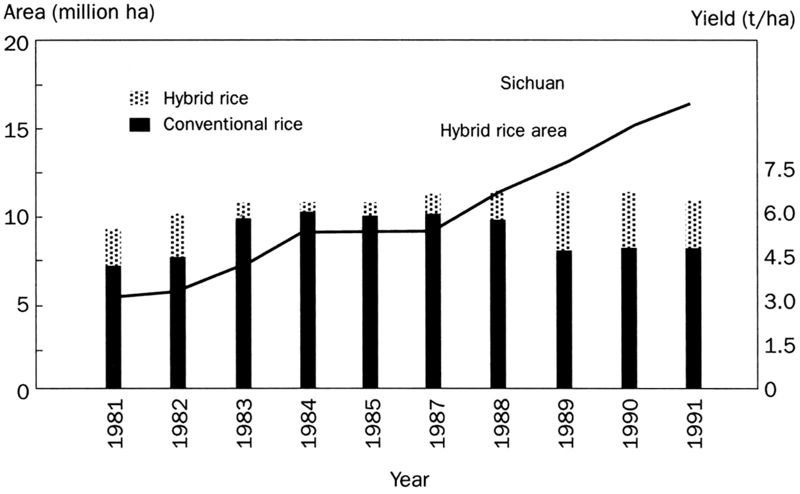
The yield of existing hybrid rice varieties, including newly developed ones, has stagnated for several years (Fig. 2). They have already reached their yield plateau and it appears that further increases in yield potential are unlikely without new methods and materials.

The sources of male sterility-inducing cytoplasm that can be used for developing better CMS rice lines are poor. Currently, about 93% of the A lines used in commercial production still belong to the WA type. This situation could be disastrous in the long run if the hybrids were vulnerable to a destructive pest.

The heterosis level in japonica hybrids is not as good as that in indica hybrids. In addition, the sterility of current japonica CMS lines (BT type) is not stable enough to produce very pure F_1 seeds. Therefore, the planting area of japonica hybrids has remained at around 0.2 million ha for many years, and, what is worse, is now declining.

The grain quality of existing hybrids is medium. This will become unacceptable as the living standard in China improves.

To break through the constraints, new technological approaches are being explored. The most successful one so far is the development of hybrids using the two-line method. This method is based on two new kinds of genetic tools, photoperiod-sensitive genic male sterile and thermosensitive genic male sterile lines. Exploitation of these MS lines has many advantages over the classical three-line method. A number of better



2. Area and yield of hybrid rice in China, 1981-91.

intervarietal and intersubspecific F_1 hybrids have been produced through the two-line system, and regional and farmer's field trials have been made. The results are promising; some combinations outyielded the check hybrids by 5-20%. It is expected that two-line hybrid varieties will be released for commercial production soon (Yuan 1990).

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Authors' addresses: L. P. Yuan, Hunan Hybrid Rice Research Center, Changsha, Hunan, China; Z. Y. Yang, Liaoning Academy of Agricultural Sciences, Shenyang, China; and J. B. Yang, Fujian Academy of Agricultural Sciences, Fuzhou, Fujian, China.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in Japan

H. Kato, K. Maruyama, and H. Uchiyamada

Hybrid rice has been studied in Japan since the 1950s. Cytoplasmic male sterility (CMS) from *Oryza sativa spontanea* and an indica variety, Chinsurah Boro II, was transferred to a few japonica varieties, which mainly acted as maintainers. Based on such materials, the Ministry of Agriculture, Forestry, and Fisheries (MAFF) backcrossed these japonica varieties with several other japonica varieties to introduce CMS on a small scale. The MAFF started its hybrid rice breeding program in 1983. There are five rice hybrids bred by the MAFF and they are now being tested. Zen-Noh, the National Federation of Agricultural Cooperative Association, and several private companies are also developing hybrid rice and some of them are being tested in production trials. The RAMM Hybrid International Cooperation is testing the adaptability of several hybrid lines which have been developed in cooperation with China. Hybrid rice breeding in Japan aims to achieve a higher and more stable level of heterosis (by producing indica/japonica hybrids, and japonica/japonica hybrids), breed hybrids that satisfy Japanese grain and cooking quality requirements (by including indica and japonica varieties with the required characteristics as genetic resources of parents and utilizing glutinous and dull genes), and to increase and facilitate hybrid seed production (by using thermosensitive genic male sterility [TGMS)) instead of CMS, male-sterilizing chemicals, artificial seeds, apomixis, and mixed planting of parents). Of these, breeding of good-quality hybrids is the most difficult to achieve in Japan.

History of hybrid rice breeding in Japan

Hybrid rice has been studied in Japan since the 1950s. Katsuo and Mizushima (1958) discovered cytoplasmic male sterility (CMS) in *Oryza sativa spontanea* and two japonica varieties. They studied the seed set percentage of hybrids between the two japonica varieties, Fujisaka No. 5 and Kamenoo, and a wild strain of *spontanea.* When the japonicas were used as females, the hybrids did not show sterility, but when the *spontanea* was used as a female, the hybrids were sterile. They concluded that the *spontanea* used in their experiment had a male sterile cytoplasm against japonica nucleus.

Shinjyo and Omura (1966) and Shinjyo (1969) reported that the indica Chinsurah Boro II possessed a sterile cytoplasm and a fertility-restoring system, while the japonica Taichung 65 acted as a maintainer. Based on such materials, Zen-Noh and the Ministry of Agriculture, Forestry, and Fisheries (MAFF) started backcrossing Taichung 65 with several japonica varieties to introduce CMS on a small scale. Basic studies on CMS itself were also done by the MAFF. Kadowaki et al (1988) reported that restriction fragment length polymorphism was observed among the mtDNAs in CMS lines.

Current situation of hybrid rice breeding in Japan

The MAFF started its hybrid rice breeding program in 1983. Five rice lines bred by the MAFF are now under testing. In Table 1, three of them are shown in comparison with Akihikari, which is one of the leading high-yielding varieties in Japan. The three hybrids show 15-20% heterosis. Kanto cross 1 was bred by the National Agriculture Research Center. The female parent is CMS Nekken 2, which has a wide compatibility gene between indica and japonica. The male parent is a line derived by crossing a japonica and a Korean indica. Both parental lines have the same heading date and only the male parent has phenol reaction, so it is possible to cultivate them in a mixed form and separate hybrid seeds from pollen parent seeds using a photoelectric separation machine. Ouu cross 1 is a hybrid obtained by crossing an indica variety directly with a japonica. Its female parent is a Chinese indica, Xinqingai 1. Its heterosis is the highest among the three, but its taste is least suited to Japanese demand because it is not sticky. Shu cross 4781 is a hybrid obtained by crossing a japonica and a line derived from an indica and a japonica. Unfortunately, the taste of all these three hybrids does not reach the minimum Japanese standard because of their low cooking quality.

Zen-Noh has been developing hybrid rice since 1983. They are breeding hybrid parents and testing yields of 40-50 hybrids every year. The performance of their hybrids is shown in Table 2. These hybrids are basically japonica/japonica crosses. The heterosis level of released hybrids is roughly 5-15%. Grain quality is better than hybrids bred by the MAFF but is still below the level of standard inbred lines. Their

Table 1. Agronomic traits of hybrids [a] bred by the MAFF.

Hybrid	Heading date	Culm length (cm)	Panicles/ plant (no.)	Biomass (t/ha)	Grain weight [b] (t/ha)	Relative grain weight	Grain quality[c]
Kanto Cross 1	9 Aug	94.5	16.5	15.67	6.20	116	7
Ouu Cross 1	9 Aug	101.0	17.0	15.54	6.35	119	7
Shu Cross 4781	3 Aug	83.0	17.0	14.42	6.19	116	7
Akihikari (Check)	3 Aug	88.5	18.5	13.13	5.34	100	4

[a] Transplanted 6 Jun 1991. N,P_2O_5, K_20:0.056 t/ha each. [b] Brown rice. [c] 1 = highest, 9 = lowest.

Table 2. Agronomic traits of released hybrids[a] bred by Zen-noh in 1988 and 1989 (Shinjyo et al 1990).

	Headomg date	Culm length (cm)	Panicles/m^2 (no.)	Biomass (t/ha)	Grain weight[b] (t/ha)	Relative grain weight	Grain quality[c]
Wakahonohikari	19 Aug	76.0	270	10.74	4.42	106	4.6
Wakahonomegumi	14 Aug	85.0	246	11.30	4.80	114	6
Wakahonominori	15 Aug	80.0	245	10.80	4.65	111	6
Todorokiwase (check)	16 Aug	83.0	284	10.40	4.26	100	4

[a] Transplanted on 19 May 1988, N,P_2O_5,$K_2$0:0.05 t/ha. Transplanted on 16 May 1989, N,P_2O_5,$K_2$0:0.09 t/ha. [b] Brown rice. [c] 1=highest, 9=lowest.

Table 3. Agronomic traits of the highest yielding hybrids[a] under testing from 1988 to 1991 by Zen-Noh.

Year	Line	No. of days from sowing to maturity	Culm length (cm)	Grain weight[b] (t/ha)	Relative grain weight	Grain quality[c]
1988	F_1	131	85	5.75	116	6
	Japonica inbred	138	81	4.95	100	3
1989	F_1	160	75	5.22	133	7
	Japonica inbred	143	68	3.92	100	4
1990	F_1	137	87	5.93	125	5
	Japonica inbred	127	82	4.73	100	3
1991	F_1	118	90	6.27	129	4
	Japonica inbred	134	82	4.87	100	4

[a] F_1 hybrids are different from year to year. Sowing dates are 19 May in 1988, 16 May in 1989, 15 May in 1990, and 13 May in 1991. Fertilizer levels are N,P_2O_5,$K_2$0:0.05 t/ha each in 1988, 0.09 t/ha in 1989, 0.072 t/ha in 1990, and 0.092 t/ha in 1991. [b]Brown rice. [c]1=highest. 9=lowest.

hybrids under testing show more than 30% heterosis and almost the same level of grain and cooking quality as standard inbred lines (Table 3).

RAMM Hybrid International Cooperation started a hybrid rice program in 1986. They are testing the adaptability of several hybrid lines in farmers' fields. Their hybrids are developed in cooperation with China. Heterosis is about 20% compared with standard inbred varieties, and eating quality is about the same as the standard level (Dr. T. Fujimura, Plant Biotechnology Department, Mitsui Toatsu Chem. Inc., Apr 1992, pers. commun.). These three research groups are breeding hybrid rice using conventional breeding technology.

Kirin Brewer Co., Ltd. is also working on hybrid rice. They are trying to make artificial seeds and tissue-cultured seedlings. They have also produced seed-sorting machines which separate seeds by their own color or phenol-reacted black. They can separate hybrid seeds from pollen parent seeds which are harvested together in mixed planting hybrid seed production fields (Suzuki et al 1990). A private company, Sumitomo Chemical Co., is conducting experiments on plant growth regulators (Nishikawa et al 1990) and gametocides for hybrid rice seed production. They are also conducting mutation breeding by ethyl methanesulfonate and anther culture for the breeding of hybrid parents (Nishikawa et al 1989).

Aims and strategies of hybrid rice breeding in Japan

The aims of hybrid rice breeding in Japan are to achieve a more stable and higher level of heterosis, to breed hybrids with the grain and cooking quality preferred by Japanese consumers, and to increase and ease hybrid seed production.

To achieve a more stable and higher level of heterosis, two strategies are being followed. One is through producing japonica/japonica hybrids. Zen-Noh is mainly following this strategy. Getting good grain quality is comparatively easy. The other one is through producing japonica/indica hybrids. The MAFF is mainly following this strategy. We can anticipate higher heterosis, but there are some problems arising from this (Table 4). Hybrid sterility is a big problem. Most of the japonica/indica hybrids show some hybrid sterility. In some cases, seed fertility is lower than 10%. To overcome this problem, the MAFF is using *S-5*^{n}, which was found in javanica by Ikehashi and Araki (1985), and introduced to japonica and indica. By introducing it to one of the parents, the fertility of the hybrid becomes normal. Taller plant height is another problem because it increases the risk of lodging. To deal with this, the MAFF

Table 4. Problems in japonica-indica hybrids and their solution by respective breeding strategy.

Problem	Solution by breeding strategy
Hybrid sterility	Use of wide compatibility gene (S-5^{n})
Excessive elongation of plant height	Use of *sd-1* gene (both parents)
Late maturity	Use of nonphotosensitive line
Sensitivity to cool temperature	Elimination of cool temperature-sensitive line
Shattering	Elimination of dominant severe shattering gene
Pest and disease resistance	Use of dominant resistance gene
Grain quality	Improvement of indica lines
Cooking quality	Use of *Wxb* or dull gene (both parents)

is introducing a stronger semidwarfing gene of Korean indicas, *sdw-1,* to both parental lines. Longer growth duration is another problem associated with dominant complementary photosensitivity (Araki 1988). We are selecting parental lines which are early-heading and nonphotosensitive to avoid this problem.

Breeding for desirable grain and cooking quality in hybrids is as important as improving yield. High amylose content is not favored in Japan. However, high amylose is a dominant character, and 3/4 of the grains are high in amylose content (Ish Kumar and Khush 1988). This type of rice was graded extremely low in cooking quality evaluations conducted in Japan. Indica and japonica varieties with good taste and low amylose content should be used for parental lines. Utilizing glutinous or dull genes may help lower the amylose content in hybrids.

To increase and ease hybrid seed production, we are using a thermosensitive genic male sterile (TGMS) line, PL12 (H89-1) (Maruyama et al 1991), which was induced by irradiation. It becomes male sterile under high temperature, above 30 °C, and becomes fertile below 26°C. High temperature for 1 h/d is enough to reduce the seed set ratio. The thermosensitive stage becomes clear about 3 wk before heading. This TGMS is controlled by a single recessive gene and will be useful in hybrid seed production. There are several advantages of TGMS over CMS in hybrid breeding and seed production. Multiplication of TGMS seeds is easier; there is no need to establish a CMS line by backcrossing, thus recurrent backcrossing is not necessary; and breeding can be done irrespective of restorer genes. Cytoplasmic male sterile of gametophytic types like BT (cytoplasm originated from Chinsurah Boro II) reduces the pollen number to half and promotes cold damage (Sato et al 1990). Theoretically, hybrids produced by TGMS under recessive genetic control may not be sensitive to cold weather.

Mixed planting of parents for higher hybrid seed yields and the accompanying selection system of mixed hybrid seeds are also being studied. In China, hybrid seeds are obtained by planting male sterile and pollen parent lines in alternate rows. However, by mixed planting of parents, we can ensure a higher seed set ratio on the male sterile lines (Maruyama et al 1991). This is because the pollen parents and the male sterile plants are closer. All the seeds are harvested together. Separation of the hybrid seeds from the pollen parent seeds can be made if they are different in terms of color, phenol-reacted black color, size, or other traits. Furthermore, if the pollen parents are female sterile or herbicide-sensitive, unmixed hybrid seeds alone can be obtained. To utilize this advantage, herbicide sensitivity to bentazon (3-(1-methyethyl)-(1H)-2,1,3-benzothiodiazin-4-(3H)-one-2,2-dioxide) (Mori 1984) has been introduced into our breeding lines to destroy pollen parents before self-seeding.

Breeding lines for parents of hybrids obtained by MAFF

Table 5 shows a number of lines bred for hybrid parents to solve the above mentioned problems. Indica/japonica, indica/japonica//indica and indica/indica combinations are for male parents in the CMS system because these lines have the *Rf* gene. We are shifting from indica/japonica to indica/japonica//indica combinations because we expect much higher heterosis in the latter. Japonica/japonica combinations are for female parents.

Table 5. Number of lines for hybrid parents which have *sd-1,* nonshattering and nonphotosensitive genes. National Agriculture Research Center, MAFF, 1991.

Combination from which lines are derived	Lines with *S-5*^{n} wide compatible gene	Lines with *S-5*^{n} or *S-5*^{j}
Indica/japonica	Most have *Rf* gene Include waxy lines	Most of them have *Rf* gene Include waxy lines and Bentazon-sensitive lines
Indica/japonica//indica	Most have *Rf* gene Include waxy lines, Bentazon-sensitive lines and good tasting lines	Most of them have *Rf* gene Include waxy lines, Bentazon-sensitive lines and big grain lines
Indica/indica		Most advanced lines:F$_5$ Most of them have *Rf* gene Include waxy and good tasting lines
Japonica/japonica	Include waxy lines, Bentazon-sensitive lines, big grain lines and good tasting lines	Including waxy lines

Table 6. Number of TGMS lines for hybrid parents which have *sd-1,* nonshattering and nonphotosensitive genes. National Agriculture Research Center, MAFF, 1991.

Combination from which lines are derived	Lines with *S-5*^{n} wide compatible gene	Lines with *S-5*^{n} or *S-5*^{j}
Indica/japonica		Most advanced lines:F$_6$ Include waxy lines
Indica/japonica//Indica		Most advanced lines:F$_5$ Include waxy lines
Japonica/japonica	Most advanced lines: F$_4$ Include waxy lines and good tasting lines	Most advanced lines:F$_4$ Include waxy lines and Bentazon-sensitive lines

Some are being introduced to CMS. Most of the four types of combinations have nonphotosensitive character and *sd-1* semidwarfing gene. Some of them are good tasting, waxy, dull, and possess selectability when mixed with pollen parents. We are making hybrids using parents with synchronized flowering times because it is required for mixed planting seed production and mechanized operation. Table 6 shows the number of TGMS lines for hybrid parents. They are fewer than the non-TGMS lines (Table 5) because the breeding program started later. Recently we have added photoperiod-sensitive genic male sterile lines (Kobayashi et al 1992) to our breeding programs.

Cooking and eating quality of hybrids is the greatest problem in Japan at present. The reason is that indica/japonica hybrids which offer distant combinations are necessary to obtain high heterosis. However, the grain and cooking qualities of such hybrids are usually not acceptable.

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Notes

Authors' addresses: H. Kato and K. Maruyama, National Agriculture Research Center, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki 305, Japan; and H. Uchiyamada, Zen-noh Agricultural Technical Center, Hiratsuka, Kanagawa 254, Japan.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in India

E. A. Siddiq, P. J. Jachuck, M. Mahadevappa, F. U. Zaman, Vijaya Kumar, B. Vidyachandra, G. S. Sidhu, Ish Kumar, M. N. Prasad, M. Rangaswamy, M. P. Pandey, D. V. S. Panwar, and Ilyas Ahmed

Hybrid rice research in India was slow until a national research network involving 12 research centers was established in 1991. Accelerated research under the network has enabled the development and multilocation evaluation of more than 200 experimental hybrids. Promising hybrids yielding over 1 t/ha more than the highest-yielding check variety have been identified for extensive testing and on-farm verification. An improved package of practices for hybrid/cytoplasmic male sterile (CMS) seed production yields more than 1.5 t/ha. Yield performance of hybrids and seed production packages are highly location- and season-specific. Impressive progress has been made on various aspects of basic research, notably on diversification of CMS, gametocide-based two-line breeding, and conservation of F_1 yield through dihaploid breeding.

Self-sufficiency and reasonable stability in rice production in India since the early 1980s were made possible by the development and widespread cultivation of plant type-based, high-yielding varieties. To sustain the same level of self-sufficiency, the country will have to increase yield by 3 million t each year. This is a challenging task, as the area under rice cannot be expanded. Plateauing of yields in areas of assured irrigation and our failure to make any significant improvement in yield levels of dwarf varieties during the last two and a half decades make the task ahead much more difficult. Maximizing yield in low productivity areas and exploring ways to raise the genetic yield ceiling in areas where average farm yields are approaching potential yield are considered to be rational strategies for achieving the production goals. Among various approaches for raising the yield ceiling further, exploitation of hybrid vigor is widely acknowledged as having the most potential.

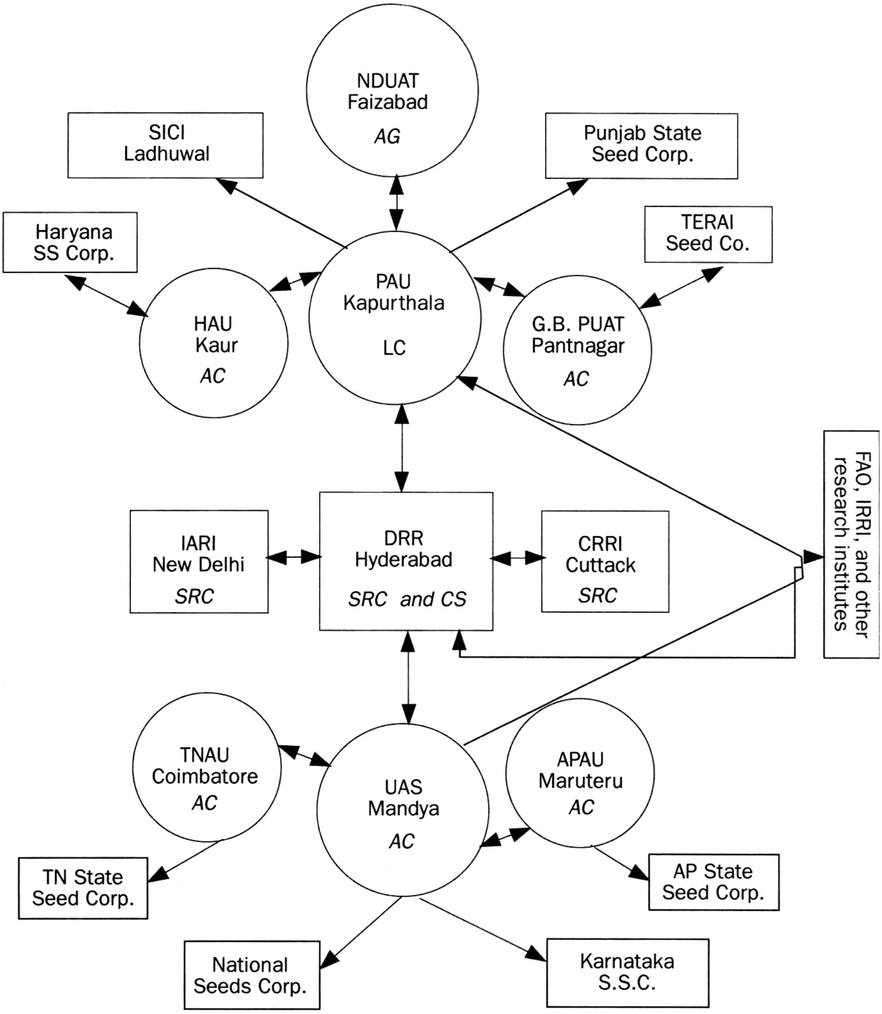
Chinese scientists developed and demonstrated the commercial feasibility of hybrid rices almost 15 yr ago. However, no country outside China was able to take advantage of this new technology until recently. The Chinese materials proved unsuitable for direct exploitation, and skepticism about the economic viability of seed production delayed research into hybrid technology. Impressive progress made at the International Rice Research Institute (IRRI) and elsewhere in breeding parental lines suited to typical tropical ecologies and in optimizing seed production techniques have motivated India to revive its interest in hybrid rice technology. Convinced of its potential, the Indian Council of Agricultural Research (ICAR) identified hybrid breeding as a priority area for future research. This led to the formulation and implementation of the ICAR-United Nation Development Programme-sponsored research network on development and use of hybrid rice technology in September 1991. The network, coordinated by the Directorate of Rice Research (DRR), comprises 2 lead, 7 associate, and 3 strategic research centers and national/state seed production agencies located in the respective regions (Fig. 1). The cooperative research effort broadly aims to i) evolve superior hybrids for irrigated ecologies, ii) optimize seed production techniques, iii) develop productive packages for hybrid cultivation, iv) develop lines for hybrids for rainfed lowlands and export purposes, and v) undertake basic research on all aspects of hybrid breeding. A little over 2 million ha spread over the irrigated areas of all southern states except Kerala, and the northwestern states, constitutes the initial target environment for exploiting hybrid vigor (Fig. 2).

The major accomplishments made during the last few years in applied and basic aspects of research by the network are discussed in this report.

Evolution and evaluation of hybrids

Systematic evaluation of hybrids began in 1989, with 18 test entries. The number rose to 126 over the next 2 yr, with a steep increase in the proportion of nominations from the national program. Yield performance of most of the experimental hybrids averaged over test locations was not significantly superior to the highest yielding check varieties of the region. However, entries with standard heterosis above 15% yielding over 1 t/ha more than the checks were not uncommon in the national as well as state level trials (Table 1). Hardly any hybrids performed comparably well at more than one location. This location-specific performance appears to depend on the type of parental lines involved. In general, hybrids involving cytoplasmic male sterile (CMS) lines IR62829 A and IR58025 A were found promising in southern parts, while those involving Punjab male sterile lines like PMS3 A, PMS5 A, and PMS10 A were better in the north. No combination involving either V20 A or ZS97 A performed well. Promising restorers also varied with the region—IR10198-66-2 R, R29723-143, ARC11353, and IR9761-19 proved productive in the south; PAU1106-6-2 and PAU1126-15-3, in the north. Cluster analysis of restorers with location-specific marker restorers would help identify appropriate pollinator parents for these and other regions.

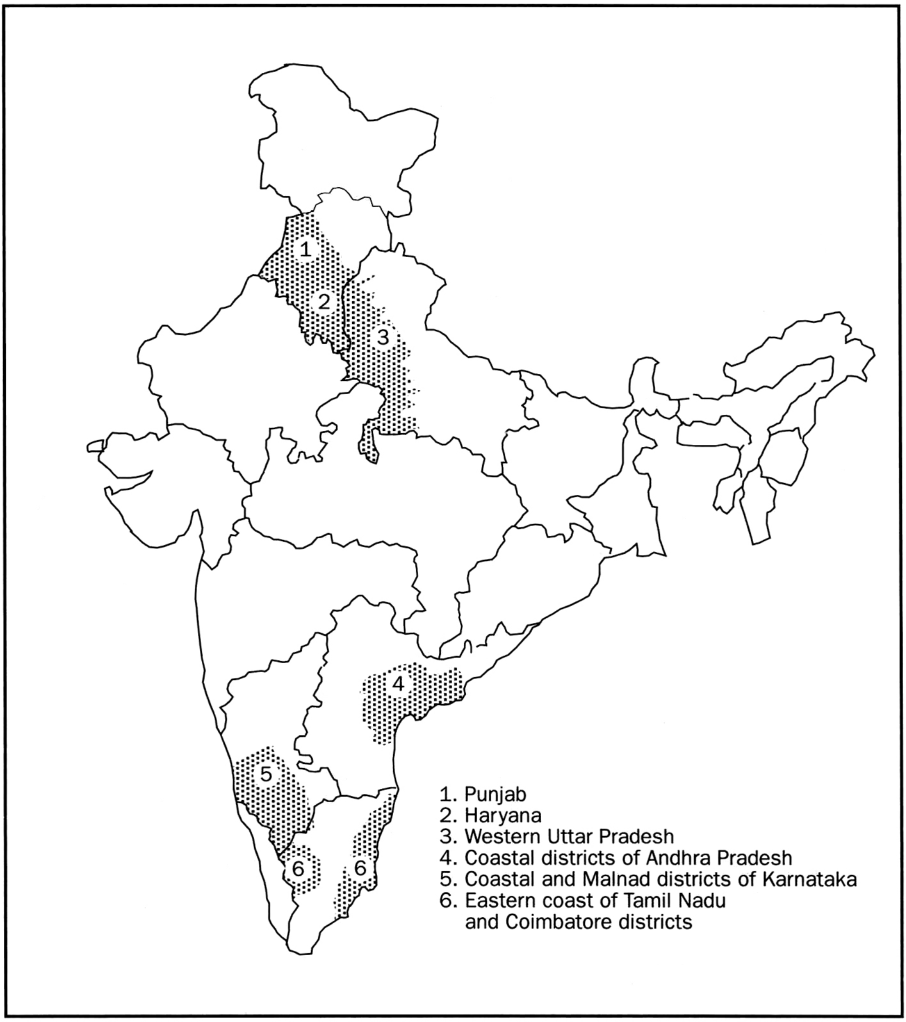
While the performance of all promising hybrids must be confirmed for consistency, the best performing hybrids have been chosen for simultaneous large-scale, on-farm verification in the respective regions during 1992 wet season (WS).



1. Schematic representation of the organization setup of the ICAR-UNDP Project on Development of Hybrid Rice Technology in India. LC = lead center, AC = associate center, SRC = strategic research center, CS = coordinating center.

Identification of potential male sterile and pollinator lines

Research has emphasized evolving male sterile lines that are agronomically superior and better adapted to local agroclimatic conditions than the Chinese lines. More than 30 improved CMS lines evolved through conversion at IRRI and in India have been evaluated for their relative stability for male sterility over locations/seasons, outcrossing potential, and combining ability. A few IRRI lines, such as IR46829 A, IR46830 A, IR54755 A, IR54758 A, IR58025 A, and IR62829 A were consistently stable with close to 100% pollen sterility at most test locations. The rest either segregated for male



2. Target areas for proposed cultivation of hybrid rice.

sterility or percentage sterility was inconsistent (Table 2). Among the lines developed in India and being used in hybrid development, Punjab male sterile lines PMS2 A, PMS3 A, PMS4 A, PMS7 A, and PMS10 A were as stable as V20 A at all locations. There is still scope for improving their stability through purification and proper maintenance. Other CMS lines of both wild abortive (WA) and indigenous sources have been developed (Table 3). Intensive study of these lines is now under way and may help increase the list of potential CMS lines further. As for combining ability, those that gave several heterotic combinations—IR62829 A, IR58025 A, PMS3 A, PMS5 A, PMS8 A, and PMS10 A—are promising.

Table 1. Best performing hybrids in the 1989-91 trial.

Hybrid	Year/season	Days to 50% flowering	Yield (t/ha)		Yield increase (t/ha)[a]
			Hybrid	Check	
ANDHRA PRADESH					
Hyderabad					
IR62829 A/IR10198-66-5	91 DS	90	6.8	5.3 (Rasi)	1.5 (28.7)
IR62829 A/IR29723-143	91 DS	90	6.4	5.2 (Rasi)	1.1 (21.3)
IR62829 A/ARC 11353	91 WS	93	7.3	6.1 (Jaya)	1.2 (19.3)
IR58025 A/IR29723-143	91 DS	103	6.2	5.2 (Rasi)	0.9 (17.7)
IR62829 A/Swarna	91 WS	108	7.1	5.1 (Jaya)	1.0 (15.7)
Maruteru					
IR62829 A/Milyang 46	90 WS	75	4.3	3.4 (IR36)	0.9 (27.3)
KARNATAKA					
Mandya					
IR62829 A/IR9761-19	90 WS	90	9.5	8.1 (Annada)	1.4 (17.9)
IR58025 A/IR29723-143	91 DS	90	7.0	5.7 (Jaya)	1.3 (22.3)
PUNJAB					
Kapurthala					
PMS 5 A/PAU1126-15-3	91 WS	102	8.5	7.2 (Jaya)	1.3 (14.1)
PMS 3 A/PAU1106-6-2	91 WS	106	8.9	7.2 (Jaya)	1.7 (19.2)
HARYANA					
Karnal					
IR62829 A/IR10198-66-24	91 WS	95	5.6	4.6 (IR36)	1.0 (21.7)
PMS 10 A/PAU1106-6-2	91 WS	104	10.9	9.2 (LC)	1.7 (17.7)
PUNJAB					
PMS10 A/PAU1106-6-2		109	9.5	8.3 (PR 106)	1.2 (14.5)
PMS8 A/IR1106-6-2		113	9.2	8.1 (PR 106)	1.1 (12.6)
ANDHRA PRADESH					
IR54752 A/Vajram		-	9.2	7.2 (MTU 1714)	2.0 (28.1)
IR54752 A/Swarna		-	6.5	5.3 (IR64)	1.2 (23.7)
KARNATAKA					
IR58025 A/IR9761-19-1R		88	7.4	6.4 (Jaya)	1.0 (15.7)

[a] Figures in parentheses are percent values.

The conversion program now under way in the network is systematic and organized, with each center responsible for developing CMS lines for a particular situation or ecosystem. The Central Rice Research Institute (CRRI) at Cuttack, for instance, is developing CMS lines for hybrids suited to rainfed lowlands. The Indian Agricultural Research Institute (IARI) in Delhi and the Punjab Agricultural University in Kapurthala are developing CMS lines of basmati quality (Table 4).

All available effective restorers were evaluated for percentage of fertility restoration, stability of restoring ability over locations/seasons, and combining ability. The results showed that restorer performance depended on the CMS lines (Table 5). The difference in fertility restoration in CMS lines with identical WA cytosterile system

Table 2. Relative stability of promising CMS lines, 1991 wet season (WS).

CMS line	Pollen sterility (%)								
	Hyderabad	Mandya	Maruteru	Coimbatore	Kanpur	Karnal	Pantnagar	Faizabad	Karjat
V20 A	99	100	80	95	100	85	100	90	100
IR62829 A	100	99	95	90	72	94	99	91	100
IR58025 A	100	99	96	96	100	94	100	94	100
PMS2 A	100	100	–	95	100	87	100	–	–
PMS3 A	100	100	99	–	100	87	98	–	–
PMS4 A	100	100	–	–	100	95	99	–	–
PMS5 A	98	25	–	–	100	95	100	–	–
PMS7 A	100	90	–	–	100	89	95	–	–
PMS8 A	100	25	–	–	100	97	100	–	–
PMS10 A	93	95	98	–	100	97	100	–	–

Table 3. Additional CMS lines developed In India.

CMS line	Source	CMS line	Source
CRMS 1	Ratna	Rajeswari A	WA
CRMS 2	Dunghansali	Bharati A	WA
Krishna A	Kalinga-1	Kiran A	WA
Madhu A	WA	Archana A	WA
Sarasa-I A	WA	Madhuri A	WA
Sarasa-II A	WA	Deepa A	WA
Pusa 33 A	WA	Pusa 4-1-11 A	WA
Pragathi A	WA	Adt. 34 A	WA
MW 10 A	WA	Suphala A	WA
Henna A	WA		
Krishna A	WA		

could be because the CMS lines had varied nuclear backgrounds. Restorers that showed a consistently high degree of restoration in CMS lines of varied nuclear background, such as WGL 3962, would be of value in a commercial hybrid breeding program if restoration ability were combined with high combining ability.

Restoring ability was found to vary with location. A study of a set of restorers at 5 centers against 2 stable CMS lines suggests fertility variation of 15-25% between the best and poorest locations (Table 6). Information of this kind might be of value when choosing locations for hybrid seed production.

Optimizing seed production

Rice is predominantly a self-pollinated crop, and this leads to skepticism about the economic viability of hybrid seed production. Development of economical and efficient seed production packages has been given the same research emphasis as improving male sterile lines. Results of the last 2 yr show the possibility of raising the yield level beyond 2 t/ha (Table 7). The level of success, however, varied with hybrid, location, and season even with optimum seed production package. The yield differences between hybrids could not be related to either of the parents (although crosses

Table 4. Rice cultivars being converted into CMS lines at various centers in India.

Purpose	CMS source	Center	Line(s) being converted	Stage of conversion
Basmati rice	WA	Kapurthala	Pusa Basmati 1	BC_2
		Pantnagar	Pusa Basmati 1	BC_1
		Delhi	Pusa Basmati 1	BC_1
			Pusa 150	
			Pusa 615	
			Pusa 1041	
Bacterial blight resistance	WA	Kapurthala	PR108	BC_2
			PR106-1	BC_2
			HKR126	BC_2
Medium late for coastal Andhra Pradesh	WA & ARC	Maruteru	WGL3010	BC_3
			WGL4584	BC_3
			MTU9991	BC_3
			IET7581	BC_3
Rainfed lowland (shallow water)	WA	Cuttack	Anamika	BC_1
			Prasad	
			CR624-21-1	
Irrigated (Medium and early)	WA	All	Several	BC_{14}

Table 5. Fertility restoration ability of various elite lines with different CMS lines[a]

Line	V20 A	IR46830 A	IR58025 A	IR62829 A
NLR30426	PM	M	PR	PM
WGL 13943	PR	R	PM	R
WGL 3935	R	R	PM	R
WGL 3962	R	R	R	R
WGL 18011-15	R	PM	R	PR
WGL 44645	PM	M	M	PR
IET8110	R	PR	R	R

[a] PM = partial maintainer, M = maintainer, PR = partial restorer, R = restorer.

Table 6. Restoring ability of promising restorers at different locations.

Restorer	Fertility (%)									
	IR62829 A					IR58025 A				
	Hyderabad	Coimbatore	Kanpur	Cuttack	Mandya	Hyderabad	Coimbatore	Kanpur	Cuttack	Mandya
IR10198-66-2 R	93	89	68	71	75	76	86	71	83	73
IR9761-19-1 R	81	78	76	73	75	80	87	77	64	76
IR29723-143-3-2-1 R	83	81	72	64	77	92	81	74	74	77
Pusa 150 R	79	84	61	66	74	77	78	76	58	76

involving V20 A have been known to give relatively low seed yields reportedly due to poor panicle exsertion, which is characteristic of the CMS line). As for influence of location and season, the seed yield of A lines was generally found to be relatively higher during the dry season (DS) than during WS (Table 8).

While attempts are being made to improve the floral traits of both male sterile and pollinator lines to improve % outpollination, various cultural and supplementary pollination techniques have also increased seed yields. Study of row ratio of A:B/R over locations revealed no consistency. However, the effective number of A rows to B/R was lower in the northern and western regions (2A:1B/R) but higher in the south (3:1, 6:2, 8:2) (Table 9). The effective ratio varies with flowering behavior of parental lines, wind direction and velocity, etc., so the row ratio for every hybrid identified for commercial exploitation must be standardized.

Inconsistency is common with supplementary pollination techniques, too. Twenty different combinations of supplementary pollination techniques, including GA_3, urea, and boric acid application, rope pulling, and flag leaf clipping, showed that GA_3 (60 ppm at 10% flowering) was the most important component at most test locations. Initial observations on the effectiveness of urea were encouraging, but later findings have failed to confirm this. With the exception of Mandya, where simple rope pulling gave

Table 7. Progressive improvement of seed yield of CMS lines (IR62829 A).

	Year	Seed yield (t/ha) at optimum package			
		Hyderabad	Mandya	Delhi	Karnal
Before	1989	<0.1	<0.2	<0.1	–
	1990	0.7	1.0	1.4	1.9
	1991	1.7	2.5	2.0	2.1

Table 8. Yield range of hybrid seed during 1990-91 DS and WS, Hyderabad.

Hybrid	Yield (t/ha)
DS	
IR58025 A/Pusa 150 R	1.1
IR62829 A/C 1359-8-1 R	1.7
IR58025 A/IR35366-40-3-3-3-1 R	2.5
IR62829 A/IR27315	1.6
V20 A/IR15324	0.8
V20 A/ARC 11353	0.3
WS	
IR62829 A/IET 9844	1.3
IR62829 A/Suweon 318 R	1.0
IR62829 A/C711097	0.7
IR58025 A/209-Chourigora	0.8
IR58025 A/HKR-119	1.1
IR58025 A/IR9761-19-1 R	0.5

Table 9. Hybrid rice seed yield in row ratio trials conducted at different locations with IR62829 A, 1991 WS.

Row ratio	Yield (t/ha)						
	Hyderabad	Mandya	Maruteru	Coimbatore	Karnal	Karjat	Faizabad
2:1	1.4	1.0	0.5	0.5	2.8	1.6	2.1
3:1	1.6	0.9	0.6	0.7	2.8	0.8	1.6
4:2	1.6	1.0	0.4	1.0	2.1	0.6	1.6
6:2	1.2	1.0	0.4	0.8	2.0	0.7	1.3
8:2	1.2	1.3	0.6	0.6	1.9	0.7	1.0
12:2	1.1	0.9	0.6	0.8	1.4	0.6	1.0
12:4	1.1	0.3	0.4	0.9	1.9	0.8	0.9

Table 10. Comparison of different treatments for increasing seed yields of CMS line (IR62829 A).

Treatment	Yield (t/ha)					
	Hyderabad	Mandya	Faizabad	Pantnagar	Karnal	Delhi
GA_3 (60 ppm)	1.6	1.7	1.2	1.1	1.8	1.7
Urea (2%)	1.3	1.8	1.0	1.2	1.6	1.6
GA_3 + urea	1.5	1.8	1.0	1.4	1.8	0.9
Most effective treatment[a]	1.7 (GA_3+ FL1)	2.5 (RP)	1.4 (GA_3+FL1+RP)	1.5 (GA_3+U+RP)	2.0 (GA_3+U+FL1+RP)	2.1 (GA_3+(FL1+RP)

[a] GA_3 = 60 ppm GA_3 at 10% flowering, U = urea (2%) spray, FL1 =flag leaf cutting, 2 d before panicle initiation, RP = rope pulling twice a day during anthesis.

the highest yield, the most effective package in general included GA_3 (Table 10). Despite its high cost, use of GA_3 is inevitable. The cost may be appreciably reduced by combining GA_3 with other chemicals or by resorting to ultralow volume spray techniques.

Variability for flowering behavior and floral traits

More than 1,500 accessions for floral characteristics that determine the extent of outpollination were screened at the University of Agricultural Sciences (UAS), Bangalore. Wide variations were revealed (Table 11). Accessions that could be utilized for improving the floral traits of parental lines were identified. These showed good panicle exsertion (Bilikagga, Mandya Vijaya, Biliakku), prolonged anthesis and additional flushes of flowering (Adokkan, CGP1351, IMD1-14), prolonged glume opening (Sarkar Longdong), large anther (Halugidda, Pokkali, T2952), large stigma surface (Halugidda, Karidadi, HR42, Kumkum Kesari), and good stigma protrusion (Halubbalu, Chandravathi, Mingolo, Type 2).

Table 11. Floral characteristics favorable to outcrossing in traditional (TV) and improved varieties (IV).

Character	Varieties
Good stigma protrusion	TV: Chandravathi, Pokkali, Halubbalu, Mingolo, Type 2
	IV: IET5656, IR50-31, IR5795–232, PR109, Pusa 205, IET6155, 6155, IET12016
Wider glume opening	TV: Halubbalu, Pokkali, Doddi,Mingolo, Carolisa, Puttarbatta, HB42, Tapasta, Kumkum Kesar
	IV: IR19792-18, IR10179-2-3, IET12016, IET12010, IET8586, IR42
Prolonged glume opening	TV: Sarkar Longdong, Indersan
	IV: IR42, IR25869-9, IR50-14, Swarna
Large stigma	TV: Halugidda, Karidadi, Kumkum Kesari, Pokkali
	IV: IR42, IR18350-73, IET5656
Panicle exsertion	TV: Bilikagga, Biliakki, Halugidda, Sarkar Longdong, Mingolo, ARC11353, China 6
	IV: Mandya, Vijaya. IR2797-125, Jyothi, Ratna
Large anther	TV: Halugidda, HWR2, Mingolo IV: IR27315, IR11418-15-2

Genetic studies

Floral characters

Some floral traits follow simple modes of inheritance. Inheritance of anther size and stigma protrusion in two crosses studied at the Tamil Nadu Agricultural University, Coimbatore, indicated that long anthers and fully exserted stigmas are controlled by a single, dominant gene.

Fertility restoration

The genetics of fertility restoration have been studied in diverse CMS systems. Fertility-restoring ability varies according to the number and strength of the two dominant restorer genes identified earlier, and the nature of the modifier complex, which again varies with the nuclear background of the CMS lines. Attempts have been made at Cuttack and Kapurthala to understand the genetics of some of the partial and effective restorers in WA, Wu 10 A, and Pankhari 203 A. The findings revealed that whereas partial restorers of Wu 10 A were governed by a single dominant gene, partial and effective restorers of V20 A and Pankhari 203 A had two dominant genes. It was also observed that penetrance and expressivity of the fertility restorer gene depended mainly on the environment and nature of CMS lines used (Table 12). Similar studies

Table 12. Segregation pattern for pollen fertility in crosses involving V20 A (WA), Pankhari 203 A (TN1), and Wu 10 A (BT) cytosterile lines and their partial and effective restorers, 1986 WS.

Genotype	F_2 plants (no.)						
	Fertile	Fertile	Partially Sterile	Total	x^2	Genetic ratio	Probability
V20 A × Rohini	118	34	48	200	0.676	9:3:4	0.50-0.75
V20 A × Vikas	112	31	11	154	0.462	12:3:1	0.75-0.90
Pankhari 203 A × Rohini	151	90	10	251	2.905	9:6:1	0.10-0.25
Pankhari 203 A × Mahsuri	148	40	13	201	0.201	12:3:1	0.90-0.95
Pankhari 203 A × Radha	131	47	51	229	1.122	9:3:4	0.50-0.75
Wu 10 A × Rohini	40	71	38	149	0.376	1:2:1	0.75-0.90
Wu 10 A × Rasi	-	116	36	152	0.140	3:1	0.50-0.75

Table 13. Spikelet fertility of plants in F_2 populations of crosses of CMS lines with restorer lines.

Cross	No. of plants					
	Fertile	Partially sterile	Partially fertile	Completely sterile	Total	x^2 9:3:3:1
V20 A/PR103	291	85	86	27	489	2.179
V20 A/PR106	283	81	107	38	509	4.826
IR54752 A/ PAU1124-36-1	232	85	92	34	443	3.630
IR54752 A/ PAU1126-1-1	239	94	85	25	443	2.162

carried out at Kapurthala on WA source suggest that fertility restoration is governed by two independently segregating dominant genes (Table 13). The two genes appeared to have additive effects, one being stronger than the other in restoring fertility. The findings of both centers agree with those of Prof. L. P. Yuan and Dr. S. S. Virmani.

Combining ability studies

The combining ability of yield and yield-supporting characters was studied through line/tester analysis involving four cytoplasmic genetic male sterile lines (V20 A, Zhen Shan 97 A, IR46829 A, and IR46830 A) as lines and 34 restorers as testers. The variance due to general combining ability (*gca*) and specific combining ability (*sca*) effect indicated that nonadditive gene action was predominant for number of panicles per plant, number of spikelets per panicle, test grain weight, total dry matter accumulation, spikelet fertility, and grain yield. Additive gene action was predominant for days to 50% flowering and plant height. CMS lines V20 A and IR46830 A were found to be good general combiners for most of the characters. Among the restorers, Savitri, Phou-oi-bi, Pokkali, Mahsuri, and White Ponni were found to be good combiners for grain yield and other yield components. Most of the crosses with high *sca* effects had at least one parent with high *gca*. This study indicates that yield and yield components are predominantly controlled by nonadditive gene action. Hence, heterosis breeding is an appropriate approach for improving rice yields.

Diversification of cytoplasmic male sterility

More than 95% of the male sterile lines used in indica hybrids in China belong to the WA system. The same is true of many improved CMS lines now being tested in India and elsewhere. Dependence on a single source for such an important trait could render the hybrids highly vulnerable to sudden outbreaks of diseases and insect pests, so alternate sources of CMS are being investigated. Research efforts to diversify the sterility system are under way in India. New CMS sources from both cultivars and wild species of the genus *Oryza* and restorer genes for male sterile lines already developed which have no restorers are being sought. CRRI has developed CRMS1, CRMS2, and CRMS21 (Ratna MS, Dunghanshali MS, and Krishna MS) which look different from the WA source. Research efforts of the last 2 yr have indicated the presence of exploitable male sterility in 1-2 accessions each of 5 species of A genome, *O. glaberrima, O. nivara, O. rufipogon, O. barthii,* and *O. longistaminata.* With one backcross using *O. sativa* as the recurrent parent, achievable sterility has gone up to 100% (Table 14) (Hoan, unpubl.).

MS577 and IR66707 A are potential male sterile lines as stable as WA-based CMS lines, but they cannot be used without effective restorers. They are believed to have

Table 14. Evaluation of interspecific crosses for alternate sources of sterile cytoplasm. DRR, Hyderabad.

Cross	F_1		BC_1	
	Pollen sterility (%)	Spikelet fertility (%)	Pollen sterility (%)	Spikelet fertility (%)
O. nivara/O. sativa (Acc. 1-1) (IR70)	86	5.0	95	2.5
O. nivara/O. sativa (Acc. 1-2) (IR64)	90	5.0	100	0.0
O. rufipogon/O. sativa (Acc. 2-1) (IR70)	70	10.0	90	3.5
O. rufipogon/O. sativa (Acc. 2-2) (IR66)	100	0.0	100	0.0
O. rufipogon/O. sativa (Acc. 2-3) (IR64)	100	0.0	100	0.0
O. longistaminata/O. sativa (Acc. 3-1) (IR70)	100	0.0	–	–
O. barthii/O. sativa (Acc. 4-1) (IR58025B)	100	0.0	–	–

originated from closely related wild species and were crossed with a large number of Indian and exotic accessions of A genome species. None of the accessions tested were effective restorers, but a few partial restorers were identified (Hoan, unpubl.). The level of fertility restoration may be improved by intercrossing among the partial restorers of wild origin and with single- and two-gene-governed restorers of WA source.

Chemical and genetic approaches for developing two-line breeding

For many years, two-line breeding through chemical emasculations was regarded as an alternative to the conventional three-line breeding approach for exploiting hybrid vigor in a variety of crops, including rice. Early reports described the effectiveness of Ethrel—(2-chloroethyl) phosphonic acid—in India and elsewhere and arsenic compounds like zinc/sodium methyl arsenate in China. Attempts were made at IARI, Delhi, to look for male gametocides less toxic but as potent and selective as arsenates (Ali, unpubl.). The test chemicals included three oxanilate formulations, ethyl 4'fluoro-oxanilate, ethyl4' chloro-oxanilate, and ethyl3'methoxy-oxanilate. A 25% emulsifiable concentrate of the oxanilates prepared in chloroform with 5% Tween 80 was diluted with water and tested at concentrations of 0.050, 0.075, and 0.1% on four varieties at panicle initiation and boot leaf stages. Sodium methyl arsenate at corresponding concentrations was the check gametocide. Efficacy of the oxanilates was rated on the basis of pollen and spikelet sterility. Of the three formulations, ethyl4' fluoro-oxanilate was the most effective, comparable with sodium methyl arsenate (Table 15), closely followed by ethyl 3'methoxy-oxanilate. The effect appears to be highly variety-specific, irrespective of stage of treatment and concentration. Pusa 150 proved to be the most responsive variety at both stages and all concentrations, with pollen sterility ranging from 95 to 100%. There were, however, indications of ovule sterility as well. Exploiting the variety specificity of the chemical treatment, varieties such as Pusa 150 could be used as the female parent for hybrid seed production. It is, however, important to look for chemicals that would be effective on a wide spectrum of varieties.

Following the discovery of temperature- (TGMS) and photoperiod-sensitive genic male sterility (PGMS) systems in China and Japan, efforts are being made to isolate such genes through screening of germplasm and induced mutagenesis in India. Preliminary findings suggest that recovering a TGMS source is possible.

Table 15. Relative efficacy of gametocides.

	Pollen sterility (%) at concentrations	
Chemical	1000 ppm	1500 ppm
Ethyl 3' methoxy oxanilate	80.84	99.30
Ethyl 4' fluoro-oxanilate	98.52	100.00
Sodium methyl arsenate	98.02	99.82

Conservation of yield vigor in F_1 hybrids

Apomixis, an asexual means of seed production, is a natural genetic mechanism that conserves hybrid vigor in certain plant species. If we find a strong source of apomixis in rice or closely related germplasm, it would pave the way for developing true-breeding hybrids.

Dihaploid (DH) lines from heterotic hybrids, now possible through anther culture, could help in conserving yield vigor of F_1 hybrids. Assuming that heterosis is primarily due to dispersion of genes in parents that display directional dominance, some of the DHs derived from highly heterotic combinations could retain the yield advantage of the F_1 hybrid. Each DH plant represents a distinct array of genes and, due to chromosome doubling, they assume the homozygous state. In DHs, the problem of low additive variance, which hinders selection in the early generations in the pedigree system, is not encountered. Furthermore, the probability of obtaining desirable recombinants is high. To take advantage of these possibilities, several DHs derived from a few selected heterotic crosses through anther culture were evaluated for their yield potential in comparison with the best yielding parent, F_1 hybrid, and the standard check at IARI (Bui Ba Bong, unpubl.). Two of the nine DH lines obtained in the cross Pusa 743-1-l/IR66, A26-2 and A10-2, yielded 6.5 and 10.0% less than the F_1 hybrid, and 17.4 and 14.5% higher than the standard check variety Pusa 150, respectively. Similarly, two of the three DH lines obtained in the cross Pusa 743-1-1/IR72 yielded about 11% below the F_1 hybrid and around 17% higher than the check variety (Table 16). In terms of absolute yield, the advantage was close to 1 t/ha, which is the level we are trying to achieve through heterosis breeding. The lines are now being tested in several locations under the All India Coordinated Trials.

Similar efforts made at the DRR have led to the development of several DH lines from some of the most consistent best performing hybrids, such as IR58025 A/IRBB7.

Table 16. Performance of promising dihaploid lines in comparison with F_1, parents, and standard check.

Cross	DH line	Yield (t/ha)	Yield increase/decrease (t/ha)[a]		
			F_1	Better parent	Standard check*
Pusa 743-1-1/IR66	A26-2	6.6	-0.4 (-6.5)	1.1	1.0 (+17.4)
	A10-2	6.3	·0.7 (-10.0)	0.8	0.7 (+14.5)
Pusa 743-1-1/IR72	A4-2	6.7	-1.2 (-10.5)	1.2	1.0 (+17.5)
	A1-3	6.6	-1.3 (-11.0)	1.1	0.9 (+16.4)

[a] Figures in parentheses are % yield increase/decrease as compared with F_1 hybrid.

Table 17. Performance of experimental hybrids as main crop (1988 DS), ratoon crop (1988 WS), and stubble crop (1988 WS), Bangalore.

Hybrid	Grain yield (t/ha)		
	Main	Ratoon	Stubble
IR54752 A/IR46 R	9.8	3.4	4.9
IR54752 A/IR54	8.2	3.9	6.8
IR54752 A/IR13319	7.3	2.6	4.4
IR54752 A/IR29512	7.1	2.6	2.7
IR54752 A/IR25912	7.2	1.3	2.3
IR54752 A/IR19392	7.1	1.0	2.9
Jaya	6.6	–	–
Mangala (seedling check)	–	–	4.3

Promising lines with 80-90% of the potential of the hybrids are being evaluated in replicated trials.

Ratooning and stubble planting

One of the major advantages of the rice plant is its amenability to ratooning and vegetative propagation. Basic studies increasing the overall yield of hybrids and seed yield of hybrid/CMS lines through ratooning have been under way at the UAS, Bangalore, for several years. Some of the hybrids yielded 1.1-3.9 t/ha in the ratoon crop, or 20-35% of the main crop, which yielded 7.1-9.7 t/ha.

Stubble planting can yield up to 90% of the main crop, depending on the cross. For hybrids with yields close to the main crop, the prospects of stubble planting for commercial adoption should be explored. Ratooning in seed plots as a cheap and effective way of increasing seed yields also needs to be investigated (Table 17).

Notes

Authors' address: E. A. Siddiq, P. J. Jachuck, M. Mahadevappa, F. U. Zaman, Vijaya Kumar, B. Vidyachandra, G. S. Sidhu, Ish Kumar, M. N. basad, M. Rangaswamy, M. P. Pandey, D. V. S. Panwar, and Ilyas Ahmed, Directorate of Rice Research, Rajendranagar, Hyderabad 500030, India.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in the Philippines

R. J. Lara, I. M. dela Cruz, M. S. Ablaza, H. C. dela Cruz, and S. R. Obien

An IRRI-bred F_1 hybrid, IR64616 H, was tested in national coordinated trials and showed 0.7-0.8 t/ha yield superiority over check varieties (4.7-5.1 t/ha) in certain parts of the country. The IRRI-bred cytoplasmic male sterile (CMS) lines IR62829 A and IR58025 A appear to be nearly stable and suitable for developing heterotic rice hybrids for the Philippines. Hybrid seed production trials with CMS line IR62829 A (the female parent of the heterotic hybrid) were conducted in several parts of the Philippines. Seed yields ranging from 1.0 to 2.3 t/ha were obtained. Heterotic rice hybrid and associated seed production technology are being evaluated in verification trials in selected areas by prospective seed growers. Cost of producing hybrid seeds obtained in research-managed seed production plots was US$0.72/kg, with additional income derived from the yield of the pollen parent ($362/ha). Based on these encouraging results, some prospective seed growers from Cagayan Valley were trained in hybrid rice seed production technology in collaboration with IRRI. Policies and guidelines in hybrid testing, release, seed production, and certification are being developed. Trials are in progress to study agronomic management of the elite rice hybrids and further improvement of seed production techniques to increase seed yield and reduce seed cost.

Rice production in the Philippines has doubled during the past two decades as a result of widespread adoption of improved varieties, associated technologies, and a strong institutional support system for farmers. Increased production has made the country self-sufficient in rice. However, steadily decreasing land-to-population ratio and a soaring food demand underline the need to produce more on less land. Demand for rice alone in the Philippines is expected to increase by about 3% per year during the next decade, and production increases will have to come primarily through increased yield per unit area.

Average yields have reached high levels of 6-9 t/ha. Adoption of hybrid rice might reduce total rice area, leading to opportunities to diversify into other crops, livestock, and household industry to increase the earnings of farm households.

Results from China and IRRI encouraged researchers at the Philippine Rice Research Institute (PhilRice) to explore the potential of hybrid rice in the Philippines. Research began in 1989, when some IRRI cytoplasmic male sterile (CMS) lines were tested. Results on the performance of experimental hybrids and seed production trials at research-managed fields are encouraging. Verification trials are now being done by selected farmer-seed growers in northern Philippines.

Promising CMS, maintainer, and restorer lines

Some CMS lines and their maintainers were acquired from IRRI. These were evaluated and used to develop hybrids.

Stable CMS lines were V20 A and IR46830 A (both with CMS WA cytoplasm), and IR54755 A (CMS ARC cytoplasm). Cytoplasmic male sterile lines IR58025 A and IR62829 A were nearly stable for male sterility (Table 1). On the other hand, IR54755 A, IR58025 A, and IR62829 A showed slight to no infection with tungro viruses. Outcrossing potential of IR62829 A, IR58025 A, and V20 A was acceptable. Cytoplasmic male sterile lines flowered at 81-102 d in IRRI and San Mateo but at 102-116 d in Banaue (a high-altitude location).

Table 1. Performance of some CMS lines in three locations in the Philippines, PhilRice, 1990 DS.

Line	Location	Pollen sterility[a]	Seed setting (%) of bagged panicles	Reaction to RTV[b]	Outcrossing potential[c]	Days to 50% flowering
V20 A	IRRI	CS	0	S	3	83
	Banaue	CS	0	R		102
	San Mateo	CS	0	I		81
IR46830 A	IRRI	CS	0	I	9	86
	Banaue	CS	0			108
	San Mateo	CS	0	I		89
IR54755 A	IRRI	CS	0	R	9	81
	Banaue	CS	0	R		108
	San Mateo	CS	0	R		88
IR58025 A	IRRI	CS	0	I	3	102
	Banaue	CS	0	R		116
	San Mateo	S	0.33	R		90
IR62829 A	IRRI	CS	0	I	1	85
	Banaue	PS	2.20	R		105
	San Mateo	S	0.05	R		84

[a] CS = completely sterile (0% fertility), S = sterile (1-10% fertility), PS = partially sterile (11-30% fertility). [b] RTV = rice tungro viruses, R =no infection, I = slight infection, S = severe infection. [c] Outcrossing potential on 1-9 scale: 1 = high, 9 = low.

Elite lines and varieties with good agronomic characteristics—e.g., high-yielding ability, pest and disease resistance, and good grain quality—were selected from the ongoing inbred breeding program. These were testcrossed as single plants using V20 A, IR62829 A, IR58025 A, IR66707 A, IR54755 A, and PR1 A to identify maintainers and restorers. Pollen sterility of 98-100% in the testcross F_1s indicated that the male parent was a maintainer and could, therefore, be converted into a CMS line by recurrent backcrossing. Testcross F_1s with normal seed setting (>75%) indicated that their male parent was a restorer which could be used to develop heterotic rice hybrids. Thirty-three maintainers and 70 restorers have been identified (Table 2).

Maintainer lines have been backcrossed 2-6 times to convert them into CMS lines. Restorers are being purified by re-testcrossing single plants before these are used for yield testing.

Performance of promising rice hybrids

The F_1 rice hybrids tested in the Philippines since the 1990 wet season (WS) were mostly developed at IRRI. Three IRRI-bred and one Cargill-bred experimental rice hybrids were nominated for testing in the national coordinated trials (NCTs) under irrigated conditions. Among the four hybrids, one (IR64616 H) showed significant superiority over check varieties IR50 and PSBRc4 and the best inbred breeding line entries during 1990 WS, 1991 DS, 1991 WS, and 1992 DS (Table 3). This hybrid was also compared with the best local varieties in seven farmers' fields in northern Philippines. The hybrid appeared superior in five locations, with a 13-60% yield advantage, and demonstrated higher daily productivity per hectare (Table 4). It is being tested further in the NCTs and in more locations under farmers' field conditions.

Eighty-two experimental rice hybrids were tested in preliminary yield trials in 2-4 locations from 1990 DS to 1992 WS. Thirteen hybrids yielded higher than the check by 8-29% (Table 5). The most promising entry will be further tested and included in the NCTs.

Progress in hybrid rice seed production technology

Several studies have been undertaken based on the hybrid rice seed production models developed in China and at IRRI. These include

- the effects of different hybrid rice seed production practices on outcrossing rate and seed yield of CMS lines in several locations,
- maximizing the efficiency of gibberellic acid (GA_3) in hybrid seed production,
- economics of hybrid rice seed production in different parts of the Philippines, and
- verification trials of hybrid rice technology among Cagayan Valley seed growers.

Seed production practices, outcrossing rate, and seed yield of CMS lines

Cytoplasmic male sterile line IR62829 A and its maintainer was grown with a 2:6 male-to-female row ratio in three locations in Luzon (IRRI, Maligaya, and San Mateo) in the 1990 DS. Four basic components of hybrid rice seed production, GA_3 spraying, flag

Table 2. Maintainer and restorer lines identified at PhilRice, Maligaya, Muñoz, Nueva Ecija, 1990 WS - 1992 WS.

Cultivar	Tester CMS line
Maintainers	
PR1B	PR1 A
PR4B	PR4 A
MRC17283-308	IR54755 A
MRC22387-859	V20 A
BPI 121-407	IR62829 A
IR5537-32D-Bulk	IR62829 A
IR57893-26	IR62829 A
	IR58025 A
IR55543-51-B-Bulk	IR58025 A
	IR62829 A
	IR54755 A
IR60080-45	IR62829 A
IR55543-51-B-Bulk	IR54755 A
	IR58025 A
IR57934-02	IR54755 A
IR60077-09	IR54755 A
IR55537-2-02	IR54755 A
IR60080-41	IR54755 A
Hualien Yu	IR54755 A
Latsidahy	IR62829 A
KSY1154	IR62829 A
	R58025 A
MRC19399-1224	IR62829 A
IAC/IRAT112	IR64 A
BPI 76/Palawan/Taichung 65-1	IR64 A
BPI 76/Palawan/Taichung 65-3	IR64 A
IR55543-31-13	IR64 A
PR19390-1215	IR54755 A
YOU2-16B	D71-72 A
YS-37B	D71-72 A
Shanghai	IR62829 A
MRC23348-30	IR62829 A
PSB Rc 8	IR54755 A
MRC23253-1336	IR64 A
IR64608B	IR64 A
HURI 356	IR54755 A
	IR64 A
MRC22918-7-2	IR64 A
BPI Ri10	IR64 A
Restorers	
BPI Ri10	IR58025 A
MRC18186-611	IR62829 A
MRC22367-807	IR62829 A
IR66	IR62829 A
PR21209-389-5	IR62829 A
RP1057-393	IR62829 A
BRB111-461-1	IR62829 A
BR425-189-1-6-2-1-1	IR62829 A
BR316-154-4-1	IR62829 A

Table 2 continued.

Cultivar	Tester CMS line
MRC22016-126	IR64 A
MRC22564-50	IR64608 A
Intan	IR64608 A
Guandong	IR64608 A
BPI Ri4	IR64608 A
RP1714-14-7	IR54755 A
PR1714-14-7	IR54755 A
PR19926-229-5	IR54755 A
Malidu	IR54755 A
Huri 356	IR54755 A
MRC19366-122	IR54755 A
PR23161-11-46	IR58025 A
PR22892-235	IR58025 A
PR21283-553	IR58025 A
IR64 B	IR58025 A
IR26	IR58025 A
IR22	IR58025 A
PR23468-4	IR62829 A
PR23408-3	IR62829 A
PR23271-1386	IR62829 A
PR22896-225	IR62829 A
PR22892-239	IR62829 A
Minantika	IR62829 A
CT4617-2-1-2P	PR1 A
Fortuna	PR1 A
Ginaracia	PR1 A
IR28238R	PR1 A
IR40750R	PR1 A
IR64B	PR1 A
MRC18798-23	PR1 A
PR23383-15	PR11 A
PR23405-9	PR1 A
SLK-8-2	PR1 A
IR28238R	PR 1A
MRC23383-3	PR 4 A
BE2	IR58025 A
Bengawan 1	IR58025 A
Bengawan 2	IR58025 A
Elon-elon	IR58025 A
FK178A	IR58025 A
Gyena 1	IR58025 A
MRC8945-161	IR58025 A
PR22349-789	IR58025 A
Bengawan	IR62829 A
Betalka	IR62829 A
Bengawan 2	IR62829 A
Brondal Putch	IR62829 A
Buenkitan	IR62829 A
C12	IR62829 A
CT4617-2-1-2P	IR62829 A
Elon-elon	IR62829 A
Tortuna	IR62829 A
IR26933-16-2-3	IR62829 A
K39-96-1-1-1-2	IR62829 A

Table 2 continued.

Cultivar	Tester CMS line
MRC22969-130-15	IR62829 A
PR23405-9	IR62829 A
PR23272-138	IR62829 A
PR23383-15	IR62829 A
RAU4045-2A	IR62829 A
SLK3-8-2	IR62829 A
RAU4045-2A	IR64608 A

Table 3. Yield of F_1 rice hybrid (IR64616 H) evaluated in multilocation national coordinated trials in the Philippines.[a]

Season/ year	Yield (t/ha)										
	BEST[b]	CMU	CPU	CVES	DES	Mali- gaya	Mid- sayap	UPLB	USM	VES	Season mean
1990 WS	6.4**	5.8*	4.3**	5.7	4.0	3.3	4.3	3.5*	7.0**	6.1**	5.0
1991 DS	2.8**	5.7**	4.9*	5.7**	–	7.2	4.4	4.2**	5.4**	4.4**	5.8
1991 WS	6.9	5.1	–	–	–	–	7.2**	–	4.3	5.2**	5.7
1992 DS	5.9	–	5.4	6.3**	6.3	5.9**	6.3**	5.1	–	3.9	6.3

[a] Mean yield of check variety for the same trial duration: IR50 = 4.1 t/ha; PSBRc 4 = 5.3 t/ha. [b] BEST = Bicol Experiment Station, CMU = Central Mindanao University, CPU = Central Philippines University, CVES = Cagayan Valley Experiment Station, DES = Dingras Experiment Station, USM = University of Southern Mindanao, VES = Visayas Experiment Station.

leaf clipping (Flc), supplementary pollination (Sp), and urea (U) spraying were tried individually and in all possible combinations. Two new growth regulators (Nevirol [phthalamic acid or N-phenyl thalamic acid] and Berelex [10% technical grade of GA_3]) were also tested.

Observations on seed yield, outcrossing rate, seed weight, panicle exsertion, plant stature, and seed discoloration of the crop were recorded. Statistical tests were used to verify the equality of variances among test locations. Results showed that the error variances for seed yield of the three locations were not significant. A combined analysis was done since the data were homogeneous.

The effects of different components of seed production on seed yield are given in Table 6. Seed yield ranged from 0.7 to 2.3 t/ha. Yields were higher at Maligaya and San Mateo (1.7 t/ha) than at IRRI (1 t/ha). Yield differences between locations were basically due to variations in crop growth and development, which can be attributed to varying environmental conditions and levels of management.

In San Mateo, plots treated with GA_3 + Sp had the highest seed yield. This was followed by GA_3 + U + Flc, GA_3 + U + Flc + Sp, GA_3 alone, GA_3 + Flc + Sp, Berelex, and GA_3 + Flc; these treatments gave similar seed yield levels. Gibberellic acid contributed significantly to seed yield increase. Flag leaf clipping alone and Sp alone had negligible effects, while application of U alone and Nevirol reduced seed yield. Flag leaf clipping improved seed yield when combined with any of the three other components.

Table 4. Performance of rice hybrid IR64616H compared with conventional varieties during 1991 WS.

Location	Cultivar tested	Growth duration (d)	Pest reaction	Yield		
				t/ha	kg/d	% of check
San Mateo, Isabela	Hybrid	108	20% leaffolder	7.8	72.2	142
	IR60	110	20% leaffolder	5.6	50.9	
Aurora, Isabela	Hybrid	110	20% bacterial leaf blight	8.2	74.5	116
	IR72	118	20% bacterial leaf blight	7.6	64.3	
Santiago, Isabela	Hybrid	112	30% bacterial leaf blight	4.0	35.8	160
	IR72	119	30% leaffolder	2.7	22.4	
San Mateo, Isabela	Hybrid	114	20% stem borer	5.8	51.0	89
	IR72	120	10% stem borer	6.9	57.3	
Cabanatuan, Isabela	Hybrid	112	20% rice tungro virus	7.1	63.7	98
	IR72	117	-	7.6	65.0	
Aurora, Isabela	Hybrid	110	20% bacterial leaf blight	5.6	51.3	155
	IR72	117	20% bacterial leaf blight	3.9	33.0	
Cordon, Isabela	Hybrid	108	-	6.3	57.9	113
	IR72	115	-	5.9	51.1	
Mean	Hybrid variety	111	6.4	58.1	125	
	Conventional variety	117	5.4	49.1		

Table 5. Leading hybrid rice combinations tested in preliminary yield trials in different locations, 1990 DS - 1992 WS.

Cross	Yield (t/ha) over location[a]				% of check	Growth duration (d)
	Maligaya	San Mateo	Midsayap	Iloilo		
IR62829 A/IR32809 R	4.2 ns	5.8**	-	-	111	108
IR58025 A/IR32809 R	5.2 ns	6.6*	-	-	116	117
IR58025 A/IR35366 R	4.8 ns	6.1 ns	-	-	122	98
IR58025 A/IR29723 R	6.4 ns	4.9 ns	5.2*	2.5 ns	112	119
IR62829 A/IR29723 R	6.8 ns	5.2**	3.7**	1.9 ns	129	109
IR62829 A/IR54742 R	6.0 ns	4.7 ns	2.9 ns	2.5 ns	110	110
IR58025 A/IR9761 R	7.3 ns	6.7 ns	-	-	117	117
IR58025 A/IR10198 R	2.3/	2.5 ns	5.2**	4.0**	109	109
IR62829 A/IR20933 R	7.3 ns	8.0**	-		122	118
IR58025 A/IR70 R	7.4 ns	7.3 ns	-	-	113	117
IR58025 A/IR15324 R	7.8*	6.7 ns	-	-	112	116
IR58025 A/IR39323 R	4.6*		-	-	108	119

[a] ns = not significant, * = significantly better at the 5% level using LSD, ** = significantly better at the 1% level using LSD, and / = significantly lower at the 5% level using LSD.

Table 6. Seed yield (t/ha) of IR62829 A/B as affected by components of hybrid rice seed production In three locations, 1990 DS.[a]

Treatment	San Mateo	Maligaya	IRRI	Mean
Control	1.3 fg	1.6 de	1.0 cde	1.3
Gibberellic acid (GA_3)	1.9abc	2.0 b	1.0 cde	1.6
Urea (U)	1.3 g	1.3 f	1.2abc	1.2
Flag leaf clipping (Flc)	1.5 f	1.4 f	0.9 de	1.3
Supplementary pollination (Sp)	1.4 fg	1.4 f	1.3ab	1.4
GA_3 + U	1.8 bcd	1.8 bcd	1.la-d	1.6
GA_3 + Flc	1.9abc	2.3a	0.7 f	1.6
GA_3 + Sp	2.1a	1.9 bc	1.3a	1.8
GA_3 + U + Flc	2.0ab	1.9 bc	1.1 bc	1.7
GA_3 + U + Sp	1.8 bcd	1.7 cd	1.2abc	1.6
GA_3 + Flc + Sp	1.9abc	1.7 cd	0.7 f	1.4
GA_3 + U + Flc + Sp	2.0abc	1.9 bc	1.0 cde	1.6
U + Flc	1.5 fg	1.8 bcd	0.9 de	1.4
U + Sp	1.4f g	1.4 ef	1.1a-e	1.3
U + Flc + Sp	1.8 cd	1.8 bcd	1.2abc	1.6
Flc + Sp	1.7 de	1.8 bcd	0.9 e	1.4
Nevirol (growth regulator)	1.2 g	1.4 f	1.1 b-e	1.2
Berelex (growth regulator)	1.9abc	2.2a	1.la-e	1.7
Mean	1.7	1.7	1.1	1.5
CV(%)	7.6	5.8	14.4	8.6
Level of significance	**	**	**	**

[a] In a column, means followed by a common letter are not significantly different at the 5% level by DMRT. ** = significant at the 1% level.

Gibberellic acid + Flc and Berelex produced the highest seed yield in Maligaya. Several other treatments resulted in better seed yield than the check. However, U alone, Flc alone, Sp alone, and Nevirol alone exhibited lower seed yield. The results indicated that GA_3 alone or in combination with other components had a pronounced positive effect on seed yield.

IRRI conditions showed a different trend in the effects of the different components. Although the GA_3 + Sp treatment had the highest seed yield, the application of U alone and Sp alone showed greater contributions under IRRI conditions. Gibberellic acid alone did not improve seed yield and Flc had a negative influence on seed yield.

The main effects of the four components of hybrid rice seed production on agronomic characteristics in the three locations are presented in Table 7.

Seed yield. Application of GA_3 at San Mateo and Maligaya gave highly significant increases in seed yield of 472 and 346 kg/ha, respectively. However, GA_3 had no pronounced effect at IRRI. urea was effective only at IRRI, and gave an advantage of 143 kg/ha. However, it was not effective in San Mateo or Maligaya. The increase in seed yield due to Flc was significant in Maligaya, but not in San Mateo (139 kg/ha); seed yield at IRRI was significantly reduced. Effects of Sp were not significant in all test locations, indicating that wind velocity was sufficiently high to nullify the effect of sp.

Outcrossing rate. The influence of GA_3 on seed setting varied across the three locations. Gibberellic acid significantly increased seed set at Maligaya and San Mateo

Table 7. Main effects of the four basic components of hybrid rice seed production practices in three locations, 1990 DS[a].

Character	GA$_3$			Urea			Flag leaf clipping			Supplementary pollination		
	San Mateo	Mali-gaya	IRRI	San Mateo	Mali-gaya	IRRI	San Mateo	Mali-gaya	IRRI	San Mateo	Mali-gaya	IRRI
Seed yield of A (kg/ha)	472**	346**	·54	·33	-63	143*	139	191*	–242**	96	–35	106
Seed set of A (%)	4.61**	8.13**	–2.54**	–3.29*	0.29	0.30	2.21	3.79	0.04	0.37	0.54	–0.46
1000-seed wt of A (g)	0.31*	0.25	0.01	0.06	0.12	0.34	0.06	0.12	–1.00**	0.24	0.28	0.16
Seed discoloration of A (%)	–1.49	0.21	6.71**	2.01*	0.56	1.09	1.76	0.75	8.05**	–0.88	–.31	4.87*
Panicle exsertion of A(%)	0.30	0.72	1.62	0.89	0.19	0.28	–0.80	–2.38**	–.03**	1.35	0.01	1.07
Height of A (cm)	19.75**	20.62**	11.62**	–0.25	0.38	1.38	–0.50	–3.37	–5.62**	0.25	–0.62	1.38
Grain yield of B (kg/ha)	–88*	–71*	61	37	69	130	–310**	–120**	–379**	–95*	–87*	34
1000-seed wt of B (g)	–0.22	–0.08	–0.55	1.38	–0.73*	0.23	1.30	0.19	–0.70**	1.30**	–0.01	0.11
Height of B (cm)	12.75**	18.37**	10.00*	0.75	0.87	1.25	–1.00	–2.10	–5.25**	–2.0	–1.63	1.00
Pollen load (no./li)	–	–	0.14	–	–	0.31	–	–	–0.59	–	–	0.15

[a] ** = Significant at the 1% level: * = significant at the 5% level.

but reduced seed set at IRRI. The crops in Maligaya and San Mateo had better growth and development than those at IRRI. It is therefore surmised that GA_3 gives better results in good and healthy crops.

There is no clear trend in the contribution of U to outcrossing rate. The seed parent did not respond at IRRI and Maligaya, while application at San Mateo decreased seed setting by 3%. Flag leaf clipping and Sp had no significant result on outcrossing rate across locations.

Seed weight. The 1000-seed weight of the seed parent was heavier at San Mateo with GA_3 application, but effects were not evident at Maligaya and IRRI. There was no indication that U, Flc, and Sp contribute to a heavier seed density. Instead, Flc tended to reduce seed weight on crops with marginal growth.

Seed discoloration. The different components tested did not significantly reduce seed discoloration. Flag leaf clipping, GA_3, and Sp increased seed discoloration, especially under high disease pressure. Urea also tended to cause seed discoloration at San Mateo.

Panicle exsertion. The different components did not improve panicle exsertion at any of the test locations. Flag leaf clipping reduced panicle exsertion in Maligaya and at IRRI. Genotypes like IR62829 A are clearly not receptive to elongation of the uppermost internode, even with the application of GA_3. Reassessment of GA_3 application time might be useful to maximize efficiency.

Height of seed parent. Gibberellic acid greatly contributed to height increase in all locations, while Flc significantly reduced plant stature at IRRI. Variations in the effects of Flc between locations might be due to differences in the degree of clipping of the flag leaves and crop stand.

Grain yield of pollen parent. Flag leaf clipping reduced the grain yield of the pollen parent in all locations. Gibberellic acid application in Maligaya and Sp in San Mateo and Maligaya reduced grain yield of the pollen parent.

Grain weight of pollen parent. The different components had no positive effect on grain weight. Application of GA_3 reduced grain weight of pollen parent at IRRI, and so did U at Maligaya, Flc at IRRI, and Sp at San Mateo.

Height of pollen parent. Increased height was due to GA_3 application while Flc reduced height.

Pollen load. Observations on pollen load were made only at IRRI. The different components failed to show significant contributions to increase pollen load. Flag leaf clipping seemed to reduce pollen load.

Economics of hybrid seed production

Twelve seed production plots (about 1,000-2,500 m^2 each) were established at Maligaya, San Mateo, Midsayap, and Iloilo in four crop seasons (1990 DS-1991 WS). Labor and nonlabor inputs were monitored.

The production plots gave an average hybrid seed yield of 1.3 t/ha (range, 0.5-2.3 t/ha) and an additional grain yield of 1.8 t/ha (range, 1.0-2.9 t/ha) from the pollen parent (Table 8).

Table 8. Economics of hybrid rice seed production per hectare in the Philippines, 1990-WS-1991 WS.

Item	Input/output	
Labor	Labor day[a]	Labor–animalday[b]
Seedling propagation	8.4	2.1
Land preparation	3.9	19.4
Pulling and distribution of seedlings, transplanting, and replanting	64.3	None
Care of transplanted seedlings	68.0	None
Roguing	9.9	None
Flag leaf clipping	7.1	None
GA_3 application	5.4	None
Supplementary pollination	4.8	None
Harvesting, threshing, and hauling of harvest	68.5	None
Drying, processing, and bagging	13.0	None
Total	253.3	21.5
Nonlabor	Quantity	Value (US$)
A-line seeds	20.4 kg/ha	24.50
Male parent seeds	7.2 kg/ha	2.30
Complete fertilizer (14-14-14)	4.5 bags/ha	18.00
Urea fertilizer (46-0-0)	1.5 bags/ha	6.00
Insecticide	2 q/ha	12.00
Herbicide	1 q/ha	6.00
GA_3	15 g/ha	144.00
Rat baits		
Rodenticides and		4.00
broken rices		2.00
Sacks		6.00
Needle and twine		4.00
Bagging materials		24.00
Irrigation fee	Per 150-kg rice	30.00
Total		380.80
Total variable cost (US$): 973.40		
Yield (t/ha)		
Hybrid seeds: 1.4 (1.5-2.2)		
Harvest from male parent: 1.8 (1.0-2.9)		
Production cost (US$/kg seeds): 0.72		
Additional income (harvest from the males at US$0.20/ha): 362.00		

[a] Labor-day costs about US$2.00. [b] 1 labor-animalday costs about US$4.00.

The computed cost of production was US$973/ha. Total labor inputs were 253 labor-days and 22 labor-animaldays, valued at US$593. Nonlabor inputs, such as seeds, fertilizers, pesticides, GA_3, and others, were valued at US$381.

Based on the above total variable cost sf production and seed yield, the production cost of hybrid seed was estimated to be US$0.72kg. Additional income derived from the pollen parent was US$362.

Assuming that hybrid seed will cost US$1/kg, five times higher than the price of grain and about three times higher than the price of certified seeds of conventional varieties, a net profit of about US$741 can be realized, including benefits derived from the pollen parent.

Reports have shown that hybrid seeds in China are valued highly so that profitability of hybrid seed production provides greater incentives for seed growers. Under Philippine conditions, however, there should be a balance between incentives for seed growers and those for seed users to equally distribute benefits from the technology. Government pricing policy, therefore, must consider these. If production costs remain stable, profits can be raised when yields are high. Seed yields can be increased by selecting the most suitable location, season, and cultural practices for seed production. With increased yield and the identification of an effective, cheaper substitute for GA_3, seed production costs could be further reduced.

Maximizing the efficiency of GA_3

Hybrid seed production costs could be reduced by lowering GA_3 dosage or finding a cheaper substitute. Chinese scientists recommended using GA_3 at 100-150 g/ha to increase hybrid seed yields. This amount of GA_3, however, is extremely costly under Philippine conditions. Initial findings showed that using ultralow-volume sprayers to apply GA_3 solution reduced the amount of GA_3 to 30 g/ha. This type of sprayer greatly increased the efficiency of GA_3 in hybrid seed production. The significant decrease in dosage results from the higher and more uniform distribution of the GA_3 solution.

Verification trials in Cagayan Valley

Verification trials were established in Cagayan Valley after encouraging results were obtained from the hybrid rice experiments. An orientation seminar for 24 seed growers and 6 seed production technicians was given in November 1990. The participants were provided with a hybrid rice seed production manual and seed materials for the 1992 DS trials. The trials served as a training program for producing quality seed and, at the same time, verified or generated data. The participants were convened at the end of each season to review the results of their trials and to plan activities for the next season. Results of the 1992 DS and 1992 WS trials are presented in Table 9. The number of seed growers was reduced to 16 for the 1992 WS because of poor performance.

Seed yield. Average seed yield was about 1 t/ha during 1992 DS and increased to 1.13 t/ha during 1992 WS. For hybrid rice seed production, DS planting is supposed to be more favorable than WS planting. The increase during the WS planting could therefore be attributed to experience gained by growers.

Seed rate used. Seed stocks of seed parents (A line) ranged from 6 to 59 kg/ha, with an average of 34 kg in the first season. This was reduced to 12 kg/ha during the second season. The pollen parent (R line) ranged from 3 to 35 kg/ha, with an average of 20 kg/ha in the first season. The average was 7 kg/ha in the second season.

Performance of seed growers. Among the 24 seed growers during the first season, 7 had very satisfactory performance; followed by 4, satisfactory; and 13, fair. For the second season, there were 13 with very satisfactory to satisfactory performance and only 3 with fair performance.

Economics of seed production. The cost of production averaged US$800/ha during the first season and US$745/ha during the second season. Based on the total variable cost of production and seed yield, hybrid seed production costs were estimated to be

Table 9. Hybrid rice seed production verification trials in Cagayan Valley in 1992.

Item	DS	WS
Number of seed growers	24	16
Seed yield of A (kg/ha)		
Average	997	1130
Range	687-1741	367-2130
Grain yield of R (kg/ha)		
Average	2250	2380
Range	1200-2675	1100-2845
Seed requirement (kg/ha)		
Average (A line)	34	12
Range for (A line)	6-59	6-22
Average for (R line)	20	7
Range for (R line)	3-35	3-13
Performance of seed growers (no. of growers)		
Very satisfactory		
Satisfactory	4	5
Fair	13	3
Cost of production (US$)		
Average	800	745
Range	537-970	440-872
Computed production cost of hybrid seed (US$/kg processed seed)		
Average	0.80	0.65
Range	0.45-1.16	0.34-2.02
Added income derived from the pollen parent[a] (US$)		
Average	450	476
Range	240-525	220-569
Quality of seeds produced (no. of samples)		
Very satisfactory	–	6
Satisfactory	–	4
Fair	–	1

[a] Price of grain is US$0.20/kg.

US$0.80/kg in the first season and US$0.65/kg in the second season. Additional income from the pollen parent was US$450 in the first season and US$476 in the second season.

Quality of seed product. Seed quality was evaluated using hybrid seed produced in their own fields. Varietal purity and general performance of hybrid seed were compared with those of the best local varieties in the 1992 DS. Ten seed growers produced good quality seeds on the basis of the grow-out test.

Production constraints

Policies for hybrid seed production and distribution of quality hybrid seeds are still on the drawing board. The seed production system in the Philippines is only beginning to gain strength. Even the system of certified seed production for standard conventional varieties is still inadequate. Furthermore, resource-poor farmers may not be in a position to produce hybrid seeds.

To popularize the use of hybrid rice, an effective hybrid seed production and distribution system must be established to stabilize the price of certified hybrid seed at a reasonable level. Target areas must be identified and seed growers trained periodically.

Research and development to improve seed yield must continue, especially on the aspect of identifying better pollinators (males) and receptors (females) as parents of new hybrids. Improvement in seed yield will eventually reduce the cost of hybrid rice seeds.

Conclusion and future outlook

Hybrid seed production technology could increase rice yield in the Philippines tremendously. The inherent vigor (heterosis) of hybrids and efficient management practices suggest a bright future for hybrid rice. Hybrid rice technology is most relevant in areas where land is becoming scarce and population density is increasing. The technology will be tested first in a high yield environment, where maximum production inputs can be applied to take advantage of the greater potential offered by the hybrid. The genetic tools (male sterile, maintainer, and restorer lines) essential to develop hybrid seed production techniques patterned after those developed by Chinese scientists are now being tested in seed growers' fields.

Notes

Authors' address: R. J. Lara, I. M. dela Cruz, M. S. Ablaza, H. C. dela Cruz, and S. R. Obien, Philippine Rice Research Institute, Maligaya, Muñoz, Nueva Ecija, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in Vietnam

Nguyen Van Luat, Hoang Tuyet Minh, and Nguyen Van Suan

Hybrid rice research in Vietnam began in 1983 at Haugiang, Mekong Delta, in the south and Hanoi, Red River Delta, in the north. Many cytoplasmic male sterile (CMS) lines introduced from China and IRRI were evaluated. Three lines, V20 A, IR58025 A, and IR62829 A, showed complete and stable male sterility. Several prospective maintainers and restorers were identified for these CMS lines. Some were used either to develop F_1 hybrids or in backcross breeding programs. Studies on hybrid seed production revealed that hybrid seed yields of up to 2.0 t/ha were possible, using suitable techniques such as GA_3 spray combined with flag leaf clipping and rope pulling. The hybrids tested in the Mekong and Red River deltas showed yield advantages of 15-40% over check varieties. Promising hybrids identified were IR54757 A/IR64 R (7.50 t/ha), IR54752 A/IR64 R (7.20 t/ha), IR58025 A/IR29723 R (7.56 t/ha), IR62829 A/IR29723 R (6.73 t/ha), and IR62829 A/Pusa R (9.05 t/ha). In demonstration plots, hybrid varieties yielded an average of 20% more than the best conventional varieties.

Hybrid rice research in Vietnam began in 1983 at Haugiang (10° latitude) in the Mekong Delta (MD) and Hanoi (20° latitude) in the Red River Delta (RD). These are the most important and productive rice areas in the country.

The original research program had the following objectives:

- To evaluate cytoplasmic male sterile (CMS) lines and identify prospective maintainer and restorer lines,
- To develop suitable techniques for enhancing hybrid seed production, and
- To evaluate the yield advantage of F_1 hybrids and identify promising hybrid combinations.

Evaluation of CMS lines and identification of maintainer and restorer lines

Evaluation of CMS lines

Twenty-eight CMS lines were evaluated for pollen and spikelet sterility. Three lines, V20 A, IR58025 A, and IR62829 A, showed almost complete and stable male sterility (Table 1).

IR58025 A and IR62829 A also possessed good phenotypic acceptability. These lines have been used to develop F_1 hybrids and to transfer CMS to elite breeding lines to develop new CMS lines. IR58025 A was found to be aromatic with long slender grains. This line could be used to develop hybrids with good grain quality.

Studies on the reaction of CMS lines to diseases revealed that V20 A, Zhen shan 97 A, and Yar-Ai-Zhao A were moderately resistant to bacterial leaf blight (*Xanthomonas campestris* pv. *oryzae*) and blast (*Pyricularia oryzae*), but susceptible to sheath blight (*Rhizoctonia solani*). IRRI-bred CMS lines, such as IR58025 A, 1R62829 A, IR54725 A, and IR46830 A, were found to be resistant to diseases and insect pests under field conditions.

Identification of maintainer and restorer lines

Thirty-eight cultivars/lines of very early and early maturity duration were testcrossed as single plants with CMS line IR58025 A in MD and with IR62829 A in RD. The testcross F_1, their corresponding male parents, and check varieties were grown in rows with 1 seedling/hill.

The F_1 combinations were examined for pollen sterility and spikelet sterility on bagging. If a testcross showed 95-100% pollen sterility, its male parent could be considered a prospective maintainer. If it showed normal pollen and spikelet fertility (>80%), its male parent was identified as a prospective restorer. The results (Table 2) revealed that OM725-10, S818B, OM59-71, and IR52287-15 were prospective restorers for IR58025 A in MD. V52, V62, and V15 were prospective restorers for IR62829 A in RD. Eight cultivars/lines, OM59-7, OM43-26, IR13240-108, OM554, IR50404, OM570, IR13428, and IR44535, were identified as prospective maintainers for IR58025 A in MD. The maintainers identified for IR62829 A in RD included IR8423, DT10, Basmati, and N8. Interestingly, most of the prospective maintainers had good agronomic characteristics and high adaptability to local conditions. The transfer of CMS to these lines to develop new CMS lines is under way.

Techniques for enhancing hybrid seed production

Natural outcrossing in CMS lines

The extent of natural outcrossing and seed yield in CMS lines V20 A, IR58025 A, IR54752 A, and IR62829 A was investigated. The natural outcrossing rate ranged from 12.4% in IR54752 A/IR64 R to a maximum of 20.0% in IR58025 A/B (Table 3). cytoplasmic male sterile seed yield varied from 183 kg/ha in V20 A/B to 728 kg/ha in IR58025 A/B.

Table 1. Pollen and spikelet sterility of some CMS liner in Mekong Delta and Red River Delta, Vietnam.[a]

CMS line	Location	Pollen sterility		Spikelet sterility on bagging (%)	
		WS	DS	WS	DS
V20 A	MD	CS	CS	100	100
	RD	CS	CS	100	100
IR58025 A	MD	CS	S	100	100
	RD	CS	S	100	100
IR62829 A	MD	S	S	92.6	94.2
	RD	CS	CS	99.6	99.2
IR54752 A	MD	PS	S	73.7	97.5
	RD	–	CS	–	–
IR46830 A	MD	PS	S	72.5	90.0
	RD	CS	CS	–	–

[a] WS =wet season, DS = dry season, MD = Mekong Delta, RD = Red River Delta. CS =completely sterile (100% sterility), S = sterile (90-99% sterility), PS = partially sterile (70-89% sterility).

Table 2. Maintainer and restorer lines identified in Mekong Delta (MD) and Red River Delta (RD), Vietnam, 1991 WS.

Line	Pollen sterility (%)	Spikelet sterility on bagging (%)
Tester: CMS line IR58025 A in MD		
Maintainers		
0M59-7	100.0	100.0
0M43-26	100.0	100.0
IR13240-108	98.5	99.2
0M554	98.0	98.0
IR50404	96.9	99.0
0M570	95.7	96.8
IR13428	94.2	93.5
IR44535	93.6	96.8
Restorers		
0M725-10	18.1	19.2
S818B	19.2	19.8
0M59-71	18.2	19.8
IR52287-15	19.8	20.0
Tester: CMS line IR62829 A in RD		
Maintainers		
IR8423	94.7	85.0
DT10	93.8	91.0
Basmati	96.0	84.0
N8	95.0	89.0
Restorers		
V52	4.0	7.5
V62	4.2	8.4
V15	3.5	4.8

Table 3. Natural outcrossing rate and seed yield in CMS lines in Mekong Delta.

Combination	Outcrossing rate (%)	Seed yield (k/ha)
1989 DS		
V20 A/B	15.4	183
IR58025 A/B	20.0	471
IR62829 A/B	17.3	624
IR54752 A/IR46 R	18.1	–
IR54752 A/IR20723 R	16.7	–
IR54752 A/IR68 R	15.8	–
IR54752 A/0M80 R	14.6	–
IR54752 A/IR64 R	12.4	–
1990 WS		
IR58025 A/B	18.1	728

A significant difference in outcrossing potential between CMS lines was observed. IR58025 A and IR62829 A seemed to possess higher outcrossing potential than V20 A and IR54752 A.

Effect of various cultural practices on outcrossing and seed yield in CMS lines

The low natural outcrossing rate of rice (normally below 20% in MD) is the major limitation in hybrid seed production. To popularize hybrid rice in tropical countries like Vietnam, hybrid seed production must be enhanced to economically viable levels. Hybrid research in Vietnam has, therefore, focused on improving seed production technology. Experiments on seed production techniques using IR62829 A/IR29723 R were conducted in three successive seasons, 1990 WS, 1991 DS, and 1991 WS. Row ratios (A:R) of 4:2 and plant spacing of 15 × 20 cm were followed. Row direction was perpendicular to the prevailing wind direction during anthesis. Flowering synchronization between A and R lines was adjusted by transplanting IR62829 A 20 d after IR29723 R. The treatments were as follows:

- Gibberellic acid (GA_3) spray + flag leaf clipping (Flc) + rope pulling (R)
- GA_3 + Flc
- GA_3
- Flc + R
- Flc
- R
- Control (untreated)

Gibberellic acid (60 ppm) was sprayed at 5% heading. A second spray of GA_3 (30 ppm) was done at 50% heading. Flag leaves were clipped at 1/2 the length at late booting stage, just before panicle emergence. Rope pulling was done 3-4 times a day during the period of maximum spikelet blooming.

The results obtained over the three seasons showed that all treatments except R significantly enhanced outcrossing rate and hybrid seed yield (Table 4). Their effects could be graded as follows: GA_3 + Flc + R = GA_3 = Flc + R > Flc. The treatment GA_3 + Flc + R showed maximum outcrossing rate of 32.7% and hybrid seed yield of

Table 4. Effect of cultural practices on outcrossing rate and hybrid seed yield obtained from the combination IR62829 A/IR29723 R in Mekong Delta, Vietnam.[a]

Cultural practice	1990 WS		1991 DS		1991 WS	
	Outcrossing rate (%)	Yield (t/ha)	Outcrossing rate (%)	Yield (t/ha)	Outcrossing rate (%)	Yield (t/ha)
GA_3 + Flc + R	23.4	1.4	32.7	2.2	18.6	0.7
GA_3 + Flc	22.5	1.1	27.3	2.1	17.6	0.8
GA_3	18.7	1.0	26.1	1.8	17.0	0.7
Flc + R	18.8	1.0	25.5	1.5	15.8	0.6
Flc	16.3	0.9	22.6	1.5	14.9	0.6
R	14.1	0.9	20.5	1.2	11.5	0.6
Control	13.7	0.8	20.2	1.2	11.5	0.5
CV(%)	10.6	7.2	20.5	19.7	21.4	22.7
LSD (0.05)	2.9	0.1	-	0.2	4.9	0.2

[a] WS =wet season, DS = dry season. GA_3 = gibberellic acid (60 ppm) spray, Flc = flag leaf clipping, R = rope pulling.

2.20 t/ha during 1991 DS, compared with an outcrossing rate of 20.2% and seed yield of 1.23 t/ha observed in the control. In 1990 and 1991 WS, seed yields obtained from the same treatment were 1.38 and 0.74 t/ha, respectively. These levels were almost double the controls seed yield. The GA_3 + Flc and GA_3 + Flc + R treatments showed similar effects. They were found to be more effective than GA_3 spray only or Flc + R.

It appeared from the results that GA_3 + Flc + R or GA_3 + Flc enhanced hybrid seed production. Further, it was obvious that seed production in MD was significantly higher in DS than in WS. The climatic conditions in DS favored cross pollination. High rainfall in WS may be responsible for the decrease of outcrossing rate and seed yield.

In CMS and hybrid seed production plots, the combination IR52025 A/B showed 22.5% outcrossing and 1.23 t/ha seed yield with GA_3 sprayed at initial heading (Table 5). The combination IR58025 A/IR29723 R (for hybrid seed production) had an outcrossing rate of 32.6% and seed yield of 1.53 t/ha when GA_3 was sprayed at initial heading and flag leaves were clipped.

Yield advantage of F_1 hybrids

Yield trials of F_1 hybrids

Data from yield trials of F_1 hybrids in MD are presented in Tables 6, 7, and 8, while RD data are shown in Table 9.

In MD, five hybrids—IR54757 A/IR64 R, IR54752 A/IR64 R, IR54752 A/OM80 R, IR54757 A/IR68 R, and IR54757 NOM80 R—were superior to the best local check (MTL 61) in 1989-90 DS. These hybrids showed grain yields of 5.76-7.50 t/ha, compared with 5.18 t/ha of the local check (i.e., 11-42% standard heterosis). The most promising hybrids were IR54757 A/IR62 R (7.50 t/ha) and IR5472 A/IR64 R (7.20 t/ha).

In 1990 WS, three hybrids showed higher yields than the local check (5.18 t/ha): IR58025 A/IR29723 R (7.56 t/ha), IR62829 A/IR29723 R (6.73 t/ha), and IR58025 A/

Table 5. CMS seed production (combination IR58025 A/B) and F_1 hybrid seed production (combination IR58025A/IR29723 R) In Mekong Delta,Vietnam, 1990-91.

Combination	Outcrossing rate (%)	Seed yield (t/ha)	Cultural practices
IR58025 A/IR29723 R	22.5	1.2	GA_3 spray at initial heading
IR58025 A/IR29723 R	32.5	1.5	GA_3 spray at initial heading + Flc

Table 6. Grain yield of F_1 rice hybrids and their parental lines in Mekong Delta, Vietnam, 1989-90 DS.

Hybrid/line	Grain yield (t/ha)
IR54757 A/IR64 R	7.5
IR54752 A/IR64 R	7.2
IR54752 A/OM80 R	6.7
IR54757 A/IR68 R	6.2
IR54757 A/OM80 R	6.2
IR54752 A/IR68 R	5.8
OM80	5.7
IR64	5.3
IR68	4.8
MTL 61 (local check)	5.2
CV(%)	5.1
LSD (0.05)	0.1

Table 7. Grain yield of F_1 rice hybrids in Mekong Delta, Vietnam, 1990 WS.

Hybrid/line	Grain yield (t/ha)
IR58025 A/IR29723 R	7.6
IR62829 A/IR29723 R	6.7
IR58025 A/IR9761 R	6.0
IR62829 A/IR9761 R	5.9
IR62829 A/IR24 R	5.6
V20 A/IR9761 R	5.5
V20 A/Milyang 46 R	5.4
MTL 58 (local check)	5.3
MTL 61 (local check)	5.2
CV(%)	7.7
LSD (0.05)	0.8

IR9761 R (6.03 t/ha). In 1991 DS, the hybrids IR62829 A/IR29723 R and IR58025 A/IR29723 R again had the highest grain yields, 6.06 and 6.03 t/ha, respectively. Local check yield was 4.96 t/ha.

In RD, the 1991 DS yield trial showed two promising hybrids, V20 A/CR203 R (7.00 t/ha) and IR62829 A/Pusa R (9.05 t/ha).

Table 8. Grain yield of F_1 hybrids and their parental lines in Mekong Delta, Vietnam, 1990-91 DS.

Hybrid/line	Grain yield (t/ha)
IR62829 A/IR29723 R	6.1
IR58025 A/IR29723 R	6.0
IR62829 A/IR10198 R	5.6
IR62829 A/IA976 R	5.6
IR58025 A/IR9761 R	5.2
MTL 61 (local check)	5.0
IR29723-143-3-2-1 R	4.9
IR9761-19-1 R	4.8
IR10198-66-2 R	4.1
CV (%)	4.7
LSD (0.05)	0.4

Table 9. Grain yield of F_1 rice hybrids and their parental lines in Red River Delta, Vietnam, 1990-91 DS.

Hybrid	Grain yield of hybrid (t/ha)	Grain yield of R line (t/ha)
V20 A/CR203 R	7.0	3.9
V20 A/VCX83 R	6.1	3.9
V20 A/CN2 R	5.8	3.7
IR62829 A/Pusa R	9.1	7.3

Demonstration plots of rice hybrids

Some hybrids introduced from China (Tapgiao 1, Tapgiao 3, and Tapgiao 4) and some developed in Vietnam (IR58025 A/OM80 R, IR62829 A/IR29723 R, etc.) were grown in demonstration plots in both MD and RD.

In RD, the hybrids showed a maximum yield of 10.2 t/ha and average yields were 6.5-8.5 t/ha. Yields were 13-14% above the check variety (CR203), and 18-21% above other conventional varieties grown in 1990-91 DS. In a few cases, a yield advantage of 30% over the check variety was obtained. In areas near the border between Vietnam and China, in Quang Ninh and Lang Son provinces (22-23° latitude), the Chinese hybrids were planted to about 300 ha. The average yield of these hybrids was 3.5-4.5 t/ha, against 2.1 t/ha of the check variety Tran Chau Lun.

In MD, demonstration plots were smaller (500-1,000 m^2). The hybrids yielded 6.0-8.0 t/ha, an increase of about 20% over the best conventional check varieties.

Notes

Authors' addresses: Nguyen Van Luat, Cuu Long Delta Rice Research Institute, O Mon, Haugiang, Vietnam; Hoang Tuyet Minh, Plant Genetics Institute, Tu Liem, Hanoi, Vietnam; and Nguyen Van Suan, Agricultural Scientific and Technical Institute, Van Dien, Hanoi, Vietnam.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P. O. Box 933, Manila, 1099, Philippines.

Hybrid rice research in Indonesia

B. Suprihatno, B. Sutaryo, and T. S. Silitonga

Hybrid rice research in Indonesia began in 1983. Among the first group of cytoplasmic male sterile (CMS) lines introduced in 1980, ZS97 A, V20 A, and V41 A were found to be stable for pollen sterility and grew well, but they were susceptible to most insects and diseases, especially sheath rot. A second group consisting of seven IRRI CMS lines was introduced during 1983-84. IR46828 A, IR46830 A, and IR48483 A showed wider adaptability but appeared to have poor combining ability and outcrossing rate. IR54752 A, which was introduced later, showed some resistance to a few major insects and diseases. However, sterility of IR54725 A was later found to be very unstable. At present, IR62829 A and IR29744 A are the most promising CMS, both highly uniform and stable in terms of sterility, but they are susceptible to bacterial blight. Most of the latest CMS lines introduced (IR64608 A, IR64607 A, Krishna A, Pragathi A, and IR66707 A) show high sterility and have some good agronomic traits. Several new Indonesian CMS lines, IR9774 A, IR19809 A, Tondano A, and M8601 A, are being developed. Yield trials conducted during 1980-85 gave standard heterosis for yield ranging from 3.3 to 69.8%, with an average of 22.1%. Hybrids were generally earlier than the best check, and standard heterosis for productivity per day ranged from 3.0 to 91%, with an average of 44.7%. Hybrid yield advantage was due primarily to more spikelets per panicle and greater 1,000-grain weight. The hybrids, however, were all derived from Chinese CMS lines, which were found to be highly susceptible to most insects and diseases. Yield trials conducted during 1986-91 showed that in all F_1 hybrids using IR54752 A, there were many sterile plants due to instability. Therefore, we stopped using IR54652 A for hybrid development. Hybrids from combinations using IR62829 A and IR29744 A seemed to be quite promising. IR62829 A has shown outcrossing rates of ± 17.0%. Techniques of hybrid seed production developed in China are being adapted to Indonesian conditions. At present, sources of dominant genes for resistance to BPH biotype 3 and stem borer in restorers are very limited. This hinders progress in developing good F_1 hybrids for Indonesia.

Indonesia began research on hybrid rice in 1983, coordinated by the Sukamandi Research Institute for Food Crops (SURIF). Research was also conducted by the Bogor Research Institute for Food Crops and the Maros Research Institute for Food Crops. The objective of the research was to explore the prospects and problems of using hybrid rice in Indonesia. The research included studies on heterosis, male sterility and fertility restoration systems, and hybrid seed production techniques.

The successful development of hybrid rice in Indonesia depends largely on the availability of good cytoplasmic male sterile (CMS) lines (high outcrossing rates, stable sterility) with resistance to brown planthopper (BPH), stem borer (SB), and/or bacterial leaf blight (BB). Good restorers possessing genetic resistance to some pests and diseases are essential. Grain quality is another important consideration.

Performance of some F_1 hybrids

Hybrid rice was introduced when SURIF received two F_1 rice hybrids (ZS97 A/IR26 and V20 A/IR26) after the late Dr. B.H. Siwi visited China in 1980. The two hybrids were tested against some superior varieties and elite lines. Yields were 5.1 t/ha for ZS97 A/IR26 and 4.6 t/ha for V20 A/IR26. The superior varieties and elite lines yielded from 2.8 t/ha for IR42 to 4.5 t/ha for IR36 (Danakasuma 1985).

Yield trials were conducted between 1982 and 1985. The highest yield was almost always obtained from one or more of the hybrids tested. Standard heterosis of the best hybrids ranged from 2.6 to 69.8%, with an average of 22.1% (Table 1). The hybrids were generally earlier than the best checks (or even earlier than IR36), and the standard heterosis for productivity per day ranged from 3.0 to 91.2%, with an average of 44.7% (Suprihatno 1986).

In the 1984 dry season (DS) yield trial in Sukamandi and Kuningan, yield of F_1 hybrids derived from IR46829 A and IR46831 A (IR46829 A/IR54, IR46829 A/IR36, and IR46831 A/IR54) ranged from 3.1 t/ha for IR46831 A/IR54 to 4.9 t/ha for IR46829 A/IR36 at Kuningan. Yields of the other combinations at Sukamandi, such as IR10179 A/IR13524-21-2-3-3-2, IR747 A/IR50, IR10154 A/IR13419-113-1, MR365 A/IR36, and IR10154 A/IR15795-232-3-3-3-2, were 5.1, 4.9,4.8,4.7, and 4.1 t/ha, respectively. The best check in this trial was Kerala (3.7 t/ha). The F_1 hybrids gave standard heterosis ranging from 1.9% for IR10154 A/IR15795-232-3-3-2 to 26.6% for IR10179 A/IR13524-21-2-3-3-2. At Kuningan, yields ranged from 3.6 t/ha for IR10154 A/IR15795-232-3-3-3-2 to 4.7 t/ha for MR365 A/IR36. Yields of all F_1 hybrids with V20 A as the female parents (also tested in this trial) were even higher. The highest yield was 6.9 t/ha for V20 A/IR13419-113-1 (Table 2).

In yield trials conducted between 1986 DS and 1989-90 wet season (WS), F_1 hybrids derived from IR54752 A gave the highest yield in 1986 DS and 1986-87 WS. In these two seasons, F_1 hybrid yields ranged from 5.6 t/ha for IR54752 A/IR29512 to 7.8 t/ha for IR54752 A/IR29512. Standard heterosis ranged from 13.9 to 70.6% (best check was IR64) (Table 3). In the following seasons, yields of hybrids using IR54752 A as the female parent were generally low. However, in 1988-89 WS and 1989 DS, four hybrids—IR54752 A/IR21916, IR54752 A/IR19392, IR54752 A/IR29723, and

Table 1. Yield and productivity per day of experimental F_1 hybrids and superiority over the best check variety in 1982-85 yield trials (Suprihatno 1986).

Hybrid	Location	Year and season	Yield (t/ha)	Standard heterosis (%)	Productivity (kg/ha per d) (%)	Standard heterosis	Best check
IET3257/IR42	Muara	1982 DS	6.1	12.6	53.0	19.3	IR42
IET3257/IR54	Muara	1982 DS	4.8	11.8	41.3	3.0	IR54
V20 A/Suweon 294	Muara	1983 DS	5.0	62.1	53.8	74.1	IR36
V20 A/Semeru	Muara	1983 DS	4.2	28.0	49.3	56.5	IR26
V20 A/IR42	Maros	1982-83 WS	7.2	15.3	72.2	32.7	IR42
ZS97 A/IR26	Maros	1983 DS	8.9	33.6	100.4	71.0	IR42
V20 A/M66b	Maros	1983 DS	8.5	27.5	90.7	54.0	IR42
V20 A/IR26	Maros	1983 DS	8.1	21.5	91.3	55.5	IR42
V20 A/IR42	Maros	1983 DS	7.6	14.0	81.2	38.3	IR42
V20 A/IR54	Maros	1983 DS	7.3	9.2	82.1	39.8	IR42
IR1015 A/IR15795	Sukamandi	1983 DS	7.5	17.1	90.0	31.2	IR54
97 A/Suweon 294	Sukamandi	1983 DS	7.0	9.5	71.3	18.5	IR54
V20 A/IR54	Sukamandi	1983-84 WS	6.9	10.7	79.4	22.1	IR36
V20 A/Sadang	Sukamandi	1983–84 WS	6.8	8.9	73.9	13.7	IR36
97 A/Sadang	Sukamandi	1983–84 WS	6.7	7.4	74.4	14.4	IR36
97 A/IR54	Sukamandi	1983-84 WS	6.5	3.3	71.6	10.1	IR36
V20 A/IR54	Sukamandi	1984 DS	5.0	41.5	59.8	65.2	IR50
V41 A/IR42	Sukamandi	1984 DS	4.9	39.9	55.8	54.1	IR50
V20 A/Sadang	Sukamandi	1984 DS	4.9	39.0	56.7	56.7	IR50
V41 A/Sadang	Sukamandi	1984 DS	4.8	35.3	54.6	50.8	IR50
V20 A/IR13419	Sukamandi	1984 DS	6.9	69.8	78.2	91.2	Kerala
V20 A/Milyang 46	Sukamandi	1984 DS	5.9	45.6	67.8	65.7	Kerala
V20A/IR9761	Sukamandi	1984 DS	5.9	44.4	70.5	72.3	Kerala
97 A/Semeru	Sukamandi	1984 DS	5.3	30.6	61.5	50.3	Kerala
V41 A/IR54	Sukamandi	1984–85 WS	5.2	4.0	60.7	28.6	IR54
V20 A/IR54	Sukamandi	1985 DS	4.3	12.7	50.0	57.7	Cisadane
V20 A/IR9761	Sukamandi	1985 DS	4.1	8.4	47.0	48.2	Cisadane
V20 A/IR9761	Maros	1985 DS	4.6	9.3	59.1	55.1	IR42
V41 A/IR54	Maros	1985 DS	4.4	6.7	57.6	51.2	IR42
V20 A/IR26	Maros	1985 DS	4.3	3.6	54.5	43.0	IR42
V20 A/IR54	Maros	1985 DS	4.3	2.6	54.0	41.7	IR42
Mean			5.9	22.1	66.89	44.70	

IR54752 A/IR46—yielded ± 7 t/ha, but the highest standard heterosis obtained was only 12.3% (IR64 was best check). In general, standard heterosis of other hybrids using IR54752 A for parent materials was negative due to high sterility. IR46830 A/IR9761, V20 A/IR42, and Tondano A/IR54 (developed in Indonesia) yielded 6.0, 5.9, and 5.1 t/ha, respectively.

In 1990 DS, hybrid yields in t/ha were 6.4 (Tondano A/IR29512), 6.3 (Tondano A/IR25912), 6.3 (Tondano A/Sadang), 6.2 (Tondano A/Cimanuk), 6.2 (Tondano A/M66b), 6.0 (Tondano A/IR54), 6.0 (Tondano A/IR19058), 5.8 (Tondano MR21916), and 5.8 (Tondano A/IR29723). Standard heterosis ranged from -4.6 to 5.4%, compared with IR64 as the best check variety (Table 4).

Six new hybrids introduced from IRRI—IR64610H(IR9761), IR64611 H (IR58025 A/IR9761), IR64615 H (IR58025 A/IR29723-143-3-2-1R), IR64616 H (IR62829 A/

Table 2. Yield, standard heterosis, and productivity per day of some F_1 hybrids, Sukamandi and Kuningan, 1984 DS (Suprihatno and dan Satoto 1986).

Hybrids	Yield (t/ha)		Standard heterosis (%)		Productivity (kg/ha per d)		Standard heterosis (%)	
	Sukamandi	Kuningan	Sukamandi	Kuningan	Sukamandi	Kuningan	Sukamandi	Kuningan
V20 A/IR13419-113-1	6.9	5.2	70.1	−10.8	78.2	52.0	91.2	−5.5
V20 A/Milyang 46	5.9	–	45.9	–	67.8	–	65.8	–
V20 A/IR9761-19-1	5.9	6.7	44.7	15.6	70.5	75.9	72.3	37.9
Sadang	–	5.8	–	–	–	52.4	–	–
ZS97 A/IR2307-247-2-2-3	5.3	5.5	30.8	−5.5	61.5	58.7	50.4	6.5
Cisadane	–	5.4	–	–	–	46.1	–	–
V20 A/IR13420-6-3-3-1	5.2	–	29.3	–	61.5	–	50.4	–
V20 A/IR2307-247-2-2-3	5.2	5.8	27.5	0.3	60.7	65.9	48.4	19.8
IR10179 A/IR13524-21-2-3-3-2	5.1	3.4	26.6	-41.9	57.5	36.1	40.7	−34.4
V20 A/IR54	5.0	4.0	22.7	−30.1	59.9	46.4	46.4	−15.6
V20 A/IR2798-105-2-2-3	4.9	–	22.0	–	54.3	–	32.7	–
IR747 A/IR50	4.9	4.3	19.3	−24.9	53.3	46.7	30.3	−15.2
IR10154 A/IR13419-113-1	4.8	–	17.2	–	53.4	–	17.2	–
MR365 A/IR36	4.7	4.7	16.0	−14.3	52.8	49.7	29.1	-9.7
IR46829 A/IR54	4.7	4.0	15.6	−31.1	49.8	41.9	21.7	−23.9
IR46829 A/IR36	4.5	5.0	10.4	−14.2	49.1	53.3	20.1	−3.1
IR46831 A/IR54	4.4	3.1	8.4	-46.4	45.3	30.4	10.7	-44.8
IR10154 A/IR15795-232-3-3-3-2	4.1	3.6	2.0	−38.1	45.3	38.6	10.7	−29.9
Kerala[a]	4.1	5.6	–	–	40.9	51.3	–	–
Bogowonto	3.8	5.3	–	–	36.4	49.0	–	–
IR50[b]	3.7	5.8	–	–	38.6	55.0	–	–
MR365 A/IR17494-32-1-1-3-2	3.7	1.6	−9.6	−73.3	39.8	16.8	−2.7	-69.4
MR365 A/IR13524-21-2-3-3-2	3.7	3.4	-11.4	-41.9	39.0	36.1	-4.6	-34.4
IR36	3.4	4.7	–	–	33.3	43.1	–	–
MR365 A/Milyang 54	3.2	2.3	-20.3	−59.5	33.3	23.6	−18.6	−57.1
MR365 A/IR50	3.0	3.4	-26.7	-40.7	32.6	36.1	−20.2	−34.4
IR54	2.5	5.6	–	–	24.7	48.3	–	–
MR365 A/IR13420-6-3-3-1	1.8	1.5	-58.8	−74.6	18.4	15.5	−55.1	−71.9

[a] Best check at Sukamandi. [b] Best check at Kuningan.

IR29723), IR64617H (IR58025 A/IR10198), and IR64618H (IR62829 A/IR10198)—were evaluated in replicated yield trials in 1990-91 WS. All the hybrids tested gave negative standard heterosis, the highest yield was obtained by IR64 (6.8 t/ha). Among the six hybrids, only IR64616 H and IR64618 H yielded quite high, giving 6.3 and 5.2 t/ha, respectively (Table 4). All the hybrids were affected by BB. However, in 1991 DS, IR62829 A/M66 B, IR62829 A/IR64, and IR29744 A/M66b gave positive standard heterosis (36.1-49.3%) compared with IR64. Yields of hybrids derived from IR58025 A ranged from 1.1 t/ha for IR58025 A/IR32809 to 5.9 t/ha for IR58025 A/IR10198, with standard heterosis ranging from -82.1 to 0.0% (Table 4). There were only 3 hybrids with yields not significantly lower than IR64. The rest of the hybrids yielded significantly lower than IR64. High percent sterility of the hybrids was one of the reasons for the low yield, and this was probably due to the unusual dry season in 1991.

At present, the most promising hybrids are derived from IR62829 A and IR29744 A.

Table 3. Yield of F_1 hybrids and extent of their superiority over the best check variety in 1986 DS and 1989-90 WS yield trials.

Experimental hybrid	Location	Year and season	Yield (t/ha)	Standard heterosis (%)	Best check
IR54752 A/IR19392	Sukamandi	1986 DS	5.9	20.5	IR64
IR54752 A/IR29512	Sukamandi	1986 DS	5.6	13.9	IR64
IR54752 A/IR29512	Sukamandi	1986-87 WS	7.8	70.6	IR54R
IR54752 A/IR54R	Sukamandi	1986-87 WS	5.8	25.1	IR36
V20 A/IR42	Sukamandi	1986-87 WS	5.9	30.0	IR54
IR54752 A/Kruang Aceh	Sukamandi	1987 DS	5.5	4.0	IR64
IR54752 A/Sadang	Sukamandi	1987 DS	5.4	0.0	IR64
Tondano A/IR54	Muara	1987 DS	5.1	70.0	Cisadane
IR46830 A/IR9761	Kuningan	1987-88 WS	6.0	-10.3	IR64
IR54752 A/Kruang Aceh	Kuningan	1987-88 WS	5.2	-22.3	IR64
IR54752 A/IR21916	Sukamandi	1988-89 WS	7.8	12.3	IR64
IR54752 A/IR29723	Sukamandi	1988-89 WS	7.4	6.5	IR64
IR54752 A/IR19392	Sukamandi	1988-89 WS	7.4	6.8	IR64
IR54752 A/IR46	Mertoyudan	1989 DS	7.1	9.9	IR64
IR54752 A/IR46	Kuningan	1989 DS	6.8	5.4	IR64
IR54752 A/IR19392	Kuningan	1989 DS	7.0	9.2	IR64
IR54752 A/M66b	Sukamandi	1989-90 WS	4.5	-10.1	IR64
IR54752 A/IR29512	Sukamandi	1989-90 WS	4.0	-19.8	IR64

Performance of CMS lines

The first CMS lines from China were introduced to Indonesia in 1980 (ZS97 A, V20 A, V41 A, Er-Jiu-Nan 1 A, and Wu 10 A) (Table 5). Subsequently, CMS lines from IRRI were introduced periodically for evaluation in Indonesia. ZS97 A, V20 A, V41 A, Er-Jiu-Nan 1 A (wild abortive [WA] type), Yar-Ai-Zhao A (Gambiaca cytoplasm), Pankhari 203 A (TN1 cytoplasm), Wu 10 A (Chinsurah Boro II or BT cytoplasm), and MS577 A (*O. sativa. spontanea* cytoplasm) were not suitable for developing F_1 hybrids for the tropics. ZS97 A, V20 A, V41 A, Er-Jiu-Nan 1 A, Yar-Ai-Zhao A, and MS577 A were susceptible to major diseases and insects, while Pankhari 203 A had unimproved plant type. ZS97 A, V20 A, and V41 A were found to be stable for pollen sterility in Indonesia and grew well, but they were susceptible to most insects and diseases, especially sheath rot (Table 5).

IR46826 A, IR46827 A, IR46828 A, IR46829 A, IR46830 A, IR46831 A, and IR48483 A from IRRI were evaluated in 1984 (Table 6). Of these, IR46828 A, IR46830 A, and IR48483 A showed wider adaptability. IR46828 A and IR46830 A were also reported to be stable for pollen sterility and remained unaffected by environmental influences (Virmani et al 1985). These CMS lines, however, appeared to have poor combining ability and low outcrossing rate.

In 1986 DS, IR54752 A, IR54753 A, and IR54754 A were evaluated. IR54752 A was found to be a good parent and had some resistance to a few major insects and diseases. However, IR54752 A was later found to have very unstable sterility (Table 7). Hybrids produced using this particular CMS line were always found to be impure.

Table 4. Yleid of experimental F_1 hybrids and superiority over the best check variety in 1990-91 DS yield trials.

Experimental hybrid	Location	Year and season	Yield (t/ha)	Standard heterosis (%)	Best check
Tondano A/IR29512	Sukamandi	1990 DS	6.4	5.4	IR54
Tondano A/IR25912	Sukamnadi	1990 DS	6.3	4.6	IR64
Tondano A/Sadang	Sukamandi	1990 DS	6.3	3.4	IR64
Tondano A/Cimanuk	Sukamandi	1990 DS	6.2	2.3	IR64
Tondano A/M66b	Sukamandi	1990 DS	6.2	2.3	IR64
Tondano A/IR54	Sukamandi	1990 DS	6.0	-0.5	IR64
Tondano A/IR19058	Sukamandi	1990 DS	6.0	-0.9	IR64
Tondano A/IR21916	Sukamandi	1990 DS	5.8	-4.3	IR64
Tondano A/IR29723	Sukamandi	1990 DS	5.8	-4.6	IR64
M8601A/IR26912	Sukamandi	1990-91 WS	6.2	-3.8	IR64
M8601A/IR28178	Sukamandi	1990-91 WS	5.9	-9.3	IR64
IR64616 H	Sukamandi	1990-91 WS	6.3	-7.7	IR64
IR64618 H	Sukamandi	1990-91 WS	5.2	-24.3	IR64
IR64610 H	Sukamandi	1990-91 WS	4.9	-28.1	IR64
IR64611 H	Sukamandi	1990-91 WS	4.7	-32.0	IR64
IR64617 H	Sukamandi	1990-91 WS	3.8	-44.4	IR64
IR64615 H	Sukamandi	1990-91 WS	3.5	-48.7	IR64
IR6289 A/M66b	Sukamandi	1991 DS	4.4	36.1	IR64
IR29744 A/M66b	Sukamandi	1991 DS	4.8	49.3	IR64
IR62829 A/IR64	Sukamandi	1991 DS	4.8	48.4	IR64
IR58025 A/IR10198	Kuningan	1991 DS	5.9	0.0	IR64
IR58025 A/IR15324	Kuningan	1991 DS	5.4	-8.9	IR64
IR58025 A/Pusa150	Kuningan	1991 DS	5.2	-11.2	IR64
IR58025 A/IR40750	Kuningan	1991 DS	5.0	-14.9	IR64
IR58025 A/IR37839	Kuningan	1991 DS	4.7	-20.1	IR64
IR55025 A/IR54742	Kuningan	1991 DS	4.4	-25.0	IR64
IR58025 A/IR29723	Kunignan	1991 DS	1.6	-73.4	IR64
IR58025 A/IR32809	Kuningan	1991 DS	1.1	-82.1	IR64

At present, the most promising CMS lines available are IR62829 A, IR58025 A, and IR29744 A. IR62829 A and IR58025 A were evaluated in 1989-90 WS (Table 8). IR62829 A and IR29744 A are actually the same, they are stable in sterility, early-maturing, and have uniform medium-short stature. Unfortunately, they are susceptible to BB and their outcrossing rates in Indonesia are moderate (just above 10%), IR58025 A was reported to have stable sterility (IRRI), medium to tall stature, medium maturity, and dense panicles, but it is still not uniform. This CMS line seems to be more tolerant of BB, but is agronomically undesirable.

Five more IRRI CMS lines—IR64608 A, IR64607 A, Krishna A, Pragathi A, and IR66707 A—were tested in 1991. All showed high sterility (100%) except IR64607 A (97.65%). They also had better agronomic traits (Table 9).

Several new CMS lines, including IR19774 A, IR19809 A, Tondano A, and M8601 A, are still being purified.

Table 5. Evaluation of the first CMS lines introduced to Indonesia, Sukamandi, 1991 DS.

Line	Days to 50% flowering	Plant height (cm)	Panicles/ hill (no.)	Pollen Sterility (%)	Spikelet sterility (%)	Panicle exsertion (%)	Reaction[a] to	
							BPH	Sheath rot
ZS97 A	67	72	24	99	99	73	7	7
ZS97 B	69	72	26	0	2	79	7	7
V20 A	66	73	26	100	99	72	7	7
V20 B	65	73	25	0	0	77	7	7
V41 A	67	71	26	100	99	72	7	7
V41 B	67	71	26	0	4	79	7	7
Er Jiu Nan 1 A	64	64	14	97	95	70	7	7
Er Jiu Nan 2 B	64	65	11	5	5	74	7	7
Wu 10 A	62	65	10	95	94	71	7	7
Wu 10 B	62	65	10	6	3	74	7	7
Yar-Ai-Zhao A	68	69	15	96	90	78	5	5
Yar-Ai-Zhao B	68	69	15	3	7	80	5	5
MS577 A	69	70	19	97	91	78	5	5
MS577 B	70	70	19	97	91	78	5	5
Pankhari 203 A	70	74	11	94	93	77	5	5
Pankhari 203 B	70	74	12	7	7	75	5	5

[a] Evaluation based on *Standard evaluation system for rice.*

Table 6. Evaluation of CMS lines introduced to Indonesia in 1984.

Line	Days to 50% flowering	Plant height (cm)	Panicles/ hill (no.)	Pollen sterility (%)	Spikelet sterility (%)	Panicle exsertion (%)	Reaction[a] to	
							BPH	Sheath rot
IR46826 A	80	79	14	93	90	78	5	5
IR46826 B	81	80	14	7	9	79	5	3
IR46827 A	79	80	12	90	90	80	5	3
IR46827 B	79	80	13	7	8	80	5	3
IR46828 A	71	75	20	99	98	83	3	1
IR46828 B	72	76	20	2	3	85	3	1
IR46829 A	80	81	15	95	90	77	5	3
IR46829 B	82	81	14	7	10	79	5	3
IR46830 A	76	75	22	99	99	84	3	1
IR46830 B	77	76	23	0	1	85	3	1
IR46831 A	80	79	15	90	91	79	5	3
IR46831 B	80	80	14	5	6	80	5	3
IR48483 A	79	78	22	99	99	84	3	1
IR48483 B	79	79	20	2	1	85	3	1

[a] Based on *Standard evaluation system for rice.*

Hybrid rice seed production

Hybrid rice seed production techniques developed in China (Lin and Yuan 1980) have been used and evaluated in Indonesia. The techniques were evaluated in CMS multiplication and hybrid seed production plots during 1983-84 WS using MR365 A as the female parent and Sadang and IR54 as restorers. The natural outcrossing rates on MR365 A were 13.7 and 19.4%, respectively (Table 10). In 1984-85 WS, CMS

Table 7. Evaluation of CMS lines introduced to Indonesia in 1986.

Line	Days to 50% flowering	Plant height (cm)	Panicles/ hill (no.)	Pollen sterility (%)	Spikelet sterility (%)	Panicle exsertion (%)	Reaction[a] to	
							BPH	Sheath rot
IR54752 A	95	90	15	93	90	88	3	3
IR54752 B	92	90	15	8	10	87	3	3
IR54753 A	96	90	12	90	90	86	3	3
IR54753 B	96	90	12	9	10	87	3	3
IR54743 A	95	91	13	90	90	88	3	3
IR54754 B	95	91	13	9	12	87	3	3

[a] Based on *Standard evaluation system for rice.*

Table 8. Evaluation of CMS lines introduced to Indonesia in 1989-90 WS.

Line	Days to 50% flowering	Plant height (cm)	Panicles/ hill (no.)	Pollen sterility (%)	Spikelet sterility (%)	Panicle exsertion (%)	Reaction[a] to BLB
IR62829 A	84	85	18	91	97	80	7
IR62829 B	82	85	18	6	10	82	7
IR58025 A	89	97	14	95	94	81	7
IR58025 B	87	97	15	8	9	81	7

[a] Based on *Standard evaluation system for rice.*

Table 9. Evaluation of CMS lines introduced in 1991.

Line	Days to 50% flowering	Plant height (cm)	Panicles/hill (no.)	Pollen sterility (%)	Spikelet sterility (%)	Panicle exsertion (%)
IR64608 A	75	61.4	10.2	97.6	100	81.1
IR64608 B	68	64.2	9.4			
IR64607 A	91	73.0	10.8	99.3	97.6	62.6
IR64607 B	99	87.2	10.8			
Krishna A	69	59.0	17.8	90.1	100	81.4
Krishna B	74	62.0	12.6			
Pragathi A	91	64.0	7.2	97.4	100	71.2
Pragathi B	91	85.0	9.8			
IR66707 A	71	71.0	9.8	99.4	100	81.2
IR66707 B	76	75.0	9.9			

Table 10. Percentage of seed set in hybrid seed production plots, Sukamandi, 1983-84 WS (Suprihatno 1986).

Combination	Row ratio	Seed set (%)
MR365 A/IR54	1:4	18.00
	1:6	17.8
	1:8	19.4
MR365 A/Sadang	1:4	13.7
	1:6	17.5
	1:8	16.0

Table 11. **Effect of row ratio on seed yield of MR365 A/B Sukamandi, 1984-85 WS (Suprihatno 1986).**

Row ratio	Seed yield/150 hills (g)	Seed yield (t/ha)
2:3	1353.2 ab	1.3
2:4	1116.9 b	1.2
2:5	1519.4 a	1.8
2:6	1114.9 b	1.3
2:7	1016.7 b	1.3
2:8	1210.7 ab	1.6

Table 12. Interaction between row ratio, flag leaf clipping, and GA_3 concentrations on seedset per hill (Sutaryo et al 1990).[a]

Row ratio	Unpruning			Pruning		
	GA_3 (ppm)			GA_3 (ppm)		
	0	30	60	0	30	60
1:4	17.2C	24.7B	30.1A	17.1C	29.2B	33.7A
	b	a	a	b	b	a
1:6	17.9C	21.6B	30.1A	18.9C	21.8B	20.8A
	b	b	a	a	c	c
1:8	19.9C	21.7B	28.5A	19.88	31.6A	31.2A
	a	b	b	a	a	b

[a] Means followed by a different letter differ significantly at the 5% level.

multiplication plots using different row ratios were planted; seed yield ranged from 1.2 to 1.8 t/ha (Table 11).

The effects of gibberellic acid (GA_3) application, flag leaf clipping (Flc), and row ratio on V20 A/IR54 seed production were investigated in Sukamandi in 1986-87 WS. Application of GA_3 at 60 ppm increased yield, seed set, panicle exsertion, and plant height. In the treatment combinations (1:4, no Flc, and 60 ppm GA_3) and (1:4, Flc, and 60 ppm GA_3), seed set was 30.1 and 33.7%, respectively (Table 12). Seed yield was not significantly different and plant height was reduced as a result of Flc. There were correlations between seed set and yield, panicle exsertion and yield, and plant height and yield.

Experiments to evaluate the effects of plant growth hormones on percent seed set and seed yield of CMS lines IR54752 A and V20 A and F_1 hybrid IR54752 A/Sadang were conducted in 1989 DS and 1989-90 WS in Sukamandi. In CMS multiplication, applications of 2% urea and Sitozim significantly increased seed yield in DS, but not in WS. Interaction between lines and plant growth hormones was significant (Table 13).

Among the three male-female ratios and the six plant growth hormones tested, hybrid seed yield was found to be insignificantly different in both DS and WS. There was no interaction between row ratios and plant growth hormones in all the traits studied (Table 14).

Table 13. Effect of plant growth hormones on yield of IR54752 A, Sukamandi, 1989 DS and 1989-90 WS.

Plant growth hormone	Yield (t/ha)	
	1989 DS	1989-90 WS
Urea	1.2 a	0.5 a
Sitozim	1.2 a	0.5 a
Massabielin	1.2 ab	0.4 a
Boric acid	1.1 ab	0.5 a
GA_3	1.1 ab	0.5 a
KNO_3	1.1 ab	0.5 a
Control	0.9 b	0.5 a
CV(%)	16.8	30.6

Table 14. Effect of plant growth hormones on yield of IR54752 A/Sadang, Sukamandi, 1989 DS and 1989-90 WS.

Plant growth hormone	Yield (t/ha)	
	1989 DS	1989-90 WS
Urea	0.5 a	0.3 a
Sitozim	0.5 a	0.3 a
Massabielin	0.4 a	0.3 a
Boric acid	0.5 a	0.3 a
GA_3	0.5 a	0.3 a
KNO_3	0.5 a	0.3 a
Control	0.5 a	0.3 a
CV(%)	16.5	34.1

Table 15. Pollen sterility, spikelet fertility on bagged panicles, and some agronomic characteristics of several candidates for new CMS lines, Sukamandi, 1989-90 WS.

CMS line	Pollen sterility (%)	Spikelet fertility (%)	Days to 50% flowering	Plant height (cm)	Panicles/hill (no.)	Panicle exsertion (%)	Reaction to BB[a]
IR29744 A	99.8	0.7	84	86	19	81	7
IR19774 A	99.6	1.0	83	84	18	80	3
IR19809 A	99.7	0.9	82	85	18	82	3
Tondano A	99.8	1.1	90	99	15	87	3
M8601 A	99.7	0.8	92	98	16	88	3

[a]Based on *Standard evaluation system for rice.*

Problems in developing hybrid rice

Instability of sterility in the CMS lines

IR54752 A was introduced early and was expected to be a good parent. However, it was later found to have very unstable sterility. IR58025 A was found to have stable sterility but showed highly variable height and seemed to be still segregating; it was also agronomically undesirable.

At present, IR62829 A and IR29744 A are the most promising CMS lines. IR62829 A has shown outcrossing rates of ± 17%. Several candidates for new CMS lines are being developed, including Tondano A and M8601 A (Table 15).

Low outcrossing rates

Percent seed set of up to 31% has been obtained using MR365 A and V41 A in CMS production plots. In hybrid seed production plots, seed set of up to 19% was obtained using MR365 A as female parent (Suprihatno 1986). IR62829 A was reported by IRRI to have high outcrossing rates, stable sterility, and high uniformity. In Indonesia, this CMS line is also promising, but its outcrossing rate is still low.

Limited sources of pest and disease resistance

Pests and diseases are a major concern. Brown planthopper biotype 3 is one of the worst problems threatening rice farmers in Indonesia. IR64 is the main variety used to cope with this problem, and it has been widely adopted by farmers. Other varieties that have some degree of resistance to BPH biotype 3 are Kerala, IR46, Bahbutong, IR72, and Bahbolon. However, they are not widely adopted because of their poor grain quality.

Bacterial blight and, in some cases, bacterial orange leaf blight (BOLB or red stripe) also cause problems. Most of the local improved varieties generally have some degree of resistance to BB. IR64 was found to be highly susceptible to BOLB and susceptible to BB.

The promising CMS line IR62829 A and hybrids derived from this line were found to be susceptible to BB. Since the CMS line and most of the restorers available do not carry the *Bph3* gene, hybrids developed using the two components are expected to be vulnerable. Therefore, new CMS and/or new restorers carrying the *Bph3* resistance dominant gene and BB resistance gene should be developed.

Another pest is white stem borer (WSB). About 60,000 ha of ricefields in Java were seriously damaged in 1989-90 WS. During this outbreak, some farmers harvested nothing. IR64, the predominant variety, was highly affected by this pest. To date, no recommended varieties are considered resistant to WSB; therefore, serious attention should be paid to this problem.

Restorer lines that have been identified and used for hybrid evaluation mostly lack genetic resistance to the abovementioned pests and diseases.

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Authors' addresses: B. Suprihatno and B. Sutaryo, Sukamandi Research Institute for Food Crops, J1. Raya 9, Sukamandi, Sabang; and T. S. Silitonga, Bogor Research Institute for Food Crops, J1. Tentara Pelajar No. 3, Bogor, Indonesia.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in Malaysia

H. P. Guok

Hybrid rice research in the Malaysian Agricultural Research and Development Institute utilizes the cytoplasmic male sterile (CMS) method. Local CMS lines, (e.g., RU2340 A, MR118 A, MR83 A, and MR112 A) were developed through backcrossing programs. To date, more than 30 desirable restorer lines have been identified for use in hybrid seed production. Forty-eight F_1 hybrids were evaluated in five separate yield trials from 1988-89 main season (MS) through 1991 off-season (OS) to identify heterotic hybrids. Four hybrids significantly outyielded check variety MR84 by 16.7-39.2%. The high-yielding hybrid IR58025 A/IR29723-143-3-2-1R was identified as a potential experimental hybrid to be multiplied in bigger quantities for multiplication testing. Other hybrids could not be evaluated further due to low outcrossing on CMS lines or unstable CMS lines. Correlation studies using 1988-89 MS yield trial data indicated that number of grains/panicle correlated significantly with yield. On the other hand, grain yield was negatively correlated with % sterility (r = -0.57, p = 0.01). Panicle number and 1000-grain weight were not significantly correlated with grain yield. Seed yields of CMS lines obtained during seed multiplication, using IR58025 A and IR62829 A, were higher in 1990-91 MS (1.0-1.6 t/ha) than in 1990-91 OS . These two CMS lines were used as female parents to produce experimental hybrids using local and IRRI restorer lines as pollinators for the production of local hybrids.

The superior performance of hybrids is due to vigor in initial seedling growth as a result of faster leaf area development (Akita 1988, 1989), vigorous root system, high tillering ability, larger and denser panicles, heavy grains, and wide adaptation and stability across many soil types and adverse environments (Yuan et al 1989). Since hybrids are known to have strong root systems, they tend to be more resistant to lodging. Trials conducted at IRRI attributed the increase in yield to more initial growth and higher sink formation (Akita 1989).

Rice cultivation covers 625,000 ha in Malaysia and ranks third after oil palm and rubber. The population is projected to increase from 17.8 million in 1990 to 40 million in 2020, but the total area under rice production is expected to decline gradually over the same period. Although per capita annual consumption of milled rice is expected to decrease from 88 kg in 1988 to 75 kg in 2000, the level of self-sufficiency in the same period will decline from 71 to 55-61 %. Consequently, annual rice imports are projected to increase from 290,000 t in 1988 to 659,000-760,000 t in 2000.

Hybrid rice offers a vital opportunity to increase rice productivity. The national average yield is only 2.7 t/ha, whereas the target average yield (by 2020) is 5-5.5 t/ha. Unless very high-yielding varieties suitable for direct seeding can be bred, hybrid rices offer the best means to substantially increase rice production in this country in the future. Since hybrid seed production is labor-intensive, it may provide employment for the rural community.

This paper reports on the progress of hybrid rice research in Malaysia, including some recent results for standard heterosis, correlation studies on yield and its components, and problems encountered in hybrid rice research.

Development of local CMS lines

Hybrid rice research in the Malaysian Agricultural Research and Development Institute (MARDI) utilizes the cytoplasmic male sterile line (CMS) method. The CMS lines were introduced from IRRI.

Testcrosses between CMS plants (used as female parents) and more than 300 local breeding lines began in 1985. The F_1 plants were evaluated for sterility reaction. The maintainers were used in the backcrossing program as recurrent parents to develop local CMS lines. A few CMS and B pairs, such as MR83 A and B, MR112 A and B, RU2340 A and B, MR118 A and B, and others, have been developed. However, none of these CMS and B pairs could be used for large-scale seed multiplication due to semisterility problems or very low outcrossing potential in the CMS lines. Hence, IRRI CMS lines were introduced for evaluation under local conditions.

Selection of suitable restorer lines

Restorer lines were selected from testcross nurseries based on fertile reaction of the F_1 plants. Re-testcross nursery was used to purify strong restorers for later use in combining ability trials. More than 30 suitable restorer lines were selected for further evaluation in A × R combinations.

Identification of heterotic hybrids

F_1 hybrids must yield 20-30% more than the best conventionally bred varieties to compensate for the high cost of hybrid seeds. This should be the target of the hybrid rice breeding program. For exploiting strong heterosis, genetically diverse parents (from modern high-yielding cultivars) should be crossed.

Table 1. Yield of 13 experimental hybrids and MR84, Bumbong Lima, 1988-89 MS.

Hybrid/variety	Yield (t/ha)	Standard heterosis (%)[a]
IR58056 A/MR77	6.2	10.1
IR58056 A/YTK38	5.4	-4.4
IR54752 A/Y958	4.7	–16.7
IR58056 A/MR84	5.9	4.6
MR83-2 A/MR84	4.9	–12.8
IR58056 A/MR81	6.9	22.0
IR58056 A/SMII	6.0	7.3
MR83-1 A/MR84	4.0	–29.1
MR83-3 A/MR84	5.4	-4.6
IR58056 A/MR1	6.0	6.7
IR58056 A/MR109	6.4	13.0
MR83-1 A/MUDA	6.6	16.7
MR83 A/MR71 A	6.9	22.2
MR84 (check)	5.6	
LSD (0.05)	0.8	

[a] Determined over MR84.

So far there are no suitable hybrids available for immediate adoption in Malaysia. However, a few promising hybrid combinations have been identified from several yield trials. A total of 48 hybrid combinations involving six CMS lines were introduced from IRRI (using IR54752 A, IR58025 A, IR62829 A, and IR58056 A from IRRI) or produced locally using IRRI and two local CMS lines (MR112 A and MR83 A). These experimental hybrids were evaluated in five separate yield trials to determine the amount of standard heterosis and to identify promising hybrids for possible immediate adoption. All the yield trials were conducted at MARDI, Bumbong Lima, Malaysia. The check varieties used were Muda, MR84, and MR103.

Main season (MS) in the west coast of Peninsular Malaysia is generally characterized by a wet season followed by dry months during anthesis/grain filling, whereas off-season (OS) is characterized by dry months during the vegetative stage, followed by wet months during the reproductive stage of the rice crop.

In 1988-89 MS, 13 experimental hybrids were evaluated. Three hybrids, MR83 A/MR71R, IR58056 A/MR81, and MR83-1 A/Muda, significantly outyielded check variety MR84 (which produced 5.6 t/ha) by 16.7-22.2% (Table 1).

These experimental hybrids were produced by hand pollination using the hot water method, but they could not be evaluated further due to weakness in the respective CMS lines. The local CMS line, MR83 A, was comparatively stable for pollen sterility, but its outcrossing potential was rather low. Consequently, this CMS line could not be used in further trials. MR83 was used to develop new maintainer lines (B) to evolve CMS and B pairs. IR58056 A was later found to be unstable for pollen sterility and it was discarded from the hybrid rice breeding program.

In 1989-90 MS, none of the 18 hybrids in the replicated yield trial outyielded the check variety MR84. In 1990 OS, the experimental materials were severely infected

Table 2. Grain yield and growth duration of rice hybrids developed by IRRI, Bumbong Lima, 1990-91 MS.

Hybrid combination	Maturity (d)	Grain yield (t/ha)	Standard heterosis (%)[a]
IR62829 A/IR9761-19-1R	103	3.7	-8.6
IR58025 A/IR9761-19-1R	103	3.4	-1.3
IR58025 A/IR29723-143-3-2-1R	114	5.6	39.2
IR62829 A/IR29723-143-3-2-1R	104	4.2	3.3
IR62829 A/IR10198-66-2R	102	3.7	-7.1
IR58025 A/IR54742-2-2-19-3R	118	4.5	11.2
MR84 (check)	124	4.0	
MR103 (check)	127	3.9	
LSD (0.05)		0.7	

[a] Determined over MR84.

with tungro virus and grain yields, especially those of check varieties, were considerably reduced. The yield differential between the hybrids and the check varieties obtained from this trial may not be a valid comparison.

In 1990-91 MS, another six IRRI hybrids were evaluated for yield heterosis. Only IR58025 A/IR29723-143-3-2-1R outyielded the check variety MR84 (4.1 t/ha), by 39.2% (Table 2). This hybrid was identified as a potential experimental hybrid possessing wide adaptation both locally and in other countries.

More hybrid combinations need to be tested in both seasons to identify heterotic combinations suited to local conditions.

CMS seed multiplication

Seed yields of CMS lines obtained during seed multiplication were higher in 1990-91 MS (1.0-1.6 t/ha) than in 1990-91 OS, using a row ratio of 4A:2B (Table 3). Seed yields obtained from natural outcrossing in 1990 and 1991 OS ranged from 0.1 to 0.2 t/ha (Table 3). This was too low for the economical production of hybrid rice.

Suitable combinations of factors, such as narrower female-male row ratios, agrochemicals (e.g., GA_3), or environments need to be evaluated to obtain higher seed set on CMS lines, especially in OS.

Hybrid seed production

Hybrid seed for heterosis evaluation can be produced by handcrossing in small quantities, or in small-scale seed production plots. Seed yields on CMS plants during hybrid seed production in 1991 OS were rather low, ranging from 0.1 to 0.2 t/ha (Guok, unpubl.). More research will be conducted, especially in MS, to produce hybrid seeds using IRRI CMS lines as female parents and local restorer lines as pollinators in order to produce locally adapted hybrids.

Table 3. Amount of CMS seeds obtained under natural outcrossing, Bumbong Lima.

Season	CMS lines	A:B	Amount of CMS seeds (t/ha)
1990 OS	IR62829 A	4:2	0.2
	IR58025 A	4:2	0.1
1990-91 MS	IR62829 A	4:2	1.3
	IR58025 A	4:2	1.6
1991 OS	IR58025 A	4:2	1.2
	IR62829 A	4:2	1.1
	MR112 A	4:2	1.1

Table 4. Simple correlation coefficients among yield and plant characters.

Character	1988-89 MS
Yield vs panicle number	-0.2035ns[a]
Yield vs 1000-grain weight	0.2049ns[b]
Yield vs filled grains/panicle	0.5020**
Yield vs % sterility	-0.5736**
Yield vs filled grains/hill	0.6897**

[a] = not significant. [b] = significant at P < 0.01.

Correlation studies

Grain yields in conventionally bred varieties are generally correlated with high panicle number. Correlation studies were conducted using the 1988-89 MS yield trial data to elucidate the relationship between yield and its components among the hybrids.

Phenotypic correlation between grain yield and yield- contributing characters for 1988-89 MS showed that grains/panicle (r=0.502**,p=0.01) and grains/hill (r=0.690, p = 0.01) were significantly and positively correlated with yield (Table 4). Further, the correlation between yield and % sterility (r= -0.574, p = 0.01) was negative and highly significant. Kim and Rutger (1988) concluded that spikelets per plant and 1000-grain weight have the largest direct effect on grain yield and suggested that the highest grain yield would come from hybrids of parents which complement each other in terms of increased spikelet numbers and heavier grains.

Four hybrids from the five yield trials significantly outyielded check variety MR84 by 16.7-39.2%. However, only one high-yielding hybrid, IR58025 A/IR29723–143–3–2–1R, was identified as a potential experimental hybrid to be multiplied in bigger quantities for testing. The other hybrids were not selected for further evaluation due to instability of male sterility in CMS lines, low outcrossing potential, or short growth duration.

Problems in hybrid rice in Malaysia

The major problems in hybrid rice research in Malaysia include lack of suitable CMS lines, instability of male sterility in CMS lines, and relatively low seed yields obtained in CMS seed multiplication (and hybrid seed production) plots, particularly in the OS. Commercial hybrid seed production, which is labor-intensive, is further constrained by the labor shortage in Malaysia. More than two-thirds of the irrigated rice area in West Malaysia is expected to practice direct seeding in the future. The potential of hybrid rice has yet to be demonstrated sufficiently to increase research and development.

The CMS method is the most commonly used method for hybrid seed production in cereal crops, including rice. Other methods, such as the two-line method, which involves male gametocides (also known as chemical pollen suppressants or chemical hybridizing agents) or thermosensitive genic male sterile lines as proposed by Maruyama et al (1990), may greatly simplify seed production. However, these methods are not yet available for adoption. A one-line method, apomixis or asexual reproduction of hybrid seeds, is considered the ultimate genetic tool for producing true-breeding heterozygotes (Kim and Rutger 1988, Yuan et al 1990).

The successful adoption of hybrid rice technology in Malaysia will ultimately depend on the availability of reasonably priced hybrid seed and sufficient standard heterosis.

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Author's address: H. P. Guok, Rice Research Division, Malaysian Agricultural Research and Development Institute, S. Perai, 13200 K. Batas, Penang, Malaysia.

Acknowledgment: The author wishes to thank the Director General of MARDI and the Director of Rice Division, MARDI, for their permission to publish this paper.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in Thailand

S. Amornsilpa, S. Potipibool, and S. Noojoy

The Rice Research Institute in Thailand started hybrid rice research and development in 1979. The wild abortive cytosterility system was transferred to many Thai rice varieties. Several breeding lines have been identified as maintainers. A yield trial conducted at the Suphanburi Rice Experiment Station in the 1991 wet season revealed that grain yields of a hybrid from IRRI were comparable with those of four Thai check lines/varieties.

Thailand produces rice for both domestic consumption and export. Although rice is the most important cereal crop in Thailand, rice farmers are still a low-income group in the agricultural sector.

Many countries that used to import rice have become self-sufficient. Some of these countries may also export rice in the near future. Therefore, rice farming in Thailand must be diversified into a multiple cropping system in order to improve economic conditions of rice farmers. At the same time, the country has to maintain the present level and growth of rice production. Increasing the productivity per unit area is fast becoming important. Improved crop management practices and the use of high-yielding varieties are being vigorously pursued to achieve this objective. One of the approaches is the development of hybrids.

The Rice Research Institute began hybrid rice research and development in 1979. Rice experiment stations at Bangkhen, Pathum Thani, and Suphanburi are working on hybrid rice research.

Initial work involved testing F_1 hybrids from China for adaptability under local conditions. The hybrids were early-maturing but failed to outyield local high-yielding varieties. From 1981 onward, hybrid rice research expanded in collaboration with IRRI, and more CMS systems and hybrids were tested. The results of these tests have been reported (Chitrakon et al 1986). This paper summarizes progress since 1987.

Development of CMS lines

Since the introduced CMS lines were unsuitable, the wild abortive cytosterility system was transferred to several selected local varieties/lines. The new CMS lines presently available are RD21 A, RD25 A, IR17492 A, BS4 A, KDML105 A, SPRLR76102-21-1-1 A, and SPRLR75001-68-2-2 A.

Identification of restorers

A large number of high-yielding local lines have been tested. Four were identified as good restorers. They are SPRLR83136-14-2-2-1-1, SPRLR836260-143-1-1, SPRLR82216-26-1-1, and SPRLR82216-26-1-3.

Yield ability of hybrids

In a yield trial, 17 IRRI-developed hybrids were tested against seven local high-yielding lines/varieties at the Suphanburi Rice Experiment Station in the 1991 wet season. The objective of this experiment was to test the yield potential of the new IRRI hybrids. Grain yields of nine of the hybrids were comparable with four checks used in the experiment (Table 1). Grain quality characteristics of the hybrids tested were not as good as those of the checks (Table 2).

Table 1. Yield duration and plant height of hybrids and local checks tested, 1991 wet season (WS), Suphanburi Rice Experiment Station, Thailand.

Hybrid/variety	Yield (t/ha)	Maturity (d)	Plant height (cm)
IR62829 A/IR29723-143-3-2-1 R	5.6a	106	94
SPR90	5.6a	120	123
IR58025 A/IR29723-143-3-2-1 R	5.5ab	114	106
IR62829 A/IR40750-82-2-3-3 R	5.3abc	114	106
SPR60	5.3abcd	105	94
IR62829 A/IR54742-19-3 R	5.2abcde	111	103
SPRLR85153-7-2-1	5.2abcde	114	111
IR62829 A/IR44675-3-3-2-2 R	5.2abcde	106	100
IR62829 A/IR9761-19-1 R	5.0abcdef	106	93
SPRLR83030-7-3-2-1-2	5.0abcdef	114	117
IR58025 A/IR66 R	4.9abcdef	106	102
IR62829 A/IR28238-109-1-3-2-2 R	4.8abcdef	114	100
IR58025 A/IR15324-13-3-3-2 R	4.8abcdefg	106	107
IR62829 A/IR10198-66-2 R	4.7 bcdefg	106	102
IR58025 A/Pusa 150-9-3-1 R	4.6 bcdefg	106	104
IR58025 A/IR54742-22-19-3 R	4.5 cdefg	113	109
RD23	4.5 defg	117	113
IR58025 A/IR10198-66-2 R	4.4 defgh	111	111
RD7	4.4 defgh	123	113
IR58025 A/Milyang 46 R	4.4 efghij	106	111
IR58025 A/IR48 R	4.2 fghijk	123	104
IR58025 A/IR35366-62-1-2-2-3 R	4.0 ghijk	109	101
IR58025 A/IR28238-109-1-3-2-2 R	3.6 hik	109	105
RD25	3.4 k	96	96

Table 2. Grain quality characteristics of hybrids and inbreds tested, 1991 WS, Suphanburi Rice Experiment Station, Thailand.

Hybrid/variety	Physical characteristics						Chemical characteristics			
	Length (mm)	Width (mm)	Thickness	Shape[a] (mm)	Chalkiness	Translucency	Amylose (%)	Gel consistency (mm)	Gel temperature[b]	Elongation ratio
IR62829 A/IR29723 143-3-2-1 R	7.37	1.12	1.74	SL	2.48	3	26.3	60	6.3	1.51
SPR90	7.50	1.31	1.84	SL	1.01	3	28.4	67	7.0	1.67
IR58025 A/IR29723 143-3-2-1 R	7.77	2.06	1.79	SL	0.42	3	23.9	75	7.0	1.65
IR62829 A/IR40750-82-2-3-3 R	7.18	2.06	1.63	SL	0.63	3	25.8	50	5.4	1.59
SPR60	7.71	2.26	1.85	SL	0.60	3	24.4	35	6.8	1.52
IR62829 A/IR54742-19-3 R	7.34	2.15	1.78	SL	1.20	3	22.7	40	4.9	1.58
SPRLR8515-37-2-1	7.31	2.22	1.79	SL	0.09	3	17.0	74	7.0	1.50
IR62829 A/IR44675-3-3-2-2 R	7.24	2.12	1.74	SL	0.66	4	24.3	63	4.9	1.71
IR62829 A/IR9761-19-1 R	6.93	2.11	1.71	SL	0.87	4	24.6	63	5.0	1.61
SPRLR83030-7-3-2-1-2	7.41	2.15	1.77	SL	0.50	3	28.3	97	6.7	1.51
IR58025 A/IR66 R	7.39	1.94	1.73	SL	0.74	3	23.9	47	6.3	1.52
IR62829 A/IR28238-109-1-3-2-2 R	6.40	2.10	1.70	I	0.66	3	24.9	37	5.2	1.70
IR58025 A/IR15324-13-3-3-2 R	7.69	2.11	1.76	SL	1.04	3	24.9	60	7.0	1.58
IR62829 A/IR10198-66-2 R	7.18	2.07	1.74	SL	1.55	3	24.9	72	6.1	1.65
IR58025 A/Pusa 150-9-3-1 R	7.49	1.98	1.70	SL	0.42	3	23.6	49	7.0	1.59
IR58025 A/IR54742-22-19-3 R	7.57	2.17	1.80	SL	0.70	3	21.4	48	6.4	1.59
RD23	7.24	2.19	1.72	SL	0.10	3	23.8	69	5.5	1.51
IR58025 A/IR10198 66-2 R	7.29	2.10	1.81	SL	0.97	3	24.4	51	6.9	1.55
RD7	7.38	2.30	1.78	SL	0.80	3	23.2	63	5.3	1.54
IR58025 A/Milyang 46 R	6.96	2.16	1.79	SL	0.46	3	17.3	78	6.7	1.76
IR58025 A/IR48 R	7.54	2.18	1.82	SL	0.92	3	22.5	36	7.0	1.55
IR58025 A/IR35366-62-1-2-2-3 R	7.50	2.13	1.76	SL	0.50	3	23.0	47	6.5	1.63
IR58025 A/IR28238-1091-3-2-2 R	7.39	2.08	1.73	SL	0.75	3	22.8	44	6.1	1.64
RD25	7.55	2.30	1.81	SL	0.24	3	25.8	48	7.0	1.55

[a] SL = slender, I = intermediate. [b] 1-9 scale.

Future plans

Grain quality is very important in Thailand. Poor grain quality of CMS and R lines is the biggest problem the program is facing. A, B, and R lines with good grain quality need to be developed. Locally adapted and accepted varieties should be used to produce the required lines and hybrids.

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Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Hybrid rice research in the Republic of Korea

H. P. Moon, M. H. Heu, and C. H. Kim

The national program of hybrid rice breeding in the Republic of Korea started in the early 1980s. The Korea-IRRI Collaborative Research Project has played a significant role in the progress of the hybrid rice program. The yearly top grain yields ofthe experimental hybrids ranged from 9.1 to 12.1 t/ha over the last 10 yr. The yield advantage of these hybrids was around 21% over leading inbred cultivars in Korea on average. The most important characters of the four yield components appeared to be the number of grains/panicle in Tongil-type (I/J) rice and the number of panicles/hill and grains/panicle in japonica. Both general combining ability (GCA) and specific combining ability (SCA) effects significantly affected hybrid grain yield, regardless of varietal group. The GCA effects of A lines, however, did not significantly affect the grain yield in Tongil-type varieties. Most of the yield components were generally affected by GCA effects of both A and R lines, except number of panicles/hill, which was affected only by GCA of the A line. The SCA effects on yield components were more important in Tongil-type rice than in japonica. Cytoplasmic male sterile lines have been developed by transferring WA-CMS and COA-ms sources into leading Korean cultivars and breeding lines. Some Tongil-type cultivars and lines were identified as maintainers to WA-CMS, and most japonica cultivars as maintainers to both WA-CMS and COA-ms. Most ofthe elite Tongil-type cultivars showed good fertility restoration for the WA-CMS system, but no japonica varieties were identified as restorers. Anther culture technique has been employed for rapid development of new japonica restorer lines with some success. The standard heterosis of japonica hybrids derived from the new japonica CMS and restorers ranged from 5 to 93%. The effects of various components of seed production for CMS and hybrid rice were evaluated. In addition to spraying GA_3 and flag leaf clipping at heading, manual supplementary pollination could increase outcrossing rate and yield of CMS and hybrid seeds. The costly, labor-intensive nature of such operations favors strongly the genetic and/or structural improvement of the plant itself.

Rice is a staple food in the Republic of Korea and occupies 59% of 2.2 million ha of arable lands. It provides 45% of the calories for 42 million people and about 50% of farmers' incomes. Rice yields have plateaued since high-yielding, semidwarf inbred varieties were introduced in the 1970s. F_1 rice hybrids provide one approach to breaking the current yield ceiling. Reviews in the literature have provided evidence of heterosis for yield and agronomic traits in rice (Davis and Rutger 1976, Virmani and Edwards 1983, Kim and Rutger 1988). The national hybrid breeding program began in 1982, using wild abortive (WA)-cytoplasmic male sterile (CMS) system from IRRI. A Korea-IRRI collaborative project on hybrid rice was developed in 1984. There is evidence of 20-30% yield heterosis in experimental F_1 hybrids between WA-CMS and elite Korean cultivars of indica-japonica. To develop japonica hybrids, CMS systems are being transferred into elite japonica cultivars. Anther culture is being used to develop japonica restorer lines quickly. The extent of natural outcrossing should be increased by breeding CMS, maintainer, and restorer lines with floral structure and agronomic characters that improve outcrossing. This paper summarizes the current status of hybrid rice research and discusses the prospects and problems of developing hybrid rice technology in the Republic.

Heterosis and combining ability studies

Heterosis for yield and yield components

Heterosis is the basis of yield advantage in hybrid rice. Jones (1926) observed heterosis for grain yield and other agronomic traits in rice. Significant evidence of heterosis has been reviewed by Chang et al (1973), Davis and Rutger (1976), Virmani and Edwards (1983), and Kim and Rutger (1988). The reality of heterosis in rice comes from 13.4 million ha of hybrid rice being grown in China, 41% of the country's rice area (Virmani et al 1990). Hybrid rices yield about 20% more than homozygous rice varieties in China.

Yield advantage and heterosis of rice hybrids. Since the national hybrid breeding program began 10 yr ago, several experimental F_1 hybrids have significantly outyielded the best inbred check cultivars (Table 1). Grain yield of the best experimental rice hybrids ranged from 9.1 to 12.1 t/ha, averaging 10.7 t/ha in replicated yield trial nurseries. Heterosis for grain yield over the best inbred check cultivars ranged from 9 to 42%, with an average of 21%. The most promising rice hybrid was a combination of V20 A/Milyang 46, which yielded 11.3 t/ha and had average standard heterosis of 25%.

The extents of heterosis, heterobeltiosis, and standard heterosis are shown in Table 2. In Tongil rice (I/J), the maximum positive heterosis in experimental plots ranged from 29 to 92% over the parental means and from 25 to 85% over the best inbred check cultivars. The results show that hybrids between WA-CMS and the elite Tongil rice cultivar have a yield advantage of 46% over the best inbred variety. Maximum standard heteroses in indica rices of 34% (Virmani et al 1982) and 41% (Yuan et al 1987) have been reported. In japonica rices, maximum standard heterosis ranged from 5 to 22% over check cultivars available on the basis of individual plants. Heterosis in japonica

Table 1. Yields of best experimental hybrids against the best check varieties in replicated yield trials in Korea, 1982-90.

Hybrid	Year	Yield	% of (t/ha)	Location check
V20 A/Suweon 294	1982	9.1	109	Suweon
V20 A/Milyang 46	1983	11.4	119	Milyang
V20 A/Milyang 46	1984	11.5	142	Iri
V20 A/Milyang 46	1985	10.0	115	Iri
HR1619 A/Iri 362	1986	9.7	118	Suweon
IR54756 A/Suweon 333	1987	9.8	115	Iri
IR5456 A/Iri 362	1988	11.8	134	Suweon
IR54756 A/Suweon 318	1989	11.0	112	Suweon
V20 A/Milyang 46	1989	12.1	124	Suweon
Milyang 55 A/Iri 362	1990	10.5	119	Milyang
Over all mean		10.7	121	

Table 2. Extent of heterosis (H), heterobeltiosis (HB), and standard heterosis (SH) for grain yield of experimental rice hybrids studied in Korea.

Varietal group	Hybrids tested (no.)	Sample type	Heterosis			Reference
			H	HB	SH	
Tongil-type	36	Hill		- 6~58		Kim and Heu (1979)
	21	10a	13~121	-14~80		Heu et al (1984)
	18	10a		- 8~86		Heu et al (1985)
	4	10a	55~92	1~48	- 4~43	Kim (1985)
	9	10a	-11~40	- 1~36	-17~19	Suh et al (1985)
Japonica-type	9	Hill	-16~85	- 22~60		Lee et al (1968)
	10				5~22	Heu and Koh (1990)

Table 3. Extent of heterobeltiosis for yield components of hybrid rice studied in Korea.

Varietal group	Hybrids studied (no.)	Panicles/ hill (no.)	Grains/ panicle (no.)	1,000 grain weight (g)	Filled grain ratio	Reference
Tongil-type	36	-10~41	-36~20	-13~7	-20~19	Kim and Heu (1979)
	21	-20~13	-18~81	0~29	- 5~11	Heu et al (1984)
	18	-15~18	-22~32	-10~5	- 30~ 7	Heu et al (1985)
	9	-23~1	-23~46	-13~4	- 32~ 3	Suh et al (1985)
Japonica-type	9	-42~35	-31~15	-16~11	- 9~ 1	Lee et al (1968)
	42	-14~10	4~7	0~4	- 8~ 9	Heu and Koh (1990)

rices is generally lower than in indica rices. Virmani et a1 (1981) reported 10-15% standard heterosis in japonica rice.

Heterobeltiosis for yield components. Heterobeltiosis for yield components is shown in Table 3. In general, the number of grains per panicle showed the greatest expression of yield heterosis, ranging from 20 to 81% in the Tongil hybrids and from 7 to 15% in the japonica hybrids. Maximum heterobeltiosis for panicles per plant ranged from 1 to 41 % in Tongil hybrids and from 10 to 35% in japonica hybrids. The heterobeltiosis for grain weight and filled grain ratio were not significant, regardless of varietal type. These results indicate that heterosis in hybrid rice is mainly due to more spikelets per panicle and panicles per plant rather than greater grain weight and filled grain ratio. Similar results have been reported by Chang et al (1973), Carnahan et al (1972), Devarathinam (1984), Hsu et al (1969), Murayama (1973), Namboodri (1963), Saini and Kumar (1973), and Singh et al (1980). However, other researchers have reported that heterosis in yield was mainly due to more spikelets per panicle and heavier 1000-grain weight (Kim 1985, Nijaguna and Mahadevappa 1983, Virmani et al 1982). However, the number of spikelets per panicle is agreed to be the most significant factor out of the four yield components in heterosis for grain yield of hybrid rice.

Combining ability

The amount of heterosis is specific to each particular cross (Falconer 1981). Successful predictions of heterotic combinations would be of great value in hybrid breeding. Heterosis can result from dominance, overdominance, epistasis, and their combinations (Comstock and Robinson 1952). If the lines are fully inbred, the variance of general combining ability (GCA) is equal to the additive variance in the base population, and that of specific combining ability (SCA) is equal to the nonadditive variance (Falconer 1981). Therefore the variance components from the two combining abilities can be predicted. Mean squares of GCA and SCA for grain yield and its components in both japonica and Tongil rice hybrids are shown in Table 4. Both GCA and SCA variances for yield were highly significant, regardless of varietal type. When GCA variance was separated into CMS and restorer variance effects, both CMS and restorer variances were highly significant in japonica hybrids while the GCA effect of CMS was not significant in Tongil rice hybrids. The relative values of GCN/SCA variance for grain yield were 0.53 in japonica hybrids and 1.11 in Tongil rice hybrids, indicating that the

Table 4. Comparison of mean squares of general (GCA) and specific combining ability (SCA) effects for grain yield and its components in japonica and Tongil-type hybrids.[a]

SV	SF	Grain yield	Panicles/hill	Grains/panicle	1000 grain weight	Filled grain ratio
			Japonica hybrids			
GCA	15	2327.0**	0.92**	47.43**	0.16*	40.78**
Male	13	266.0**	0.03 NS	6.17*	0.19**	2.39**
Female	2	1144.9**	5.09**	239.93**	0.04	219.94**
SCA	26	4368.8**	0.46	1.82	0.09	18.13**
GCA/SCA		0.53	2.00	26.06	1.78	2.25
			Tongil hybrids			
GCA	15	2090.9**	0.26*	153.2**	0.98**	1.81
Male	6	3092.8**	0.22	217.7**	0.79**	1.53
Female	9	659.5	0.33*	60.9**	1.25**	2.22*
SCA	54	1876.9**	0.11	46.8**	0.22**	3.03**
GCA/SCA		1.11	2.36	3.27	4.46	0.60

[a] *, **= significant at 5 and 1% level, respectively.

nonadditive effect is more important for yield heterosis in japonica hybrids and that additive and nonadditive effects have equal importance in Tongil rice hybrids. The GCA effects for all four yield components of japonica were significant. The SCA effects were not significant, except for filled grain ratio. In Tongil rice hybrids, all components except filled grain ratio had significant GCA effects, and all except panicles per hill had significant SCA effects. The relative values of GCA/SCA ratios for yield components were more than double, except for filled grain ratio in Tongil rice hybrids.

These results indicate that the additive effects are much more important than the nonadditive effects. This is supported by Kim and Rutger (1988), who found that both GCA and SCA variances were highly significant, with higher GCA variance than SCA.

Development of CMS lines

The discovery of the CMS system made commercial rice hybrids possible. Virmani and Wan (1988) listed 37 cytoplasm sources reported to induce male sterility in rice. Among them, the WA-CMS system developed from the cytoplasm of *O. sativa* f. *spontanea* has been the most successful in China.

Leading WA-CMS lines, such as V20 A, Zhen Shan 97 A, and V41 A, are used widely to develop commercial rice hybrids in China. They also show good combining ability and favorable floral characteristics for natural outcrossing in the Republic of Korea. However, they are not suitable for developing F_1 rice hybrids for the Republic, mainly because of unacceptable grain quality (high chalkiness and high amylose) and susceptibility to diseases and insects. Some elite genotypes of Tongil-type rice were identified as WA-CMS maintainers—Suweon 290, Suweon 296, Suweon 310, Suweon 311, Iri 342, Iri 356, Milyang 55, Wx126, Wx187, Wx498, and Wx817. Almost all japonica varieties were found to be effective maintainers.

The WA-CMS systems of V20 A, Zhen Shan 97 A, and V41 A were transferred into selected Tongil-type maintainers by backcrossing. Some japonica CMS lines were also developed by transferring the CMS systems of V20 A, Reimei A, and COA-ms into elite japonica cultivars. Sixteen new CMS lines have been developed (Table 5). Nine lines are Tongil-types, derived from indica/japonica hybridization, and seven have the genetic background of japonica. Most Tongil-type CMS lines have better grain quality and adaptability than the Chinese CMS lines, but low outcrossing rate and some instability of sterility. Virmani and Wan (1988) indicated that lack of complete pollen sterility in certain genotypes after nine backcrosses may be due to minor genes for fertility restoration present in the maintainer genotypes. New japonica CMS lines were generally lower in standard heterosis and outcrossing rate than Tongil-type CMS lines.

None of the 337 japonica rice varieties tested showed complete fertility restoration to COA-ms; 261 of them were identified as complete maintainers (Table 6). Male sterile cytoplasm COA-ms proved to be different from that of WA, TN1, Gam, Di, and *O. spontanea* sources (Heu and Koh 1990).

Table 5. CMS lines developed with the genetic background of Korean elite breeding lines and varieties.

CMS line	Line/variety converted		CMS type[b]	Origin of MS line
	Designation	Varietal group[a]		
HR1619 A	HR1619-1-2	I/J	WA	V41 A
S.310 A	Suweon 310	I/J	WA	ZS97 A
Iri 356 A	Iri 356	I/J	WA	ZS97 A
SR1628S A	Milyang 55	I/J	WA	V20 A
SR16289 A	Suweon 290	I/J	WA	V20 A
HR7019 A	Suweon 290	I/J	WA	V20 A
HR7026 A	Milyang 55	I/J	WA	ZS97 A
HR7028 A	Suweon 290	I/J	WA	ZS97 A
M.55 A	Milyang 55	I/J	WA	ZS97 A
S.304 A	Suweon 304	J	WA	V20 A
Ch.34 A	Cheolweon 34	J	HR	Reimei A
Gwanag ms	Gwanagbyeo	J	COA	Rax201 A
Seolag ms	Seolagbyeo	J	COA	Rax201 A
Samnam ms	Samnambyeo	J	COA	Rax201 A
Nagdong ms	Nagdongbyeo	J	COA	Rax201 A
Jangbaek ms	Jangbaek #6	J	COA	Rax201 A

[a]I = indica, J =japonica. [b]WA = wild abortive, COA = College of Agriculture, HR = Honam Rice.

Table 6. Segregation of grain fertility in the F_1 progenies of crosses between COA-ms and japonica cultivars from different origins.

Origin	Grain fertility (%)							
	Total	0	10	20	30	40	50	60
Korea	109	102	2	3	1	1		
Japan	121	117	3				1	
China	45	18	20	4	3			
Taiwan	24	6	12	3	2			1
USA	12	5	3	2	2			
Others	25	13	5	3	3		1	
Total	337	261	45	15	10	1	2	1
	(%)	(77)	(13)	(5)	(3)			

Fertility restoration

Screening Korean elite lines and cultivars for fertility restoration showed that many Tongil-type cultivars possessed good fertility restoration to the WA-CMS lines. No effective restorers were identified for other CMS lines such as Toyonishiki A and Reimei A (Table 7). None of the japonica cultivars tested possessed complete fertility restoration.

Several japonica restorer lines with partial fertility restoration were identified from anther culture progenies of the Suweon 304 A/Iri 362 cross (Table 8).

All japonica hybrids between S.304 A and anther culture- derived restorers headed between CMS and restorer lines. Grain yield of these japonica hybrids ranged from 6.2 to 11.3 t/ha. The yield components were satisfied and there was good fertility

Table 7. Fertility restoration of Korean varieties to the new CMS lines.

Restorer	CMS lines[a]							
	Suweon A 310	Iri A 356	Milyang A 55	HR1619 A	V20 A	Reimei A	Toyoni-shiki A	S.304 A
Suweon 287	F	F	F	F	F	PF	S	PS
Suweon 294	F	F	F	F	F	PF	PF	PS
Suweon 325	F	F	F	F	F	PF	PF	PS
Suweon 332	F	F	F	F	NH	PF	PF	PS
Iri 362	F	F	F	F	NH	PF	PS	
Iri 363	F	F	F	F	F	–	–	–
Milyang 46	F	F	F	F	F	S	PF	PS
Milyang 54	F	F	F	F	F	S	S	PS
Suweon 333	F	F	–	–	–	PF	PF	
Japonicas (28)	S	S	S	S	S	S	S	S

[a] F = complete fertility, PF = 30-70%. fertility, PS = <30% fertility, S = complete sterility, NH = nonheading.

Table 8. Performance of new japonica restorers developed by anther culture technique and hybrids in Suweon, 1991.

Genotype	Heading date	Culm length (cm)	Panicle length (cm)	No. of panicle	Spikelets/ panicle (no.)	Ferti-lity (%)	WC/ WB (0-9)[a]	Grain yield (t/ha)
Suweon 304	29 Jul	70	20	14	140	96	0/0	4.9
H0474-3-1	10 Aug	44	15	19	116	78	5/5	3.6
S.304 A/H474-3-1	2 Aug	67	19	29	153	75	2/3	10.6
HB474-57	8 Aug	46	14	26	95	83	2/4	2.4
S.304 A/HB474-57	2 Aug	65	19	35	140	81	1/2	11.3
14705-F2-3-2	16 Aug	80	25	19	166	85	2/1	5.3
S.304 A/14705-F2-3-2	12 Aug.	82	25	20	201	79	3/1	9.2
14714-F2-2-1	15 Aug.	59	16	16	151	77	1/0	5.3
S.304 A/14714-F2-2-1	8 Aug.	72	21	19	192	84	1/0	6.2

[a] WC = white center, WB = white belly of rice endosperm; 0 = clear, 9 = chalky.

restoration (more than 75%). Heterosis ranged from 12 to 211% over the mean of parents, 15 to 372% over the restorers, and 5 to 93% over the standard check cultivar (Table 9).

Another japonica restorer line for COA-ms, GP15-6, was selected from the progenies of COA-ms/Fukuhikari, and subsequently 138 homorestorer lines were developed through anther culture of the F_1s of crosses between GP15-6 and several elite japonica cultivars. This restoration system was found to be gametophytic (Heu and Koh 1990).

CMS seed production

Seed production is another important constraint in hybrid rice. The effects of several seed production components on outcrossing rate and seed yield of CMS lines were studied, including row ratios between CMS lines, maintainers, and restorers, flag leaf

Table 9. Heterosis (H), heterobeltiosis (HB), and standard heterosis (SH) for grain yield of japonica hybrids in Suweon, 1991.

Hybrid	Heterosis %		
	H	HB	HS
S.304 A/HB474-3-1	149	191	81
S.304 A/HB474-57	211	372	93
S.304 A/14705-F2-3-2	81	73	57
S.304 A/14714-F2-2-1	12	16	5

Table 10. Effects of spraying gibberellic acid (GA_3), flag leaf clipping (Flc), the supplementary pollination (SP) on outcrossing rate and seed yield of CMS line, IR62829A, in Iri, 1990.

Treatment	Outcrossing rate[a] (%)	Seed yield[a] (t/ha)
Control	11.3 d	1.43 c
GA3 + Flc	16.5 c	1.76 b
GA3 + SP	22.1 b	1.94 ab
Flc + SP	24.1 b	2.00a
GA3 + FIC + SP	27.5 a	2.05 a
CV(%)	7.0	5.7

[a]Figures with the same letters are not significantly different at the 5% level.

clipping (Flc), gibberellic acid (GA_3) application at heading stage, and manual supplementary pollination (SP).

The effects of different seed production components on outcrossing rate and seed yield of IR62829 A are shown in Table 10. The average outcrossing rate of the treatments ranged from 16.3 to 27.5%, significantly higher than the control (11.3%). The highest outcrossing rates appeared in treatments which included manual SP, 27.5% for GA_3 + Flc + SP and 25.2% for Flc + SP. The estimated seed yields of IR62829 A ranged from 1.8 to 2.1 t/ha with the extra treatments, compared with 1.4 t/ha in the control. However, if labor is considered alongside the above components, then it would be much better to enhance outcrossing ability through genetic and/or structural alterations to the plant itself.

Three new CMS lines developed in IRRI and Korea—IR62829 A, SR16282 A, and S.304 A—were evaluated for seed production with Flc and different row ratios (Table 11). SR16282 A had the highest seed production, with 1.9 t/ha with Flc and a row ratio of 8:2 CMS to maintainer. IR62829 A and S.304 A produced seed yields of around 0.2 t/ha. Flag leaf clipping at 10% heading generally gave higher seed yields, regardless of CMS line or row ratio.

Conclusions

Experimental F_1 rice hybrids yielded 10.7 t/ha on average over the last 10 yr, a yield advantage of 21% over inbred semidwarf indica/japonica cultivars in the Republic of

Table 11. Seed production of new CMS lines under different row ratios and flag leaf clipping In Suweon, 1991.

CMS line	Flc at 10% heading	No. of rows of CMS and maintainer						Av
		1:1	2:1	3:1	4:1	6:2	8:2	
SR16282 A/B	No	0.56	1.03	1.28	1.54	1.01	1.66	1.18
	Yes	0.88	1.39	1.52	1.46	1.56	1.92	1.46
IR62829 A/B	No	0.08	0.07	0.16	0.13	0.16	0.26	0.14
	Yes	0.29	0.18	0.24	0.30	0.26	0.19	0.24
S.304 A/B	No	0.23	0.13	0.14	0.13	–	–	0.16
	Yes	0.24	0.18	0.14	0.20	–	–	0.18
AV	No	0.29	0.41	0.53	0.60	0.59	0.96	
	Yes	0.47	0.58	0.63	0.65	0.91	1.06	

Korea. However, commercial rice hybrids are not yet available to the farmers in Korea. Poor grain quality and labor-intensive seed production technology are the major constraints. To meet grain quality requirements, it is essential to develop japonica rice hybrids. Anther culture technique is used to produce new japonica CMS and restorer lines quickly. To make seed production economical, parental lines need genetic and/or structural improvement to enhance outcrossing rate. Multiple resistance to major diseases and insects must also be introduced into the parental lines.

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Notes

Authors' addresses: H. P. Moon, Crop Experiment Station, Rural Development Administration (RDA), Suweon, Republic of Korea; M. H. Heu, College of Agriculture, Seoul National University, Suweon, Republic of Korea; and C. H. Kim, International Technical Cooperative Center, RDA, Suweon, Republic of Korea.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Hybrid rice research in Egypt

M. A. Maximos and I. R. Aidy

Hybrid rice research in Egypt started in 1982. Testcrosses to determine natural fertility restoration of Egyptian varieties on two Chinese cytoplasmic male sterile (CMS) lines, V20 A and Zhen Shan 97 A, were made. The work was extended to include evaluation of certain CMS lines introduced from the International Rice Research Institute and elsewhere. Yield tests were also conducted to evaluate yields and agronomic characteristics of some F_1 hybrids received from different sources. Seed production studies in isolated areas were conducted to evaluate yields and seed setting percentage of CMS lines planted with restorers or maintainer lines in a row ratio of 8A:2R or B. Studies revealed that Egyptian japonica varieties have little or no fertility-restoring ability on the wild abortive CMS source. Sterility of most CMS lines examined under Egyptian conditions was almost complete, according to microscopic tests of the pollen grains, and seed setting percent under bagged panicles ranged from 0.00 to 1.63%. In yield tests of F_1 hybrids, some gave yields comparable with the best commercial varieties. Seed yields of the hybrids in the isolated plots with row ratio of 8A:2R or B ranged from 1.0 to 1.2 t/ha.

Egypt has one of the highest rice yields per unit area in the world. Average productivity of rice in Egypt in 1991 was 7.5 t/ha. It has been demonstrated that adopting improved crop management technology alone would help farmers to harvest as much as 9.00 t/ha (Wally 1989). Adoption of innovative techniques would also help increase rice production in Egypt. One of these techniques is hybrid rice. Egypt could be an ideal place for exploiting hybrid vigor due to adequate irrigation potential and a risk-free environment (Balal 1989, Wally 1989).

Results at the International Rice Research Institute (IRRI) and elsewhere (Virmani and Edwards 1983, Lin and Yuan 1980) indicate that heterosis breeding can be exploited to develop high-yielding hybrids using cytoplasmic male sterile (CMS) and fertility restoration systems. This breeding approach allows the retention of desirable combinations and can overcome the effects of undesirable (repulsion phase) linkages found in the parents. The Egypt Rice Research Program will continue to explore the prospects of hybrid rice in increasing the yield potential of rice. Locally adapted parental lines need to be bred so that suitable heterotic rice hybrids can be developed.

The hybrid rice program in Egypt began in 1982, in collaboration with the University of California Davis (UCD) and IRRI. The hybrid rice research work has focused on four topics since then:

- Determining the prevalence of fertility-restoring ability for wild abortive (WA) cytoplasm of some Egyptian cultivars,
- Evaluating yield performance of F_1 hybrid combinations,
- Evaluating stability of sterility and phenotypic acceptability of some CMS lines, and
- Determining the outcrossing ratio and hybrid seed yields in seed production plots.

The results obtained in these above studies are summarized in this paper.

Fertility-restoring ability of Egyptian rice varieties

Crosses were made in UCD between the male sterile lines V20 A and Zhen Shan 97 A, with Egyptian cultivars as pollinators. F_1 plants of each cross and their male and female parents were grown in greenhouses at UCD during the winter of 1981-82, and in the field at the Rice Research and Training Center (RRTC) Sakha, Egypt, in the summer of 1982. At both locations, panicles were bagged a few days before anthesis to prevent seed set by outcrossing.

The results indicated that among the Egyptian materials, only Giza 180 showed appreciable fertility restoration in the cross with V20 A (59.6% in the greenhouse and 71.7% in the field) (Table 1). Giza 180 is an indica introduced from IRRI (IR579-48), while the other Egyptian cultivars are japonicas. The Egyptian japonicas showed a small amount of fertility restoration in one or both crosses, especially under field conditions. Therefore, to use the WA cytoplasm in hybrid rice breeding in Egypt, it will be necessary to backcross fertility-restoring genes into appropriate male parents, and or to convert WA cytoplasm into a japonica background.

Yield performance of F_1 hybrids

Yield tests were conducted between 1986 and 1991 at the RRTC to evaluate the potential of 34 hybrids developed by IRRI and 13 hybrids received from two private seed companies. Egyptian commercial varieties were included in the experiments as checks. The experimental design was a randomized complete block with four replications. Plots were transplanted with seven rows per F_1 hybrid at 20- × 20-cm spacing. Harvest area of each plot was 5 m^2.

The average yield of F_1 hybrids developed by IRRI ranged from 5.0 to 8.6 t/ha, while that of check varieties ranged from 7.2 to 9.8 t/ha (Tables 2, 3, and 4). The lowest yield of the hybrids was recorded in 1991 (Table 4), most of these hybrids showed high

Table 1. CMS lines possessing WA cytoplasm.

Egyptian Male parent	F_1 spikelet fertility with female parent			
	Greenhouse (UCD)		Field (RRTC)	
	V20 A	Zhen Shan 97 A	V20 A	Zhen Shan 97 A
Nahda	2.90	0.00	6.20	0.00
Giza 14	0.00	0.00	1.20	0.80
Giza 159	0.00	0.00	1.20	1.60
Giza 170	0.00	0.00	0.80	0.50
Giza 171	0.00	0.00	3.80	0.00
Giza 172	0.00	0.00	1.10	0.60
Giza 173 (Reiho)	0.00	0.00	1.50	-
Giza 180 (IR579)	59.60	-	71.70	-

Table 2. Yield potential of F_1 hybrids developed by IRRI and tested at RRTC, Sakha, Egypt, 1986 and 1989.

Hybrid	Yield (t/ha)	Days to heading	Blast reaction[a]	Grain translucency[b]	Phenotypic acceptability[b]
V20 A/IR9761-19-IR	9.2	98	R	5	5
V20 A/Milyang 46 R	9.5	100	R	5	5
V20 A/Milyang 54 R	10.5	100	R	5	5
V20 A/Iri 347 R	6.4	99	R	5	7
97 A/Milyang 46 R	9.3	105	R	5	7
97 A/Milyang 54 R	8.0	98	R	5	5
97 A/Iri 347 R	4.1	95	R	5	5
IR46828 A/Milyang 54	8.8	95	R	5	5
IR46830 A/Iri 347 R	9.8	94	R	5	5
IR46830 A/IR13292-5R	9.6	102	R	5	5
IR46830 A/Milyang 54 R	8.9	93	R	5	5
IR46830 A/IR54 R	7.3	108	R	5	6
Av (tested hybrids)	8.5	99	–	5	5.4
Giza 171 (late check)	9.3	125	S	3	3
IR28 (early check)	6.5	93	R	5	3
IR64 (international check)	5.7	93	R	5	5
Av (local check varieties)	7.2	105		4.3	3.7

[a] R = resistant, S = susceptible. [b] Determined using the *Standard evaluation system for rice*.

percent sterility (25-90%) which may have been due to late seeding in June. If we take into consideration individual performances, the hybrid V20 A/Milyang 54 showed a 13% increase over the best check variety Giza 171 in 1986 (Table 2).

Two of the hybrid varieties developed by seed companies, LIMING/8411 and Chang Fei-22A/T 230, showed high yield potential and outyielded all the check varieties except the newly released one, Giza 176 (Table 5). These two hybrids seemed to be japonica types, which are normally very successful under Egyptian conditions.

Phenotypic acceptability and other important characteristics were evaluated. In general, most of the hybrids developed by IRRI so far show poor phenotypic

Table 3. Yield potential of F_1 hybrid developed by IRRI and tested at RRTC, Sakha, Egypt, 1990.

Hybrid	Yield (t/ha)	Days to heading	Blast reaction[a]	Grain translucency	Phenotypic acceptability
IR54756 A/IR9761-19-IR	8.9	103	R	5	3
IR64610 H	9.1	100	R	3	3
IR64611 H	9.7	100	R	5	3
IR64612 H	9.1	104	R	7	5
IR64613 H	7.5	104	R	3	5
IR64614 H	8.6	111	R	4	5
IR64615 H	6.8	115	R	3	5
IR64616 H	9.3	106	R	4	5
Av (tested hybrids)	8.6	105	–	4	4
Giza 175 (early check)	10.0	100	R	3	3
Giza 176 (medium early check)	10.0	110	MR	3	3
Giza 181 (medium early check)	10.2	110	R	2	3
Giza 171 (late check)	9.1	120	S	3	3
Av (check varieties)	9.8	110	–	3	3

[a] R = resistant, MR = moderately resistant, S = susceptible.

Table 4. Yield potential of F_1 hybrids developed by IRRI and tested at RRTC, Sakha, Egypt, 1991.

Hybrid	Yield (t/ha)	Days to heading	Blast reaction[a]	Grain translucency	Phenotypic acceptability
IR62829 A/IR44675-101-3-3-2R	5.3	104	R	3	6
IR58025 A/IR66R	7.3	105	R	5	5
IR58027 A/IR54742-22-19-3R	5.5	118	R	5	7
IR62829 A/IR54742-22-19-3R	5.2	107	R	5	7
IR58025 A/IR40750-82-2-2-3R	6.5	119	R	5	7
IR62829 A/IR40750-82-2-2-3R	5.2	107	R	3	5
IR62829 A/IR28238-109-1-3-2R	4.7	107	R	3	3
IR58025 A/IR28238-109-1-3-2R	5.0	101	R	3	7
IR62829 A/IR29723-143-3-2-1R	4.5	102	R	3	5
IR62829 A/IR10198-66-2R	5.0	102	R	5	3
IR58025 A/IR10198-66-2R	5.9	106	R	5	5
IR58025 A/Pusa 105-9-3-1R	4.4	104	R	3	5
IR58025 A/IR35366-62-1-2-3R	4.2	100	R	3	5
IR58025 A/IR48 R	0.8	124	R	5	9
Av (tested hybrids)	5.0	108	–	4	5.6
IR28 (Early check)	8.9	103	R	3-5	3
Giza 175 (Early check)	7.8	103	R	3-5	3
Giza 176 (Med.Early check)	9.5	97	MR	3	3
Giza 181 (Med.Early check)	9.1	102	R	2	3
Giza 171 (Late check)	7.8	98	S	3	3
Av (Check varieties)	8.6	101	–	3-4	3.0

[a] R = resistant, MR = moderately resistant, S = susceptible.

acceptance and poor grain quality, while the majority of the hybrids developed by the seed companies have good phenotypic and acceptable grain quality because their plant type and grain quality are very close to japonica type, which is highly preferred in Egypt.

Table 5. Yield potential of F_1 hybrids developed by seed companies and tested at RRTC, Sakha, Egypt, 1987-90.

Designation	Grain yield (t/ha)	Days to heading	Blast reaction[a]	Grain transclucency	Phenotypic acceptability
Rax 2003	8.4	85	R	5	3
Rax 2851	6.4	85	S	5	3
Rax 2856	7.5	92	S	6	3
Wie You 64	8.4	99	S	5	3
Chang You 64	8.3	96	R	3	3
Xian You 64	9.0	102	R	3	5
Shu You 57	9.0	93	S	7	5
Xiou You 57	8.2	85	S	5	5
Rei You 57	8.7	95	S	5	5
LIMING/4811	10.3	86	R	3	3
Shai Jinna/8411	9.0	97	R	5	3
Chang Fei-22A/T230	10.1	91	R	5	3
Chang Fei-22A/Test 46-7	8.1	81	R	7	3
Av	8.6	91.3	-	5.1	3.8
Giza 171 (late check)	8.9	120	S	3	5
Giza 176 (medium check)	10.5	110	MS	3	3
Giza 181 (medium check)	9.1	107	R	3	3
Giza 175(early check)	8.5	100	R	4	3
IR28 (early check)	8.1	100	R	5	5
Av	9.0	107	-	3.6	3.8

[a] R = resistant, MS = moderately susceptible, S = susceptible.

Table 6. Percent pollen sterility, spikelet fertility, and some agronomic characteristics of CMS lines and their maintainers evaluated at RRTC, Sakha, Egypt.

Designation	CMS lines			Maintainer lines			
	Pollen sterility (%)	Spikelet fertility (%) Open	Spikelet fertility (%) Bagged	Days to heading	Spikelet fertility (%)	Blast reaction	Phenotypic acceptability
V20 A	100.0	36.0	1.0	76	91	R	5
97 A	100.0	24.0	0.0	90	95	R	5
Iri 356 A	100.0	7.0	0.0	96	93	R	-
IR46828 A	100.0	6.0	0.0	90	93	R	-
IR46829 A	100.0	26.0	0.0	85	90	R	-
IR46830 A	100.0	14.0	0.0	90	87	R	-
IR46831 A	100.0	3.0	0.0	99	92	R	-
IR54756 A	100.0	8.0	0.0	95	96	R	-
IR58025 A	100.0	3.0	0.0	115	90	R	5
IR62829 A	100.0	6.0	0.0	115	87	R	5
IR64605 A	100.0	4.0	0.0	119	89	R	3
IR64606 A	100.0	0.0	0.0	127	40	R	7
IR64607 A	100.0	6.0	0.2	113	79	R	3
IR64608 A	100.0	3.0	0.0	114	55	R	5
IR64609 A	100.0	24.0	0.4	111	94	R	3
Krishna A	-	8.4	0.8	100	83	R	7
Pragathi A	-	2.9	0.6	105	89	R	5
PMS1 A	-	4.7	0.3	110	81	R	7
PMS2 A	-	0.6	0.0	112	89	R	7
PMS5 A	-	2.5	1.6	117	72	R	9
PMS10 A	-	0.3	0	118	84	R	9

Table 7. Percentage seed setting and seed production of some hybrids planted in isolated fields at RRTC, Sakha, Egypt, 1990-91.

		IR58025 A		IR62829 A		V20 A	
		Grain yield (t/ha)	Seed setting (%)	Grain yield (t/ha)	Seed setting (%)	Grain yield (t/ha)	Seed setting (%)
				1990			
IR9761-1-1R	A/R	0.070	0.4	0.158	2.0	0.367	-
	R	1.573	83.0	1.573	83.0	1.573	83.0
Total		1.643	-	1.731	-	1.940	-
Milyang 46 R	A/R	0.081	0.9	0.108	3.7	0.157	4.4
	R	1.087	83.0	1.087	83.0	1.087	83.0
Total		1.168	-	1.195	-	1.244	-
IR24 R	A/R	0.066	0.2	0.069	0.6	0.054	0.2
	R	0.899	74.0	0.899	74.0	0.899	74.0
Total		0.965	-	0.968	-	0.953	-
IR29723-14-3-3-2R	A/R	0.124	1.15	0.079	7.0	0.094	0.5
	R	0.910	78.0	0.910	78.0	0.910	78.0
Total		1.034	-	0.989	-	1.004	-
Seed multiplication	A/B	0.205	3.2	0.560	6.0	0.990	5.0
	B	1.425	90.0	1.620	87.0	1.176	80.0
Total		1.630	-	2.180	-	2.166	-
				1991			
IR44675-101-3R	A/R	0.230	2.88	0.400	4.07		
	R	1.430	88.00	1.430	88.00	NT[a]	
Total		1.660	-	1.830	-		
IR66 R	A/R	-	-	0.330	12.00		
	R	-	-	1.408	97.00	NT	
Total		-	-	1.738	-		
Seed multipication	A/B	0.343	2.82	0.308	5.61		
	B	1.360	98.00	1.430	88.00	NT	
Total		1.703	-	1.738	-		

[a] NT = not tested in 1991.

Stability of sterility and phenotypic acceptance of some CMS lines

Cytoplasmic male sterile lines and their maintainers were evaluated for pollen sterility, spikelet fertility under open and bagged panicles, phenotypic acceptability, and other important characteristics. Cytoplasmic male sterile lines and their maintainers were transplanted in adjacent rows. Pollen grains of all the CMS lines examined were 100% sterile, while seed setting percent under bagged panicles ranged from 0.00 to 1.63% (Table 6). This indicates that sterility of some CMS lines is stable under Egyptian conditions and could be used as a good source of sterility for developing local CMS lines. On the other hand, some CMS lines recorded a high percentage of seed setting under open pollinated panicles—e.g., V20 A (36%), IR46829 A (26%), 97 A (24%), and IR46483 A (14%)—indicating that these lines have floral characteristics that encourage outcrossing under Egyptian conditions.

Determining outcrossing ratio and hybrid seed production in isolated plots

Isolated field tests were conducted at RRTC in 1990-91 to determine outcrossing ratio and yield of hybrid seeds and seed multiplication per hectare under Egyptian conditions. Fields were transplanted in rows with 20- × 20-cm spacing and row ratios of 8A:2R or B. Isolation distance was about 100 m from each side of the field. Supplementary pollination was done by moving a stick over the pollinators during anthesis to dislodge the pollen.

Yields of the isolated plots were low for either A lines or B or R lines (Table 7). The yields of the A lines included the area of B or R lines and ranged from 0.05 to 0.99 t/ha; yields of B or R lines included the A line area and ranged from 0.90 to 1.62 t/ha. The poor yield of A lines may be due to late seeding (done in June, normal seeding time in Egypt is May) or nonsynchronization between the male steriles and pollinators.

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Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Public sector research on hybrid rice in the United States

D. J. Mackill and J. N. Rutger

Hybrid rice has the potential to increase yields in the United States, allow easier combination of traits controlled by dominant genes, and improve seed quality and distribution of promising cultivars. Research has focused on evaluating levels of heterosis, developing seed production systems, and searching for apomixis. Heterosis among U.S. japonica cultivars appears to be low. Current efforts are directed toward increasing diversity and exploiting the wide compatibility gene for indica x japonica hybrids. Research on seed production mechanisms has focused on male sterility. Several genetic male steriles have been developed for use in breeding. Cytoplasmic male sterility is being transferred to California japonicas, but the three-line production system may be too laborious for application in the U.S. The two-line approach appears more promising; environmentally sensitive male steriles have been developed and are under evaluation. The *eui* (elongated uppermost internode, or recessive tall) gene was identified for use in the pollinator parent to facilitate outcrossing. Apomixis could be an excellent means of fixing heterosis in a rice cultivar. An exhaustive search of cultivated and wild *Oryza* species yielded no conclusive evidence of significant levels of apomixis. A more promising approach will be to identify and introduce apomixis genes from other grass species into rice by direct DNA transfer or protoplast fusion.

Rice yields in the United States, and in California in particular, are among the highest in the world. Estimated average grain yield for California in 1991 was almost 9 t/ha. Exploiting heterosis is seen as a means of increasing yields still further. An additional advantage of hybrid rice would be the ease of combining important dominant genes in a single variety. Hybrid rice varieties cannot be propagated by seed, so the breeder/owner would have more control over distribution of the variety. This may stimulate more investment in breeding research, as the return on this investment would be more assured.

There are significant bottlenecks to the exploitation of hybrid rice in the US., the major one being the economics of seed production and seed costs. All rice in the U.S. is direct seeded, and seeding rates range from 100 to 150 kg/ha (Hill et al 1990). Seeding rates could probably be reduced without seriously affecting stand establishment but would still be considerably higher than for transplanted areas. Labor costs are also considerably higher in the U.S. than in Asia. In California, where japonica rices predominate, there is the added difficulty of obtaining high enough levels of heterosis to make hybrid rice worthwhile.

Private companies have become interested in the hybrid rice market for the southern U.S., where indica and japonica varieties can be grown and higher levels of heterosis are more easily obtained. This paper will therefore focus on the problems of developing hybrid rice in California, where public-sector research in hybrid rice has been more prominent. Research in California has focused on evaluating levels of heterosis, improving seed production systems, and searching for apomixis.

Heterosis

The first requirement for producing hybrid rice is to obtain a hybrid with a sufficient level of heterosis to justify the higher seed production costs. Rice cultivars grown in California are japonica-type, deriving ultimately from Japanese and Chinese germplasm. By isozyme classification (Glaszmann 1987), the japonica group (isozyme group VI) contains both temperate and tropical germplasm, the former traditionally designated japonica and the latter javanica or bulu. Despite morphological and geographical diversity, genetic polymorphism seems to be lower in japonica rices than in indicas (Glaszmann 1987). Most researchers feel that japonica × japonica hybrids do not exhibit as much heterosis as indica × indica hybrids (Virmani et al 1981). There are some reports, however, that significant heterosis in japonica × japonica hybrids can be obtained (Cao 1988, Li and Ang 1988), and japonica hybrids are grown on a limited area.

Davis and Rutger (1976) studied heterosis of rice hybrids at Davis, California. Of 41 hybrids examined, 10 outyielded the highest yielding parent, but only two outyielded the best cultivar (by 23 and 16%). The experiments were conducted using wide spacing (30 × 30 cm) in single-row plots, so the results may not apply to direct seeded plots.

Future work must focus on increasing the narrow genetic base of California japonicas. There is considerable interest in exploiting the heterosis observed in indica × japonica hybrids. Indica × japonica crosses normally exhibit considerable sterility, but the wide compatability gene, described by Ikehashi and Araki (1986), can suppress this sterility. We are currently introducing this gene into California japonicas so that yield of indica × japonica hybrids can be evaluated. Even if genetic sterility is avoided, most indica varieties are susceptible to low temperatures at the vegetative and young microspore stages, an important limiting factor in California environments. One approach is to develop, through hybridization, lines with many indica genes but adapted to California growing conditions. Some early indica varieties like Ai-Nan-Tsao can produce fertile panicles in Davis, California, and these may form the basis of more diversification. Unfortunately, most indica types cannot meet the strict eating and milling quality standards of U.S. rices, and recovering this quality is often difficult. We are presently using molecular markers to tag genes conferring cold tolerance in indica × japonica crosses. This should improve the efficiency of introgression of indica genes into the japonicas.

Hybrid rice seed production mechanisms

Extensive research has been conducted at Davis on male sterility. Cytoplasmic male sterility (CMS) is the most useful for producing hybrid seed. An attempt was made to induce CMS in japonica varieties to avoid the long process of backcrossing these into adapted cultivars. No CMS mutants were found, but two useful male sterile mutants with higher levels of outcrossing were isolated (Rutger 1988, Hu and Rutger 1992). We are currently backcrossing CMS and restorer genes into California cultivars.

The two-line system of seed production would be highly desirable for California conditions. This system relies on a genetic male sterile gene that is sensitive to photoperiod or temperature. Two useful mutants have been identified in California. These have been termed “environmentally sensitive” due to the ambiguity of the factor inducing sterility. The mutant described by Oard et al (l991) shows a fivefold increase in fertility when plants are grown at 12-h daylength, as opposed to natural long-day conditions in the field at Davis. F_1 plants are completely fertile. Sterility was shown to be controlled by two genes with epistatic effect.

The mutant described by Rutger and Schaeffer (1989) was identified from anther culture-derived plants. This mutant is conditioned by a single recessive gene. Under long-day California conditions, the plants are sterile. But in the winter nursery in Hawaii, or when grown in the southern U.S., plants are completely fertile. This mutant would be ideal for hybrid seed production for California. Homozygous sterile seed stock could be produced in the southern U.S., and the F_1 hybrids could be produced in California.

A recessive tall mutant, designated *eui* for elongated uppermost internode, was identified in California (Rutger and Carnahan 1981). It was termed the “fourth genetic element” for facilitating hybrid seed production, the other three being CMS, maintainer, and restorer genes. Additional *eui* mutants isolated have been shown to be controlled by the same locus. This gene, when introduced into the pollen parent, should facilitate outcrossing, and the resulting F_1 plants will have normal phenotype. While conceived of as a pollinator trait, the gene has recently been introduced into CMS lines to promote panicle exsertion of the sterile plants in China (Shen and He 1989). This gene can eliminate the need to apply gibberellic acid to the female parent.

Apomixis

The ultimate seed production method would be to develop apomixis in rice as a means of fixing heterosis in a true-breeding cultivar. An extensive search for apomixis was begun at Davis in 1985 (Rutger et al 1986, Rutger 1992). Progeny of 3,728 F_1 plants were evaluated for abnormal segregation, a sign of apomixis. Only seven F_1s produced abnormal segregation, but this could not be attributed to apomixis. Another indication of apomixis is twin seedlings. Of 603 cultivars screened for this trait, four were identified that produced occasional twin seedlings. Cooperative studies on high frequency twin seedling production were also conducted with Chinese scientists (Ching et al, unpubl. data). Also 547 wild or weedy species were evaluated for abnormal embryos, an expected indication of apomixis. Sixty-eight cultivars were identified with some abnormal embryo formation.

These studies failed to confirm the existence of apomixis in rice. Furthermore, even if the observations could be attributed to apomixis, the levels would probably be too low for use in conventional breeding. The most promising approach for developing apomictic rice would be to identify the genes causing apomixis in other grasses and transfer these to rice via direct DNA transfer. Even if these genes cannot be identified, it may be possible to transfer them by protoplast fusion.

Conclusions

While the outlook for hybrid rice in the southern U.S. still appears to be relatively good, there are significant problems to overcome before it can be adopted in California. Foremost among them is identification of heterotic combinations that are adapted to California conditions while maintaining the required grain quality standard. Even if this can be achieved, it is still not certain if seed could be produced cheaply enough to make its use economical; however, the potential benefits of hybrid rice necessitate further research. Our work will continue to focus on identifying or developing adapted heterotic combinations and economical seed production systems. A useful byproduct of this research will be the development of a broader germplasm base for conventional breeding programs.

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Authors' addresses: D. J. Mackill, Research Geneticist, USDA-ARS, Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA; and J. N. Rutger, Associate Director, Mid South Area, USDA-ARS, Jamie Whitten Delta States Research Center, P. O. Box 225, Stoneville, MS 38776-02256, USA.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Hybrid rice research in Colombia

D. B. Muñoz

Hybrid rice research in Colombia began in 1983 in collaboration with the International Rice Research Institute (IRRI). Five rice hybrids were evaluated in yield trials against the predominant variety, Oryzica 1. The hybrid V20 A/Suweon 294 yielded 8.3 t/ha and showed the highest heterobeltiosis (21%) and standard heterosis (10%) for yield. Oryzica 1 yielded 7.5 t/ha more than the other hybrids. A study was conducted to determine the yield potential and yield components of 15 hybrid rices. The hybrid Oryzica 2/Cica 4 gave the highest yield (8.5 t/ha), and showed the highest heterosis (49%) and heterobeltiosis (44%). This hybrid yielded 34% more than Oryzica 1. Chinese cytoplasmic male sterile (CMS) lines V20 A and Zhen Shan 97 A were used in testcrosses with 42 male parents. Forty-five percent were identified as maintainers, 40% as partial restorers, and only 14% as restorers. The white core is the most important determinant of price, so a study was carried out with three hybrids. Two of the hybrids showed lower white core than the mid-parent. The hybrid IR46830 A/IR9761-19-1 had the lowest white core, with 0.6, and Oryzica 1, 0.4. Twelve hybrids were harvested in replicated yield trials at two locations in February 1992. IR62829 A/IR40750-82-2-2-3R was the best hybrid (5.6 t/ha) compared with Oryzica 1(4.7 t/ha). The hybrid rice breeding program is focusing on selecting and restorers better adapted to local environmental conditions.

Rice is the most important crop after coffee in Colombia and it is the second source of protein after meat. Rice area in 1991 was 352,323 ha, and average yield was 4.9 t/ha. Total production has declined annually by 1% over the last 10 yr and consumption decreased from 39 to 31 kg/person per year between 1980 and 1990.

Rice production improved during the past two decades because of the development of 14 semidwarf, high-yielding varieties. However, average yields have reached a plateau. Hybrids offer the opportunity to break through this yield ceiling. However, the economic viability of hybrids under our agroecological conditions should be analyzed.

First hybrid rices evaluated

The first study on hybrid rices was carried out in the Cauca Valley Department at the National Research Center Palmira (CNI-Palmira) of the Colombian Agricultural Institute (ICA) in 1983 and 1984 (Muñoz and Carvajal 1989). The five hybrids and their parents were introduced from IRRI and were compared with Oryzica 1, the predominant variety in Colombia (ICA-CIAT and National Rice Growers Federation [FEDEARROZ]) (Table 1).

The hybrid V20 A/Suweon 294 yielded 8.3 t/ha and showed the highest heterobeltiosis (21%) and standard heterosis (10%) for yield; the other hybrids yielded less than Oryzica 1 (7.5 t/ha) (Table 2).

All the hybrids were lower than Oryzica 1 in the following parameters: days to flowering, leaf area index, root dry weight, number of empty spikelets per panicle, and number of grains per panicle.

Hand-pollinated hybrids

A study was conducted to determine the yield potential, yield components, and some agronomic characteristics of 15 hybrid seeds which were produced by hand-pollination between varieties Cica 4, Cica 7, Oryzica 1, and Oryzica 2 and experimental lines 17396 and 11744. The experiment was planted by transplanting at CNI-Palmira of ICA. A randomized complete block design was used, with four replications (Muñoz and Castellanos 1990). The hybrids generally yielded more and had superior yield components than their parents (heterosis) and the best parent (heterobeltiosis). The hybrid Oryzica l/Cica 4 gave the highest yield (8.5 t/ha) and showed the highest heterosis (49%) and heterobeltiosis (44%). The following hybrids ranked second with 8.2 t/ha, Oryzica 2/Cica 7, 17396/11744, and 11744/Cica 4. The first two hybrids yielded 34 and 30% more than Oryzica 1, respectively (Tables 3 and 4).

Twelve out of 15 F_1 hand-pollinated hybrids showed heterosis and heterobeltiosis for grain number per panicle. Heterosis ranged from 10 to 47% and heterobeltiosis from 3 to 38% (Table 4). The hybrid 11744/Cica 4 had the highest number of grains per panicle (195) (Table 3). Mallick et al (1978) reported negative heterosis for grains per panicle in all the hybrids evaluated.

Some restorers and maintainers of wild abortive cytosterile lines

A study was initiated to identify restorers and maintainers for the CMS lines V20 A and Zhen Shan 97 A. The work was done in the Cauca Valley Department at CNI-Palmira of ICA. Pollen storage at different temperatures with different panicle development stages was tested. It was found that the best methodology for evaluating pollen sterility was with flowers located in the upper third part of the panicle before dehiscence, storage at 2-11 °C, and staining with IKI.

F_1 hybrids from the two CMS lines and 42 male parents (which were traditional), standard varieties, and elite breeding lines with different heading times were obtained. These F_1 hybrids were transplanted in the field with 16 plants to a row and percentage

Table 1. Yield and yield components of five F_1 rice hybrids and superiority over parents and best commercial variety Oryzica 1. CNI-Palmira, Colombia.[a]

Hybrid/ variety	Yield (t/ha)	Grains/ panicle (no.)	Unfilled spikelets/ panicle (no.)	1000-grain wt (g)	Panicle-bearing tillers/plant (no.)
V20 A/Suweon 294	8.3 a[b]	190 c	25 cde	29 b	23 cdef
V20 A/Milyang 46	7.5 ab	180 c	22 def	30 b	23 cdef
MR365 A/Suweon 287	5.7 de	191 c	26 cde	25 d	26 c
V20A/Suweon 287	5.6 de	144 f	10 gh	28 c	21 ef
IR747 A/IR50	4.7 ef	153 ef	15 fg	19 g	37 a
Milyang	7.0 b	162 de	19 ef	28 c	24 cde
Suweon 294	6.8 bc	244 a	30 bc	21 f	23 cdef
IR50	6.0 cd	191 c	39 a	19 g	31 b
Suweon 287	4.9 ef	182 c	16 fg	24 e	20 f
MR365 B	5.3 ef	175 cd	28 bcd	26 de	26 cd
IR747 B	5.0 ef	115 g	5 h	19 g	38 a
V20 B	4.4 f	111 g	11 gh	33 a	21 ef
Oryzica 1	7.5 ab	222 b	34 ab	25 d	22 def

[a] Av of two semesters. [b] Means with the same letter are not significantly different at the 5% level by DMRT.

Table 2. Heterobeltiosis and standard heterosis in yield and yield components in five F_1 rice hybrids. CNI-Palmira, Colombia.[a]

Hybrid	Heterobeltiosis and standard heterosis (%)				
	Yield[b]	Grains/ panicle	Unfilled spikelets/ panicle	1000-grain wt	Panicle-bearing tillers/plant (no.)
V20 A/Suweon294	21*[c]	-21^{ns}	-17^{ns}	-11^{ns}	2*
	10[d]	-14	-17	16	7
V20 A/Suweon46	7^{ns}	11^{ns}	13^{ns}	-9	-4^{ns}
	0	-19	-36	18	4
MR365 A/Suweon 287	7^{ns}	5^{ns}	-10^{ns}	2^{ns}	3^{ns}
	-25	-14	-24	-1	20
V20 A/Suweon 287	14^{ns}	-21^{ns}	-40^{ns}	-14^{ns}	-1^{ns}
	-25	-35	-71	12	-4
IR747 A/IR50	-21^{ns}	-20^{ns}	-63^{ns}	-1^{ns}	-3^{ns}
	-36	-31	-57	-24	67

[a] Av of two semesters. [b] * = significant at 5% level. [c] Heterobeltiosis. [d] Standard heterosis over Oryzica 1. ns = not significant.

sterility was determined. Eight plants, three panicles per plant, and three flowers per panicle were analyzed by the methodology suggested. Male parents of F_1 that showed 90-100% pollen sterility were designated maintainers. Male parents of F_1 that showed 21-89% pollen sterility were designated partial restorers. Male parents showing 0-20% pollen sterility were designated restorers.

Among the male parents, 6 (14%) restorers and 19 (45%) maintainers were found (Table 5). Mohanty and Sarma (1983), using V20 A, identified 26% restorers and 26%

Table 3. Yield and yield components of 15 F_1 hand-pollinated hybrids and their parents. CNI-Palmira, Colombia.[a]

Hybrid and parent	Yield (t/ha)	Grains/ panicle (no.)	Unfilled spikelets/panicle (no.)	1000-grain wt (g)	Days to flowering
Oryzica 2/17396	7.5 abcd	145 fgh	96 bc	28.7 a	105 d
Oryzica 2/11744	7.5 abcd	190 a	61 fgh	25.3 ef	106 d
Oryzica 2/Cica 7	8.2 abc	163 cde	101 b	27.0 b	106 d
Oryzica 2/Cica 4	8.5 a	181 ab	88 bcd	25.4 ef	109 c
Oryzica 2/Oryzica 1	7.3 abcde	161 cde	70 efg	28.5 a	97 g
17396/11744	8.3 ab	175 bc	64 efgh	25.9 de	108 c
17396/Cica 7	6.9 abcde	119 jk	77 def	27.0 b	105 d
17396/Cica 4	7.5 abcd	166 cd	36 j	26.7 bc	109 c
17396/Oryzica 1	4.5 f	101 l	92 bcd	28.2 a	100 f
11744/Cica 7	7.3 abcde	191 a	48 hij	23.7 g	111 bc
11744/Cica 4	8.3 ab	195 a	49 hij	23.5 g	110 c
11744/Oryzica 1	6.5 bcde	149 efgh	42 ij	25.4 ef	96 g
Cica 7/Cica 4	6.1 def	134 hij	56 ghi	24.8 f	102 ef
Cica 7/Oryzica 1	6.8 abcde	151 defg	81 cde	26.6 bc	104 de
Cica 4/Oryzica 1	7.5 abcd	164 cde	81 cde	25.9 de	106 d
Oryzica 2	5.5 ef	127 ijk	118 a	25.5 e	114 a
17396	7.3 abcde	137 ghi	40 ij	26.3 cd	114 a
11744	6.5 bcde	139 ghi	45 hij	21.8	113 ab
Cica 7	6.7 abcde	121 jk	33 j	26.7 bc	105 d
Cica 4	5.9 def	158 def	36 j	22.3 h	104 de
Oryzica 1	6.3 cde	117 k	32 j	26.6 bc	109 c

[a] Means with the same letter are not significantly different at the 5% level by DMRT.

Table 4. Percent heterosis (H) and heterobeltiosis (Hb) in yield and yield components in 15 F_1 hand-pollinated hybrids. CNI-Palmira, Colombia.

Hybrid	Yield		Grains/ panicle		Unfilled spikelets/panicle		1000-grain wt		Days to flowering	
	H	Hb	H	Hb	H	Hb	H	Hb	H	Hb
Oryzica 2/17396	17	3	10	5	21	138	11	9	-7	-7
Oryzica 2/11744	25	16	43	37	-26	33	7	-1	-7	-7
Oryzica 2/Cica 7	35	22	32	28	50	201	3	1	-3	1
Oryzica 2/Cica 4	49	44	27	15	14	143	6	0	0	5
Oryzica 2/Oryzica 1	24	16	32	27	-7	120	9	7	-13	-11
17396/11744	20	13	26	26	49	58	7	-2	-4	-4
17396/Cica 7	-1	-5	-8	-13	109	120	2	1	-3	1
17396/Cica 4	13	2	12	5	-6	0	10	1	05	
17396/Oryzica 1	-34	-38	-20	-26	157	191	7	6	-10	-8
11744/Cica 7	11	9	47	38	21	42	-2	-11	2	6
11744/Cica 4	34	28	31	23	20	36	7	5	2	6
11744/Oryzica 1	1	0	-16	7	8	31	5	-4	-13	-12
Cica 7/Cica 4	-3	-9	-4	-15	61	67	1	-7	-2	-2
Cica 7/Oryzica 1	5	2	27	25	147	154	0	0	-3	0
Cica 4/Oryzica 1	22	18	19	3	139	156	6	-8	0	2

Table 5. Parents classified according to pollen fertility. CNI-Palmira, Colombia.

Cytosterile	Restorers	Maintainers	
Zhen Shan 97 A	Cica 8	Colombia 1	Taichung 176
V20 A	IR22	Fortuna morado	Palawan
	L 11972	Fortuna blanco	Suakoko
	L 17388	Inamono	IRAT13
	Campeche A-80	Monolaya	IRAT120
	Chianung Sen Yu 23	Miramono	IRAT121
		Cacao pelao	IRAT122
		Rexoro	IRAT124
		Moroberekan	IRAT125
		Taipei 309	

Table 6. Yield and grain quality of three hybrids and their parents in comparison with Oryzica 1. [a]

Designation	Yield (t/ha)	1000-grain wt (g)	Milling yield (%)	Chalkiness [b]
IR46830 A/IR9761-19-1	8.7 abc	23.8 cde	68 ab	0.6 de
IR46830 B	7.5 bcd	23.1 de	66 b	0.5 e
IR9761-19-1	9.2 ab	22.8 e	61 c	1.3 cd
Zhen Shan 97 A/Milyang 54	8.7 abc	27.5 ab	69 ab	1.6 bc
Zhen Shan 97 B	7.3 bcd	25.9 bc	69 ab	2.5 a
Milyang 54	6.2 d	23.8 cde	66 ab	1.3 cd
V20 A/IR9761-19-1	9.9 a	27.4 ab	69 ab	2.2 ab
V20 B	6.7 cd	29.1 a	70 a	2.7 a
IR9761-19-1	9.2 ab	22.8 e	61 c	1.3 cd
Oryzica 1	9.2 ab	25.4 bcd	68 ab	0.4 e

[a] Means with the same letter are not significantly different at the 5% level by DMRT. [b] Scale 0-5: 0 = free from chalkiness. 5 = completely chalky.

maintainers out of 23 commercial varieties; from 51 advanced breeding materials, they isolated 33% restorers and 25% maintainers.

Yuan and Virmani (1988) reported that effective restorer varieties are mainly from the tropics, where indica rices are grown, and that 20% of rice varieties and breeding lines developed at IRRI possess restoration ability for wild abortive cytosterile lines.

Grain quality of some hybrid rices

Chalkiness is the major determinant of price in Colombia. Grain yield and some grain quality characteristics of three F_1 hybrids were evaluated. The replicated yield trial was done at CNI-Palmira in 1988. The yield and some grain quality data of the three F_1 hybrids and their parents compared with Oryzica 1 (best check) are shown in Table 6. Heterosis, heterobeltiosis, and standard heterosis are included in Table 7.

The F_1 hybrid V20 A/IR9761-19-1 was the only one that showed standard heterosis (8%) in grain yield and had the highest chalkiness. All of the F_1 hybrids showed heterosis in milling yield. The hybrid IR46830 A/IR97671-19-1 had the lowest chalkiness, 0.6,

Table 7. Percent heterosis, heterobeltiosis, and standard heteroris in yield and grain quality in three hybrids. CNI-Palmira, Colombia. [a]

Entry	Yield	1000-grain weight	Milling yield	Chalkiness
IR46830 A/IR9761-19-1				
Heterosis	4	4	7*	-26
Heterobeltiosis	-6	3	3	-50
Standard heterosis	-6	-6	0	67
Zhen Shan 97 A/Milyang 54				
Heterosis	28	11*	2	-16
Heterobeltiosis	18	6	0	-35
Standard heterosis	-6	8*	2	300**
V20 A/IR9761-19-1				
Heterosis	24	6	5	8
Heterobeltiosis	8	-6	-2	-20
Standard heterosis	8	8*	2	450**

[a] *, ** = significant at the 5 and 1% level, respectively.

Table 8. Yield, head rice, and chalkiness of 12 hybrids in comparison with Oryzica 1 at two locations. Colombia, 1991. [a]

Hybrid	Grain yield (t/ha)		Head rice recovery (%)		Chalkiness[b]	
	Saldaña	Bosconia	Saldaña	Bosconia	Saldaña	Bosconia
IR62829 A/IR29723-143-3-2-1R	4.6	4.6	49 ab 2/	58	2.0	3.6
IR62829 A/IR28238-109-1-3-2-2R	4.1	5.6	54 a	59	1.5	1.6
IR62729 A/IR9761-19-1R	4.3	4.2	38 cd	59	1.5	1.2
IR58025 A/IR15324-13-3-3-2R	5.0	4.9	39 bcd	53	2.0	2.2
IR58025 A/IR54742-22-19-3R	4.7	5.5	30 de	56	1.2	1.0
IR58025 A/IR54742-22-19-3R	4.7	5.1	48 abc	58	1.3	1.0
IR62829 A/IR40750-82-2-2-3R	6.0	5.0	49 abc	50	1.0	1.6
IR58025 A/IR29723-143-3-2-1R	5.0	5.1	23 e	50	1.8	2.0
IR58025 A/IR10198-66-2R	4.9	5.6	47 abc	61	1.8	1.2
IR62829 A/IR10198-66-2R	3.9	5.8	48 abc	60	1.5	2.0
IR58025 A/Pusa 150-9-3-1R	4.7	4.7	48 abc	50	1.8	0.4
IR58025 A/IR35366-62-1-2-2-3R	4.3	5.1	48 abc	54	1.8	0.4
Oryzica 1	4.0	5.3	54 a	59	0.8	0.8

compared with 0.4 for Oryzica 1. The high chalkiness of the hybrids appeared to be inherited primarily from the female parents. Recently, some F_1 combinations derived from new IRRI CMS lines have shown encouraging results for grain quality improvement.

Recent F_1 hybrids

IRRI F_1 hybrid rices recently evaluated in Colombia were harvested in February 1992. The replicated yield trials were conducted using direct seeding at two different locations. The Saldaña area is located in the central part of the country and Bosconia is on the Atlantic coast; both are irrigated.

The highest yielding hybrid was IR62829 A/IR40750-82-2-2-3R, with an average yield of 5.6 t/ha (Table 8). The best local check variety, Oryzica 1, yielded 4.7 t/ha. The two hybrids, IR58025 A/IR10198-66-2R and IR62829 A/IR10198-66-2R, with the same restorer, had the highest yield and head rice recovery at Bosconia.

The performance of most hybrids tested based on yield was similar at both locations. The most remarkable characteristic in the majority of the hybrids was the low chalkiness, which varied between 0.4 and 1.8.

These results are encouraging the continued selection of indica-type restorers in Colombia and crossing these to CMS lines IR58025 A and IR62829 A, which appear to transmit good grain quality to the hybrid. Yuan and Virmani (1988) reported that the frequency of restorer lines in indica rices is fairly high (20%).

Prospects for hybrid rice

Yields are already high in Colombia. F_1 hybrids could raise yield ceilings further. Some commercial varieties and advanced breeding lines obtained in this country have been identified as restorers. IRRI scientists are developing new CMS lines adapted to the tropics with good grain quality.

The FEDEARROZ Rice Improvement Program is developing a new CMS line by transferring the cytosterility system of the wild abortive lines V20 A and Zhen Shan 97 A into elite line Colombia 1 by backcrosssing. Since Colombia has low- and high-temperature areas in close proximity, the two-line method shows great promise for the future.

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Authors' address: D. B. Muñoz, National Rice Growers Federation (FEDEARROZ), Apartado Aeréo 52772, Bogota, Colombia.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Hybrid rice research in Brazil

P. C. F. Neves, E. M. Castro, P. H. N. Rangel, and L. P. Yokoyama

Hybrid rice has great prospects in Brazil. The first hybrid varieties are intended for release in irrigated areas, where 49% of Brazil's rice is produced. The technological level of the farmers (which results in average yields of 4.8 t/ha), the good infrastructure for seed production and distribution, and the expected improvement in the economical productivity of hybrid rice provide a good basis for developing hybrid varieties. The National Research Center for Rice and Beans is developing a hybrid rice breeding program based on the three-line method, using the wild abortive cytoplasm and the long stigma trait transferred from *O. longistaminata* A. Chev. to improve cross fertilization. The first set of identified maintainer lines are being sterilized, the combining ability tests will be done soon, and hybrid rice varieties probably will be released in the next 5 yr. To improve the available variability for varietal creation in the future, a reciprocal recurrent selection scheme has been started.

The Chinese seed production system is highly labor-intensive, so it is not economical in countries like Brazil, where rice production is fully mechanized. Therefore, an alternative technology must be developed.

Average yield of upland rice in Brazil is low (1.4 t/ha), although the climatic conditions are favorable for this crop. It is possible to increase this yield through suitable cultural practices. Average yield of lowland rice is about 4.8 t/ha. Taillebois and Guimaraes (1987) have observed F_1 hybrids with yield heterosis of about 25% over traditional varieties, so yield potential could be increased through hybrid breeding.

The National Research Center for Rice and Beans (CNPAF/EMBRAPA) is developing a research program for irrigated lowland areas with the objective of developing improved male sterile parental lines with long stigmas to increase outcrossing rate and permit hybrid seed production at a lower cost.

Irrigated and rainfed lowland rice cultivation systems in Brazil

Total rice production in Brazil averaged 10.2 million t/yr over the last 5 yr. Irrigated rice contributed about 49% of this. Approximately 5% of total production came from rainfed lowland conditions. About 23% of the total rice area in Brazil is under these two systems, the rest is under upland conditions.

The irrigated lowland cultivation system covers about 1.07 million ha, concentrated mainly in the southern region of the country. Direct mechanized seeding is practiced in 90% of this area. In the states of Rio Grande do Sul, about 766,000 ha are planted, and the most commonly planted cultivars are IRGA409, IRGA410, IRGA412, and IRGA414. Seeding is done with pregerminated seeds in the 104,000 ha of the state of Santa Catarina, where Cica8 is the prevailing cultivar. The other important areas for irrigated rice are the west-central and northern regions, with about 102,000 ha, mostly planted with cultivar Metica 1. Rainfed lowland areas are concentrated in the southeast, where Cica8 is the prevailing cultivar on an area of about 120,000 ha.

The climatic conditions vary from region to region, but this variation is less in areas where the irrigated lowland system dominates. This explains the broad geographic distribution of some cultivars. The exception is the state of Rio Grande do Sul, where the low temperatures in the autumn season favor cultivars with short cycles.

Based on the importance of irrigated rice in Brazil, the technological level in this system, and the prospect of greater economic returns through hybrid rice technology, the CNPAF gave top priority to the hybrid rice program.

There is good infrastructure for seed production and distribution in irrigated lowland regions of Brazil. In these regions, several national and international enterprises are now working with hybrid maize. Some of them are also working with vegetable hybrids. This kind of experience will be useful for hybrid rice development.

Research program for the development of hybrid rice at CNPAF

The CNPAF began its research on hybrid rice technology in 1984, concentrating on the irrigated lowland system. The work involves improving parental lines based on the three-line (A, B, and R) hybrid breeding system using short- and long-term breeding strategies.

Short-term strategy of hybrid rice breeding

The A, B, and R lines are being obtained through the identification of maintainer and restorer plants among existing Brazilian cultivars or fixed lines proceeding from the conventional breeding program.

All available purelines are crossed with a restoration tester carrying wild abortive (WA) male sterile cytoplasm. Maintainers and restorers are identified by F_1 fertility rate and anther characteristics. The A/B lines are being produced by backcrossing the long stigma trait transferred from *Oryza longistaminata* A. Chev. and the WA male sterile cytoplasm in the maintainer plants. Some indica lines are at the first cross cycle for WA male sterile cytoplasm, following introduction of the long stigma trait.

The combining ability of A and R lines will be tested for yield and other traits of economic importance. Good combining A and R lines will be used to develop heterotic rice hybrids.

Long-term strategy for hybrid rice breeding

CNPAF will apply a recurrent selection scheme to broaden the genetic variability among parental lines of the hybrids. The recurrent selection has already been applied by using genetic male sterile mutants of IR36 (developed at IRRI by Singh and Ikehashi [1981]) to develop composite breeding populations. Two populations, CNA-IRAT4 M and CNA-IRAT4 R, were formed after identifying and intercrossing maintainer and restorer plants from the CNA-IRAT4 population into the two respective groups (Taillebois and Neves 1989). To broaden the genetic bases of these male and female populations, a collection of maintainer and restorer lines was introduced. The long stigma trait was introduced into the female parent. Average intercrossing rate is 34% in the CNA-IRAT4 population after four recombining cycles, and observations show that it is possible to select for this character.

The reciprocal recurrent selection scheme used in half sib families (Neves et al 1990) will help improve the combining ability among the two populations. The allogamy characters will be improved in the maintainer population and restoration ability will be tested and selected in the restorer one.

Four generations, or 2 yr, are necessary to complete one cycle of recurrent selection. Hybrid parental lines will be created at each cycle by pedigree selection on the “per se” performance. The long stigma trait will be selected in early generations. Restoration ability will be tested on inbred lines and maintainer plants sterilized by WA cytoplasm. The tests of combining ability and restoration will be done during the normal cropping season.

Considering the progress of research, we expect that the first set of rice hybrids for Brazil will be released by 1997.

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Authors' address: P. C. F. Neves, E. M. Castro, P. H. N. Rangel, and L. P. Yokoyama, National Research Center for Rice and Bean, EMBRAPA-CNPAF, C. P. 179, Goiania, GO 74001, Brazil.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Hybrid rice research at CIRAD/IRAT

J. Taillebois, M. Jacquot, G. Clement, E. Guiderdoni, B. Courtois,
L. Seguy, and S. Bouzinac

The Institute for Research in Tropical Agriculture (IRAT) is the Food Crops Department of CIRAD (French Center for International Cooperation in Development-oriented Agricultural Research). The CIRAD/IRAT research project on hybrid rice was developed in three phases, starting in Montpellier, France, in 1981. From 1984 to 1989, the project was conducted in Goiania, Brazil, in collaboration with EMBRAPA/CNPAF. During this time, the basic knowledge and genetic materials necessary for organizing a breeding project on hybrid rice varieties were developed. Since 1990, CIRAD/IRAT has been conducting its own project, with the aim of selecting hybrid rice varieties for irrigated conditions in tropical countries of South America and in countries under a Mediterranean-type climate. The breeding research activities are carried out in France, principally in French Guyana, South America. Cytoplasmic male sterility is used. Trials on gametocides are also being conducted with private chemical companies. The Anther Culture Laboratory of IRAT in Guadeloupe, French West Indies, is participating in the project. The biotechnology laboratories of IRAT in Montpellier and Nottingham University (U.K.) are undertaking sterile cytoplasm transfer through protoplast fusion and plant regeneration. Medium- and long-term recurrent selection is ongoing. The first tests of seed production and agronomic evaluation are now being conducted in French Guyana and in the Rhone Delta near the Mediterranean. Yield tests are planned for 1993 in these areas and other tropical and Mediterranean countries. For research activities, seed production, distribution, and marketing, CIRAD/IRAT is looking for private partners.

First phase

In 1981, IRAT decided to start research on hybrid rice because of the Chinese success. The main problem in growing hybrid rice outside China was the low level of hybrid seed production, which is due to the poor outcrossing ability of *Oryza sativa.* Accordingly, IRAT, which was working on the wild allogamous species *O. longistaminata,* tried to increase the outcrossing ability of *O. sativa* by transferring the floral characters of *O. longistaminata* to *O. sativa.* This work, conducted at Montpellier, France, led to the conclusion that allogamous characters, mainly the very large stigmas of *O. longistaminata,* were transferable to *O. sativa.*

Second phase

Since IRAT already had important collaborative projects with EMBRAPA/CNPAF, and because CNPAF had active research projects on hybrid rice, it was decided in 1984 to set up a joint hybrid rice project in Brazil. The main objective of this collaborative work was to acquire the basic knowledge and genetic materials necessary for organizing a breeding project on rice hybrids. To carry out this work, six male sterile cytoplasms were obtained from IRRI; three of these—WA, GAM, and BT— were later used.

With indica material for WA cytoplasm, it is easy to find restorer lines but sterilizable lines are few. For japonica material, this cytoplasm induced good sterility, but numerous japonica varieties have a recessive gene that interacts with WA cytoplasm and gives spikelet malformation. The frequency of restorer lines among japonica varieties is very low.

We focused our studies on BT cytoplasm with japonica material. The male sterility induced by BT cytoplasm on japonica varieties is often imperfect. Japonica restorers are few and are generally introgressed with indica. Restorer gene transfer from indica to japonica is easy and the process has been done for some lines.

GAM cytoplasm, which was little studied, induces perfect male sterility in most japonica varieties.

In the short term, we decided to work with WA cytoplasm for indica rice and with BT cytoplasm for japonica rice.

Work on outcrossing character transfer initiated in France was continued and led to the creation of some A lines (WA cytoplasm, indica material) with large stigmas. But using classical breeding processes (backcrossing and pedigree selection), it became evident that transferring large stigmas and CMS cytoplasm jointly was time-consuming and complicated.

In the long term, carrying out a breeding project on hybrid rice with existing lines and varieties appeared impossible. We have now started to prepare various rice populations segregating for a male sterile gene because we felt that recurrent selection as a basis for a long-term rice breeding project was necessary. Working with this *ms* segregating gene and harvesting only the male sterile plants, we can easily achieve recombination among the different plants of the population. The *ms* gene was obtained from IRRI.

Third phase

Building on the results obtained in collaboration with EMBRAPA/CNPAF, the IRAT priorities from 1990 have been the creation and commercialization of hybrid rices in

South America and in countries with a Mediterranean climate. For tropical countries, we are working on rice suitable for both irrigated and favorable upland conditions; for Mediterranean-climate regions, we are working on irrigated rice. Most of the current work is located in French Guyana, but there has been increasing participation, mainly on Mediterranean-climate research from the French Center for Rice located in the Rhone Delta near the Mediterranean Sea. Soon, IRAT hopes to have trial facilities in Brazil. The IRAT Laboratory in Guadeloupe is assisting with anther culture. Additionally, staff in the biotechnology laboratories of IRAT in Montpellier and Nottingham University are undertaking sterile cytoplasm transfer through protoplast fusion and plant regeneration. Trials on gametocides are also being conducted in collaboration with private chemical companies. For additional participants in this project, with specific reference to its commercial aspects, IRAT has sought to find private partners in several countries.

For indica rice, and in the short term, IRAT decided to use WA cytoplasm. A good outcrossing rate on male sterile plants was observed among indica recurrent populations. As large stigma transfer associated with CMS cytoplasm transfer is a long and complex process, IRAT decided not to use the large stigma character so that a hybrid rice variety could be commercialized more rapidly.

Elite lines of different origin (from IRAT and other research organizations) are testcrossed, on a single-plant basis, to find out if they are restorers or maintainers (potential A lines). If they are restorers, a new testcross is done to confirm the restoration ability and to purify the line. Restorer lines are common but maintainer lines are few, and they are not always convertible to A lines through backcrossing. The number of A lines we can obtain through this process of screening is low. So we are breeding our own A/B lines through pedigree selection. It is complicated but necessary work. Anther culture and cytoplasm transfer through protoplast fusion would be of considerable assistance, but unfortunately, for indica rices, these methods do not give good results. We are paying special attention to elite lines derived from indica material introgressed with japonica because they are more likely to give maintainer lines.

All combinations between A and R lines are evaluated if the difference between their growth duration is shorter than 10 d. To speed the process, we begin to test A lines from the third backcross of sterilization. All hybrids are evaluated in a small trial in French Guyana to observe their general phenotype and growth duration. The most promising combinations are retested in a multilocational trial (French Guyana, Brazil, and France) for very early combinations.

Since 1991, this breeding work has been strongly backed up with research to establish adequate hybrid and male sterile seed production systems. The large seed requirements can now be met because we can produce large quantities of A seeds on a noncommercial basis.

Seed production tests and agronomic evaluations are conducted first in French Guyana and the Rhone Delta. The same tests will be conducted in Brazil soon. The end result is that IRAT expects, with private partners, to commercialize the production of hybrid indica rice within 5 yr.

For countries with a Mediterranean climate and for which IRAT is developing a japonica hybrid project, BT cytoplasm is mainly used. Some work, however, is also done with WA and GAM cytoplasms. The outcrossing rate on male sterile plants among japonica recurrent populations, unlike that among indica populations, is very low, so the transfer of large stigmas appears to be necessary. To facilitate the breeding of A lines with large stigmas, we use anther culture done at the IRAT-Guadeloupe laboratories. IRAT hopes to be able to sterilize B lines with cytoplasm transfer through protoplast fusion and plant regeneration. This last technique is currently used for japonica material in collaborative work with Nottingham University.

Future plans

In the short term, hybrid breeding depends directly on the inbred breeding program, but it will become independent. Inbred-line breeding accumulates genes that perform well under homozygous conditions, whereas the aim in hybrid breeding is to seek genes that perform well under heterozygous conditions. IRAT is preparing special breeding plans for long-term research that are based on recurrent selection. The first recurrent breeding program will be completed in 1993-94 and will probably comprise the breeding of various restorer populations in relation to some elite A lines. After that, a recurrent breeding program will need to be conducted for A lines.

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Authors' addresses: J. Taillebois, CIRAD-IRAT/Guyane, B.P. 60, 97322 Cayenne Cédex, France; M. Jacquot, G.Clement, and E. Guiderdoni, CIRAD-IRAT, B.P. 5035, 34032 Montpellier Cédex 01, France; B. Courtois, CIRAD-IRAT, Station de Roujol, 97170 Petit Bourg, Guadeloupe; and L. Seguy and S. Bouzinac, CIRAD-IRAT, A/c Dr. Tasso de Castro, B.P. 504, Agencia Central, CEP, 74000 Goiânia, Goias, Brazil.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Capabilities and limitations of the global seed industry in hybrid rice development

S. M. Sehgal

Rice is planted on approximately 145 million ha throughout the world each year. More than 97% of this area lies in the developing (middle- and low-income) countries and less than 3% is in the developed (high-income) countries. The global seed industry can be divided broadly into the hybrid seed sector and the nonhybrid seed sector. The hybrid seed industry is characterized by high research and development (R&D) costs, high prices, and high margins. It is primarily controlled by the private sector in both developed and developing countries. The nonhybrid seed industry is characterized by low R&D costs, low prices, and low margins. It is primarily in the public domain in developing countries and in the private sector in developed countries. In high-income countries, the seed industry is in the mature phase of development. In low-and middle-income countries, it is only in its embryonic stage, or just beginning the growth phase. In recent years, however, many new national and multinational seed companies have entered into the seed business in developing countries due to greater availability of hybrids in several crop species and easing of relevant government policies or deregulation. The private sector seed industry operates according to four fundamental criteria: a) breeding and associated technologies must create significant value, b) protection of the products must be possible, c) the industry must be able to recover added value through adequate pricing, and d) farmers must significantly benefit if they are to pay higher prices for hybrid seed. If the added value of an improved seed is insignificant (e.g., marginal heterosis) and if the cost of seed production is high (e.g., low female yields, high input costs, high roguing costs, etc.), the margin will not be big enough to compensate both the seed company and the farmer. In such a case, the project will not be attractive to the seed industry. However, if hybrid rice meets the four criteria listed above, then the seed industry will be able to begin seed multiplication and distribution. Given the prominence of rice in Asia, hybrid rice could have the same catalytic effect on the development of the regions' seed industry that hybrid maize had on the seed industry in

North America and hybrid sugar beet had on the seed industry in Europe. The main limitations to private sector involvement are government policies and unfair competition from the public sector. The availability of market opportunities for hybrid rice will not be a limiting factor for the private sector if government policies are made less restrictive and unfair competition is eliminated.

In a world hard pressed to feed its population, and where rice is a staple food for more people than any other crop, the potential of hybrid rice in maintaining the global food balance cannot be overestimated. The conventional wisdom is that hybrids are not suited to Third World agriculture because they require higher inputs than varietal seeds, they are more expensive, and there is no multiplier system to ensure that farmers have a constant, reliable source of seeds. However, farmers in developing countries are willing to pay for higher quality seed, if they see benefits. Hybrid seed production is best in the private sector, and national policies have a decisive effect on the willingness of the private sector to invest in the developing world.

More than 97% of the global rice acreage lies in the developing (middle- and low-income) countries and less than 3% is in the developed (high-income) world. Most rice area is concentrated in Asia. India and China together account for approximately 50% of the global total (about 145 million ha each year), with rice cultivation in 41 and 32 million ha, respectively. Thailand, Indonesia, and Bangladesh plant about 10 million ha each. Among high- and middle-income countries, Japan and South Korea are the most significant rice producers. More than 2 million ha are planted in Japan; and more than 1 million ha in South Korea.

The national average yield in Japan is about 6 t/ha; in China, more than 5 t/ha; and in North and South Korea, about 7 t/ha. Yields vary between 2 and 4 t/ha in the rest of Asia (Table 1). Seeding rate varies from 20 kg/ha (transplanted rice) to more than 100 kg/ha (direct seeded rice). The seeding rate in Japan is approximately 40 kg/ha. In Brazil, the direct seeding rate is more than 65 kg/ha.

Market characteristics

In Asia's low-income countries, the enduser of seed is typically a subsistence farmer with a small landholding. (See Table 2 for a profile of seed markets, products, and end users in the high-, middle-, and low-income countries.)

In high-, middle-, and low-income countries, farmers are sophisticated and have a keen eye for profit margins. Agricultural markets are generally highly competitive and cost-sensitive. Profitability is linked to yield, cost of inputs, grain damage at harvest, storability, and moisture content. Many farmers now rely on computers to help control these factors.

Seed markets are primarily product-driven. Hybrids with high yields and other desirable traits can become the dominant cultivar in their areas of adaptation relatively quickly. Farmers will pay high seed prices if returns on yields are good.

In developing countries, hybrids have usually been successful first among the more advanced farmers in irrigated regions. Farmers in rainfed regions are generally technically unsophisticated and slower to adopt hybrids. Furthermore, they have little

Table 1. Major rice-producing countries and yield in 1990 (FAO 1990).

Income level	Country	Area ('000 ha)	Yield (kg/ha)
High	Japan	2074	6.3
	USA	1138	6.2
Middle	Brazil	3944	1.9
	South Korea	1244	6.3
Low	India	41800	2.7
	P.R.C.	32890	5.7
	Thailand	9700	2.0
	Indonesia	10301	4.3

Table 2. Market characteristics of hybrid seed industry In high-, middle-, and low-income countries.

	High-income	Middle-income	Low-income
Enduser	Sophisticated	Nonsophisticated	Subsistence farmer
Market	Highly competitive	Competitive	Market potential with limited or no existing market
Market share	Assured growth with high value added products	Can increase market share quickly if price is reasonable	Gradual increase through expansion in market size
Product	Performance advantages over competitors important	Need substantial performance differences over competitors; qualitative differences not so important	Need gross differences over farmer varieties; qualitative differences unimportant
Quality	Excellent quality with high cold and warm test, genetic purity a must	Need acceptable quality and high warm test, genetic purity important	Need good quality and good warm test, physical appearance of seed important
Pricing	Not a price market	Price important	Price market because of poor purchasing power

or no capital to invest and are less educated than their counterparts in irrigated regions. From any farmer's points of view, adopting high-priced seed is risky if the immediate payoff is modest. Hybrid rice is therefore more likely to be initially welcomed in irrigated areas, where returns are already higher than in nonirrigated areas and where risk is correspondingly lower.

The private sector

The hybrid seed industry is characterized by high research and development (R&D) costs, high prices, and high margins. It is primarily controlled by the private sector in both developed and developing countries.

Table 3. Hybrid and nonhybrid seed industry characteristics in high-, middle-, and low-income countries.

Industry	High-income	Middle-income	Low-income
Hybrid			
Volume	High	Medium	Low
Value	High	High	High
Margin	High	High	High
Sector	Private	Private	Public and private
Stage of development	Mature	Growth	Embryonic
Nonhybrid			
Volume	High	High	High
Value	Low	Low	Low
Margin	Low	Low	Low
Sector	Private	Public and private	Public
Stage of development	Growth	Embryonic	Embryonic

The nonhybrid seed industry is characterized by low R&D costs, low prices, and low margins. It is primarily in the public domain in developing countries and in the private sector in developed countries (Table 3).

The seed industry is in its mature phase in the developed world. It is in an embryonic phase in developing countries. In recent years, however, many new companies have entered the seed business in developing countries due to greater availability of hybrids in several crop species and easing of government policies.

Government deregulation

One of the most notable examples of deregulation in the developing world is India's new seed policy, which was announced in 1988. As a result of this new policy, many new national and multinational companies entered the seed business in India. The newcomers included Indian Tobacco Co., Sandoz, Cargill, Hoechst, Ciba-Geigy, ICI, SPIC, Bejo, Hindustan Lever, Harrisons Malayalam, and JK Seeds. Similarly, deregulation in Thailand and the Philippines has led to a sizeable expansion in their hybrid seed industries over the past 5 yr. Government policymakers can learn a lesson from this phenomenon. Even modest deregulation, of the sort introduced in India, can spur enormous development in a country's seed industry.

Policymakers can continue to create incentives for expansion, as is currently happening in several developing countries. The aim of any seed policy should be to ensure that elite seed is made available to farmers. Legislation that hinders this goal is counterproductive. If the private sector is to be a partner in the effort to develop, produce, and distribute hybrid rice, the principles by which the industry operates should be considered in national policymaking.

There are at least four basic principles by which the private seed sector operates:

- Breeding and associated technologies must create significant value.
- Protection of the products must be possible.
- Industry must be able to recover added value through adequate pricing.
- Farmers must benefit significantly if they are to pay higher prices for hybrid seeds.

Table 4. Value added at different yield levels.

Yield level (t/ha)	Heterosis			
	20%	25%	30%	US$(*)
4.0	800 80	1000 100	1200 120	Kg US Dollars
5.0	1000 100	1250 125	1500 150	Kg US Dollars
6.0	1200 120	1500 150	1800 180	Kg US Dollars
6.0	1200 120	1500 150	1800 180	Kg US Dollars

(*) Assuming US$100/t Av. Commodity price (paddy rice)

Creating value

Rice yield improvement through varietal development seems to have plateaued. It seems that conventional breeding can only offer improvements in qualitative traits. By contrast, no yield plateau has been observed in wheat, which is a self-pollinated crop like rice, or in hybrid maize, which is a cross-pollinated crop.

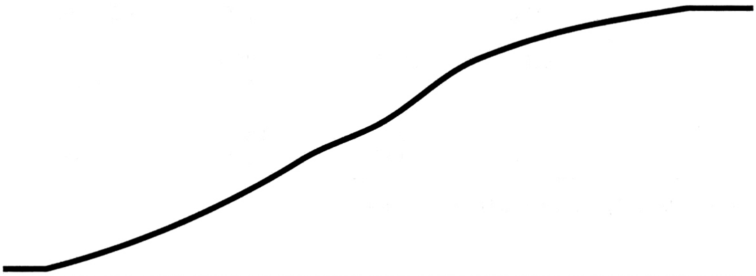
Rice researchers have turned to heterosis breeding to overcome the current yield ceiling. IRRI has already identified hybrids which give an initial yield increase of 15% or more over the best available varieties. Further increases with the next generation of hybrids appear likely. This offers hope that the success of hybrid rice in China can be repeated elsewhere in Asia. It is claimed that hybrid rice in China has more than 30% yield advantage over conventional pureline varieties and is planted on a large scale. Elsewhere, if breeders can identify hybrids which give 25% or more heterosis over current varietal yield levels of around 5.0 t/ha, the added value will be large enough to attract the private sector into hybrid rice seed production in those areas (Table 4).

Even higher yields with intersubspecific hybrids (indica × japonica, indica × javanica, and javanica × japonica) seem possible. Further efforts in heterosis breeding in this area should be made a priority. Studies in China indicate that the degree of heterosis in hybrid rice varieties has the following general trend: indica × japonica > indica × javanica > japonica × javanica > indica × indica. Indica × japonica hybrids possess the highest yield potential if fertility in the F_1 hybrids can be assured through the use of wide compatibility genes.

Protecting value

Historically, the seed industry in developed countries has expanded by developing and selling hybrids (Table 5). Nearly 40% of the total global commercial seed business of about US$150 billion is due to hybrids for various crops. The industry generally shifts toward hybrids whenever they are technically and economically feasible. With hybrids, breeders can achieve the equivalent of intellectual property protection (IPP).

Table 5. Historical representation of seed industry development in developed countries and type of protection available.

<table>
<tr><th colspan="5">Type of protection</th></tr>
<tr><td>Seed certification</td><td>Seed certification
Trade secret</td><td>Seed certification
Trade secret
PVR</td><td>Seed certification
Trade secret
PVR
Patents</td><td>Seed certification
Trade secret
Amended PVR
Amended patents</td></tr>
<tr><td colspan="5"></td></tr>
<tr><td>Embryonic</td><td></td><td>Growth</td><td>Mature</td><td>Projected</td></tr>
<tr><td>Until 1930</td><td>1930-60</td><td>1960-80</td><td>1980-90</td><td>1990+</td></tr>
</table>

They do so by keeping the parent lines required to produce the hybrid secret. With proper incentives, the private sector could become a dynamic force in hybrid seed development in developing countries without the burden of IPP legislation. Since the private sector must protect the value it creates, this can be done through hybrids. Intellectual property protection legislation is neither necessary nor desirable for developing the hybrid seed industry.

Recent activity by the private sector in developing countries in Asia and Latin America indicates that there is ample business opportunity in hybrids. Hybrids enable companies to obtain a return on their investment either directly in the form of gross margins, or indirectly in the form of royalties, or both.

Recovering value

Table 6 is based on the 1989 American Seed Trade Association's survey of the U.S. seed industry. It shows that if the cost of goods sold (COGS) is more than 60%, the business is not profitable or only marginally profitable. A private company needs at least 48-52% gross margin to be in business and show an acceptable return on sales.

The price, cost, and profit structure required by the private seed industry can be seen in Table 7. Payment to seed growers is a major seed production cost, accounting for approximately 50% of COGS. To undertake seed production, growers must be assured of at least 25-30% more revenue than would be earned by producing and selling the crop as a commodity. If seed yields are low, growers are paid a higher premium to grow the crop.

Table 6. Price/cost/profit structure in the U.S. hybrid maize seed industry (ASTA 1989).

	Top 1/3 (%)	Middle 1/3 (%)	Bottom 1/3 (%)
Net sales	100.00	100.00	100.00
Cost of goods sold	51.80	61.30	68.80
Gross margin	48.20	38.70	31.20
Selling expenses	15.30	16.70	16.70
G&A	17.10	14.90	19.50
Total operating expenses	32.40	31.60	36.20
Net operating income	15.85	7.03	-4.96
All other non-operating income	1.75	2.16	4.32
Total income	17.60	9.19	-0.64
Total non-operating expenses	2.74	3.45	5.26
Net income before tax	14.86	5.74	-5.90

Table 7. Hybrid crop price/cost/profit structure desired by industry.

	Percent
Net sales	100.00
Cost of goods sold	48.00
Gross margin	52.00
Selling expenses	15.00
G&A	15.00
R&D	7.50
Net operating income	14.50
Other non-operating expenses	1.50
Total income	16.00
Other non-operating expenses	1.50
Net income tax	14.50

For example, if the female yield is one-third of the commercial variety, seed growers are paid about three times the price of the seed procured plus the usual 25-30% premium. (The row ratio of female to male parents and the yield of the male parent are also taken into account when compensation to growers is fixed.)

The other 50% of the COGS comprises parent seed costs, transportation, certification, seed conditioning, bags, tags, and other incidental costs. If roguing, quality control, and input costs are high, the resulting COGS can make the project economically unfeasible. To reduce the COGS, higher seed set to increase yield of the female parent is essential. If male and female parents could be interplanted, a high percentage of seed set in the female parent could be ensured.

Table 8. Farmer's benefit in growing hybrid seed.

Assumptions	US$
Commodity price (paddy rice)	0.10/kg
O.P. varity seed	0.15/kg
Hybrid seed (fifteen times commodity price)	1.50/kg
Hybrid seed cost/ha (at transplanting) (Planting rate 20 kg/ha @ $1.50/kg)	30.00/ha
Less O.P. variety seed cost (Planting rate 30 kg/haa)	6.00/ha
Net increase in farmer's seed cost	24.00/ha
Minimum requirement Value added	72.00/ha
Value added at 5.0 t/ha current yield level and 25% heterosis	125.00/ha
Farmer's benefit	101.00/ha

Interplanting is possible if the male parent is made female sterile through genetic engineering, or if the male parent is made herbicide-sensitive and the female parent is made herbicide-resistant by gene transfer. In the latter case, the male parent can be eliminated by spraying with the appropriate herbicide after pollination but before harvest. Even if there is seed set in male parent plants that are not killed by the herbicide, the seeds are likely to be shriveled and can be removed mechanically during seed conditioning.

In summary, unless certain minimal requirements on costs and revenues are met, the private sector will have no long-term incentive to stay in the seed business. The recent exit from the seed business of many large chemical companies is indicative of the high costs and low margins characteristic of the seed industry today.

Farmer's benefit

Farmer's benefit is a function of the value added to improved seed. Seed companies can theoretically charge an amount up to, but not exceeding, the value they add. The farmer should get not less than three times (preferably five to six times) the return on his investment in seed.

Hybrid seed is generally priced at 10-30 times the value of the crop's commodity price, depending on the complexity of the cross and the amount of value added. This price structure gives acceptable gross margins for seed companies if COGS is kept at 48-52% of the net price. Table 8 shows that with a 5 t/ha yield base and 25% heterosis, the farmer's benefit can be four times his investment in seed. In this scenario, hybrid rice could be an attractive option for farmers and seed companies.

Growth limitations

Major constraints to the hybrid seed industry in developing countries include the following:

- Low percent heterosis, low female yield, high input costs;
- Complicated variety notification and registration procedures;
- Complex seed legislation;
- Seed subsidies to public sector;
- Restrictions on seed exports/imports;
- Restrictive quarantine laws;
- Unfavorable investment laws;
- Inadequate sources of long-term financing;
- Inadequate refrigerated storage capacity; and
- Infrastructure limits on markets for input and outputs.

Despite these constraints, there are opportunities for growth in the seed industry. Growth could be optimized if unduly restrictive constraints are removed or modified. A few lessons can be gleaned from the history of the global seed industry. Listed below are observations over the past 25 yr.

- Success is more likely when building onto an existing successful program.
- Flexible dynamic management is critical to success.
- Private sector commitment is directly related to a product's gross margin—the higher the margin, the greater the commitment.
- Seed growers are more involved and effective when their share in the profit is assured.
- Repeat business is possible only if the farmer's return on investment is high ($3-5 for each $1 spent).
- Strict quality assurance is indispensable for success.
- Capital-intensive projects are often neither necessary nor appropriate in the developing world.
- Seed production must be linked to seed demand.
- A long-term perspective is essential to success.
- Timely availability of seed in areas of use is critical.

Creating success

While seed is a small part of total farming costs, it has greater influence on productivity than any other input. Most good farmers understand the value of high quality seed. They are willing to travel considerable distances and are willing to buy in advance to ensure they get quality seed.

Since most farmers in developing countries operate at subsistence level, it has been said that they lack the resources to utilize hybrid seed. There is indeed reluctance on the part of the farmer to pay high prices for hybrid seed. Traditionally, farmers have used open-pollinated varieties, not hybrids. The former are, of course, a "free" input.

However, the experience of one of the leading seed companies in India, Proagro Seed Company Ltd., suggests that there is reason to doubt this accepted wisdom about farmers in developing countries. For the past 3 yr, Proagro's biggest constraint has been to produce enough hybrid seed to meet demand. Proagro's bottleneck has not been in creating demand, but rather in ensuring enough supply to meet demand for hybrid millet, sunflower, maize, and sorghum seed. Approximately 33-25% of sales are made prior to undertaking production. From the seed company's point of view, the importance of advance bookings is that they provide cash to make seed grower payments without getting highly indebted to banks.

Farmers will pay for hybrid rice if it benefits them, regardless of the premium. Farmers in the developing world have centuries of crop-growing experience, even if they may lack the formal education of their colleagues in the developed world. Higher input levels are no disincentive to use of hybrids.

Experience has shown that the industry is capable of providing quality seed to farmers as they need it. The same will be true of hybrid rice. Hybrid rices could have the same catalytic affect on the Asian seed industry that hybrid maize had on the seed industry in North America and hybrid sugar beet had on the seed industry in Europe.

Notes

Author's address: S. M. Sehgal, Plant Genetic Systems, Jozef Plateaustraat 22, 9000 GENT, Belgium.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

FAO's contribution to hybrid rice development

Ton That Trinh

Rice is the staple food for about 2.5 billion people, half the world's population. World rice production is second only to wheat, but about 95% of it is grown in developing countries, mainly in Asia. In 1990, world rice production reached 519 million t of paddy on 146 million ha, the average yield was 3.6 t/ha. Roughly 90% of world rice production is consumed in Asia, and only around 4% (12 million t) of milled rice reaches international markets each year.

Population growth rates and the frequent occurrence of natural catastrophes (drought, flooding, etc.) in the monsoon season have caused great concern in many rice-producing countries about the stability of the present increase in rice output and its capacity to meet national demands. The encouraging trend of self-sufficiency in rice in some countries may be reversed under unfavorable climatic conditions. Most of the land-scarce Asian countries, which depend on rice as their staple food, are anxious to increase yield to feed their growing populations.

The yield of modern semidwarf varieties seems to have stagnated over the last two decades. The International Rice Research Institute (IRRI) is attempting to develop a "super high-yielding" variety of rice capable of producing 15 t/ha in favorable irrigated conditions. Similar research, aiming at the same yield levels though with differing theoretical approaches, is being undertaken by a few strong national breeding programs.

Commercial hybrid rice developed in China provides a practical means of increasing rice yield from 15 to 20% above the local best conventional variety, particularly in irrigated areas. The longer and stronger root systems of rice hybrids may also contribute to the stabilization of rice production under rainfed conditions once this technique becomes economically viable. Some innovative developments in rice hybrid technology, such as more stable cytoplasmic male sterile (CMS) systems for tropical climates, temperature and or photoperiod-sensitive genic male sterility (two-line hybrid), apomixis, wide compatibility genes for higher heterosis in indica and japonica crosses, and higher hybrid seed yield with improved agronomic practices will ultimately extend the adoption of hybrid rice to countries outside China and the Democratic People's Republic of Korea.

The Food and Agriculture Organization (FAO) has been collaborating with IRRI, Japan, China, and some selected national agricultural research centers (Indonesia, India, Brazil, Colombia, Vietnam, People's Republic of Korea, and France) to promote hybrid rice research and development, with emphasis on the rapid transfer of any major innovation in rice hybrid technologies.

Special features of hybrid rice development

Hybrid rice comprising wild abortive (WA) CMS and restorer lines was first grown in China in 1974. Since then, the area planted to hybrid rice has rapidly increased. It is interesting to note, with regard to present Chinese rice hybrids, that

- the steady increase in hybrid rice cultivation has enabled China to use about 2 million ha for other, more profitable alternatives, particularly fish ponds and citrus cultivation.
- the labor-intensive technique used in hybrid seed production has increased employment opportunities in rural China.
- impressive progress has been made in hybrid seed production technology. Seed yield has been improved from around 1 to 2-3.5 t/ha by using improved planting methods, gibberellic acid (GA_3), long stigma and extended stigma exsertion, etc., hence reducing the cost of hybrid seed production. Two levels of hybrid seed production are practiced, CMS seed is produced by seed companies and hybrid seed is produced by contract farmers.
- the discovery of photoperiod- (PGMS) and temperature-induced genic male sterility (TGMS) in Hubei in 1983 and its recent exploitation for two-line breeding provide some hope for a wider diffusion of hybrid rice outside China. This method is much simpler than the complex three-line method based on CMS breeding. The cost of seed production could also decrease.
- most hybrid rices are of the indica type, cultivation of japonica hybrids is still limited. Even so, hybrid rice in China seems to be concentrated in central provinces, such as Sichuan, Hunan, Hubei, and Jiangsi, etc., and is exploited to a lesser extent in the warmer southern provinces, such as Guangdong. This is because WA sources of male sterility are not suitable for tropical areas. This limitation is now being overcome through the Hong-lien CMS which tolerates warmer temperatures.
- hybrid rice appears to be adopted more widely in the dry season than in the wet season, probably due to better solar radiation and fewer pests.
- although more than 90% of the hybrids have a single cytoplasmic source, WA, no serious breakdown has been observed. However, efforts have been made to diversify CMS systems and incorporate more disease resistance into hybrids.
- the demand in China is primarily for japonica-type quality. The incorporation of wide compatibility (WC) genes discovered in Japan will facilitate developing japonica-type hybrids for northern China.

Major constraints to hybrid rice production

The successful Chinese hybrid rice program has prompted many other countries and IRRI to step up research on hybrid rice by using CMS lines initially imported from China or those produced by IRRI's cooperative program. However, commercial hybrid rice has not yet materialized in most of these countries.

Major constraints seem to be the instability of Chinese and Chinese-derived cytoplasms, their susceptibility to tropical pests, the quality of hybrid rice, the adaptability of the complex systems of CMS, maintainers, and restorers, and the socioeconomic difficulty of matching national hybrid seed production to the Chinese model (labor-intensive, with high production costs). The benefit-cost ratio between increased production and hybrid seed prices (about 7-10 times the normal price of rough rice) is too low in direct seeding and in unfavorable, low-yielding rice areas to motivate farmers to adopt hybrid rice.

It is reported that commercial hybrid rice has been planted in Quang-Ninh Province in northern Vietnam, using hybrid seeds originating from neighboring Chinese provinces. The Democratic People's Republic of Korea has released one short-duration hybrid for cultivation in 1990, planted now on 10,000 ha in the eastern coastal region and the mountainous areas. In France, hybrids based on Chinsurah Boro II have been tested at Arles. Morocco reported a high yield for Chinese hybrids tested in 1990, but these tests were not resumed because the imported hybrids from China were too expensive and the benefit-cost ratio in planting hybrids was not attractive under the mechanized direct seeding system prevalent in the country.

FAO hybrid rice development program

FAO has long been interested in hybrid rice research and development, undertaken first in China and later at IRRI, and in the USA, Brazil, Democratic People's Republic of Korea, India, France, and others. The FAO Hybrid Rice Program itself really started with the recommendations of the 16th Session of the International Rice Commission (IRC) held at IRRI in 1985. These recommendations were reiterated at the 17th Session of the IRC in 1990 in Brazil, following the presentation of a paper on rice hybrids by Virmani (IRRI) and Singh (FAO).

The first symposium on hybrid rice at Changsha, China, in 1986 also requested FAO promotion of hybrid rice and seed production in Asia.

Vietnam

In 1990, FAO provided modest financial assistance to Vietnamese scientists formerly trained at IRRI to carry out research at the Cuu Long Delta Rice Research Center, the National Institute of Genetics, and the National Institute of Agricultural Sciences in Hanoi. Work consisted exclusively of testing CMS lines and hybrid rice introduced from IRRI. During 1990-91, these institutes were regularly informed of new technological breakthroughs concerning temperature-induced genic male sterility through a Japanese scientist consultant (Dr. Maruyama) who applied this new technology in Japan and cooperated with IRRI to incorporate it into IRRI indica hybrid lines. The

Government of Vietnam recognized the outstanding field performance of Chinese hybrids cultivated by farmers in northern Vietnam. At the end of 1991, FAO agreed to help Vietnam buy more hybrid seeds to extend these on-farm demonstrations to three other overpopulated and chronically rice-deficient northern provinces, Ha-Nam-Ninh, Thai-Binh, and Hai-Hung, and to train Vietnamese scientists and technician-farmers to develop the three-way production methods for hybrid seeds (based on stable CMS available from Guangdong and Guangxi provinces), using new agronomic practices to increase seed setting and yields. The Chinese will also introduce their PGMS and TGMS to initiate the less complex and less costly two-way seed production methods. This technical cooperation project will also provide financial assistance to test more stable CMS and high-performing hybrids introduced from IRRI and the IRRI TGMS hybrids which will, hopefully, be available at the end of 1992.

Democratic People's Republic (DPR) of Korea

Hybrid rice breeding began in 1976 in DPR Korea. The first hybrid was tested from 1986 to 1988 in three regions, Pyongyang, Shingge, and Kilyu. Results showed that hybrids outyielded best local checks (Samjon 1, Pyongyang 15, and Emju 1) by 11-33%. The CMS used was derived from Chinsurah Boro II, and seed yield of some lines reached 1.5-1.7 t/ha (Choi 1991). In 1989-90, the hybrid Dong Hae 1 was released for cultivation in the eastern coastal region and mountainous areas. The area cultivated with Dong Hae 1 is less than 10,000 ha because it is an early hybrid and most rice areas in DPR Korea grow long-duration cultivars. In 1987, the incorporation of WC genes with extruded stigma was initiated in Boro CMS lines. Many F_1 lines have a seed fertility rate between 81 and 89 (Lee and Kim 1991). Hybrids of japonica with WC gene crossed with indica appeared to be highly productive. Many lines outyielded the best conventional variety, Pyongyang 15, by more than 40%. Line A 241/R53 yielded 10.9 t/ha compared with 7.4 t/ha of Pyongyang 15. At the request of the Korean Government in 1986, FAO implemented a UNDP/FAO project to improve the facilities of the Rice Research Institute at Pyongyang, increase their rice germplasm collection, and train Korean scientists in the new breeding methods adopted in China, India, and other countries. IRRI consultants visited the Rice Institute to help improve many components of the Korean rice program. When the computerized greenhouse allowing for the control of photoperiod and temperature is completed, it is expected that the PGMS and TGMS two-way methods of hybrid rice development will be carried out at the Institute.

India

In 1988, The Regional Office of FAO-Bangkok formulated a Hybrid Rice Research and Development Project for India at the request of the Indian Government. An IRRI consultant redrafted this document in 1990, and the final project was begun by nationals in 1991. In line with new UNDP regulations, FAO is designated as a cooperating agency to provide fellowships, study tours, and international consultants. However, FAO will provide other assistance on request, and it will participate in the Steering Committee, which also has an IRRI representative. In 1991, better quality CMS lines with greater stability and higher resistance to tropical diseases were introduced from IRRI and identified and multiplied in India. In 1993, IRRI's tropical TGMS lines with WC gene incorporated were made available to India. Consultants from China and Japan are helping the India program to strengthen seed production technologies and set up hybrid rice seed companies.

Indonesia

Yield increase in irrigated rice is crucial if future demand for rice in Indonesia is to be met. New technologies will be needed once the yield plateau for high-yielding irrigated varieties under current levels of inputs has been reached. Indonesian scientists have agreed that hybrid rice could be a feasible way to increase yield significantly. But top scientists from the Sukamandi Research Institute for Food Crops were frustrated by the limited progress in hybrid rice breeding in Indonesia and admitted that the present approach should be revised. In fact, contrary to initial expectations, breeding a stable CMS system seems to be very difficult. It is impossible to ascertain how promising the new series of more stable CMS lines are, because they were bred on the same basis as the previous unstable ones. In the light of past varietal changes in Indonesia, there is always the threat of outbreaks of new types of pests or diseases. It is possible that any CMS line bred could break down after several years of effort. If this occurs, finding good substitutes among the CMS systems may be difficult, as they can be found only after a large number of trials (Ikehashi 1990, unpubl.). In contrast, the use of EGMS (environmentally induced genic male sterility), TGMS, and/or PGMS allows a far wider range of varietal combination, thus enabling breeders to combine a set of resistance genes in one hybrid variety.

The other important aspect of hybrid rice development—the technology for seed increase—has not been tested in Indonesian programs. A project has been formulated consisting of a new orientation on hybrid rice breeding; testing of appropriate technologies available in China and Japan to increase seed production; and, for Indonesian scientists at IRRI, a focus on TGMS incorporation into the indica background. Breeding pollinator lines and other related work at its major national center should also begin. Prospective Italian trust funds for the two-way method of producing hybrid seed and extensive on-farm demonstrations of IRRI-NARC tropical TGMS hybrids to be made available at the end of 1992 did not materialize. The project formulated in 1990 is still waiting for another source of financing.

Brazil

The hybrid rice program in Brazil was initiated through the CNPAF/EMBRAPA upland rice improvement program in 1984. However, rice was not well-targeted and the breeding procedure was not clearly designed due to excessive reliance on population breeding (which was thought more appropriate for selecting tolerance for mineral stress and fungal diseases through the integration of minor genetic contributions from diverse source materials). A genotype with a high outcrossing rate is necessary since manual labor may not be available in the large seed farms of Brazil. Population breeding delayed production of materials with high outcrossing rates. So far, field trials for outcrossing between A and B lines have not been performed. The restorers, maintainers, and hybrids are all derived from the same genetic stock, so there is little possibility of obtaining desirable heterotic combinations.

In 1989, the hybrid rice program was directed to irrigated rice, where higher returns could be expected. A reorientation of the program was proposed, with emphasis on the exchange of expertise and materials and on testing new technologies and procedures.

Breeding for high outcrossing rate should be continued. Closer linkage is required between breeders in the southern states, where higher yielding irrigated rice is concentrated, and those at the CNPAF (Goiânia) to design target types and select the best materials for backcrossing. Size of backcrossing should be reduced. The japonica male sterile lines already developed can be used with indica restorers, which may possess WC gene. If the WC gene is incorporated into B lines, any indica variety could be used as a restorer. Japonica restorers developed by transferring the *Rf* gene from indica generally show low levels of heterosis on crossing with japonica B lines. Brazilian breeders need alternative source of materials for new technologies such as TGMS and PGMS if these are not available from China. Brazilian breeders also need to monitor progress in new hybrid rice technologies by attending international meetings or by joining tours to China, Japan, and other countries.

Colombia

Hybrid rice research began in Colombia in 1983-84. Five hybrids and their parent varieties provided by IRRI were tested at the Palmira station of the Instituto Colombiano Agropecuario. V20 A/Suweon 294 gave 8.3 t/ha, 1.2 t/ha over Oryzica 1. In 1983-84, some 15 varieties were identified as maintainers and restorers of V20 A and Zhen Shan 97 A. Many of the maintainers were from among those introduced from Africa and the USA, or with upland origins, while the restorers were found in high-yielding varieties.

Since the initial testing, backcrossing has continued. The CMS donors are V20 A, Zhen Shan 97 A, and IR62829 A, to which three B lines, Colombia 1, Palawan, and Moroberekan, are being backcrossed. Restorers have been identified for them. Improvement of B lines and some maintainer lines from IRRI aims to reduce plant height, add tolerance for adverse soils, and introduce resistance to the hoja blanca virus (some IRAT lines are resistant). Performance tests of IRRI hybrids and those from Ring-Around, a private seed company in the USA, are being carried out or are in the planning stage. Hybrid rice breeding is conducted at two farms of FEDARROZ: one at Cesar Department in Bosconia City (45 ha), the other at Cordiba Department in Monteria City (15 ha). The program leader (Dr. Muñoz) has selected some B lines through which backcrossing has been advanced somewhat. Some hybrid rice varieties will be produced in the near future. A review of Colombian hybrid rice was conducted by Prof. Ikehashi, an FAO consultant, in 1991.

Hybrid rice in the Interregional Cooperative Rice Research Network for the Mediterranean Climate

The network, established in September 1990, has hybrid rice research as one of its components. So far, France, Egypt, and Russia have shown interest. In Egypt, where irrigated rice has very high yield and where seed production is well-organized, any progress in hybrid rice could be transferred rapidly to the farmers. France is already well-advanced on hybrid rice research based on CMS systems for both temperate and tropical climates. Russia began hybrid rice research at the All Union of Rice Research Institutes-Krasnoda in 1984, working on the CMS system for japonica hybrids. Restorers are being studied.

The objectives of the research on hybrid rice in the cooperative network are the following:

- diversification of CMS systems,
- CMS transfer by protoplast fusion,
- introduction and utilization of PGMS and TGMS,
- gametocide testing in cooperation with private companies,
- incorporation of WC genes by backcrossing to exploit higher heterosis in intersubspecies crosses, and
- increase in hybrid seed production and cost reduction to an appropriate level.

The system of mechanized direct seeding used in the cooperating countries of the network requires ten times more seeds than does transplanting. At present yield increase levels and hybrid seed production costs, it may not yet be economical for farmers in the Mediterranean climate to plant hybrid rice. More research is required on increasing heterosis levels through intersubspecies (japonica/indica) crossing or even wide crossing (with other *Oryza*); identifying stronger restorers for japonica rice; lowering the cost of seed production by EGMS or by using innovative methods of hybrid seed production such as mechanized mixed planting and seed sorting at harvest, mixed planting of male sterile and female sterile lines (Maruyama and al 1983), use of a recessive tall gene (*eui*) (Rutger et al 1981), and breeding exserted stigmas in japonicas by mutation. Developing a male sterile line with exserted stigma in japonica transformed from indica rices is difficult because indica varieties often possess a restorer gene for BT cytoplasm (Maruyama 1992).

Conclusion and suggestions for international collaboration in hybrid rice

Besides diversification aimed at more stable and less vulnerable CMS, new technologies (EGMS and WC genes) that make it possible to simplify the breeding approach are emerging, giving breeders more opportunities to select combinations and more flexibility to confront changing pathosystems. They could also increase heterosis and yield for both hybrids and seeds and possibly reduce production costs. Incorporation of greater tolerance for pests and diseases for tropical environments, better quality, and refined agronomic practices to increase hybrid rice seed yield would enhance the expansion of hybrid rice cultivation to countries other than China and the DPR Korea.

Efforts in developing apomictic rice in Japan, China, and in some other countries deserve all our support because apomixis would remove the need to buy new seed every year. It would also increase the opportunities for cultivating hybrid rice in rice ecologies less favorable than irrigated and rainfed lowland.

Three other aspects, however, have to be considered:

- sharing of new materials on CMS, EGMS, and apomictic germplasm in the TCDC spirit, or following the model of sharing all materials resulting from research grants, such as in the Rockefeller Foundation International Rice Biotechnology Program;

- the need to train or continuously recycle national breeders and to reorient national breeding programs to emerging technologies; and
- the setting up of national hybrid rice seed organizations with appropriate facilities.

These are the prerequisites for a rapid extension of hybrid rice among developing countries. The FAO would continue to support national programs on hybrid rice development in the future, particularly on implementing high hybrid rice seed production, promoting a TCDC network for exchanging information and seed materials from new breakthroughs, providing fellowships and study tours for scientists from developing countries to visit excellent national or international hybrid rice centers, and on-farm demonstrations of outstanding IRRI and Chinese hybrids in order to speed up their field transfer to tropical areas.

FAO looks forward to collaborating with such partners as IRRI on the research and development of hybrid rice.

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Author's address: Ton That Trinh, Plant Production and Protection Division, FAO International Rice Commission, Via Delle Terme de Caracalla, Rome.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

IRRI’s program on international collaboration on hybrid rice

S.S. Virmani

IRRI’s program on international collaboration on hybrid rice aims to expedite development of hybrid rice technology for use by national programs to increase their rice varietal yields. Over the years, collaboration has been established with several countries interested in developing and using this technology (China, India, Indonesia, Republic of Korea, Egypt, Philippines, Japan, Sri Lanka, Thailand, Vietnam, Colombia, Brazil, and Bangladesh). Collaboration with China has been limited on account of that country’s policy of restricting the sharing of hybrid rice germplasm. IRRI’s collaboration with other countries has led to the free exchange of germplasm and information and the training of scientists at IRRI. IRRI has also provided consultancy services to hybrid rice programs in India, Vietnam, Indonesia, Malaysia, the Philippines, and Egypt. IRRI does not collaborate with the private sector on hybrid rice, although it recognizes the role of the private sector in the development and transfer of this technology. However, IRRI policy on intellectual property rights and hybrid rice has been spelled out recently and this should be helpful in establishing effective and useful collaboration with the private sector. IRRI proposes to establish an International Task Force on Hybrid Rice to strengthen international collaboration and expedite development and utilization of this technology for increasing rice varietal yields.

IRRI began hybrid rice research in 1970, when studies on developing cytoplasmic male sterility (CMS) in indica rice were conducted (Athwal and Virmani 1972). For various reasons, these studies were discontinued in 1975. The successful development and use of hybrid rice in China encouraged IRRI to revive hybrid rice research in 1979 to explore its potential and problems in increasing rice varietal yields (IRRI 1980).

In 1979, formal collaboration was established between IRRI and China. As the work progressed, several other countries sought and established collaboration with IRRI to study the prospects of developing this technology. Considerable progress has been made since then. This paper presents the objectives, achievements, and future outlook on this collaboration.

Objective

The objective of IRRI's program on international collaboration on hybrid rice is to study the potential and problems of this technology jointly with interested countries and, if found useful, expedite its development and utilization in national programs to increase rice varietal yields beyond the level of semidwarf, inbred rice varieties.

Countries involved in collaboration

China was the first country in the world to develop and use hybrid rice technology commercially. IRRI established collaboration with China as soon as hybrid research at IRRI was revived in 1979. The objectives of this collaboration were to

- compare the available CMS systems and search for better sources,
- develop CMS lines with disease and insect resistance and adaptability to tropical and subtropical conditions using the available cytosterile sources,
- study the nature of hybrid vigor and identify lines with better general combining ability,
- identify germplasm with larger stigmas and longer flower opening duration and transfer those traits to male sterile lines,
- study ratooning potential of F_1 hybrids,
- investigate ways and means of perpetuating F_1 hybrids by converting them to apomicts, and
- study techniques of hybrid seed production.

As work progressed at IRRI and some positive results were reported (Virmani et al 1981,1982), several other countries sought bilateral collaboration with IRRI to explore the potential and problems of hybrid rice technology. Table 1 lists the countries which established bilateral collaboration with IRRI during 1979-92. Collaboration with Thailand, Colombia, Brazil, and Bangladesh has been informal, and collaboration with China was suspended in 1990 on account of China's policy of restricting germplasm sharing. Recently, China and IRRI have started dialogue to revive the bilateral collaboration. Currently, hybrid rice research is in progress in 14 countries (Table 2). Most of the work is being done in public sector institutes, although some private seed companies are also actively working in the Philippines, USA, India, and Japan.

Achievements

The major accomplishments of China-IRRI collaboration are the 1) introduction of three CMS sources (CMS-WA, CMS-GAM, and CMS-bo) to IRRI in 1979 and their sharing with interested national agricultural research systems (NARS); 2) introduction of IRRI-bred restorers and sources of wide compatibility (WC) genes to China; 3) development of the first short-duration rice hybrid Wei You 64 (V20 A/IR9761-19-1-

Table 1. Countries having bilateral collaboration with IRRI.

China (1979)[a]	Thailand (1984)[b]
India (1980)	Colombia (1990)[b]
Indonesia (1982)	Brazil (1991)[b]
Republic of Korea (1983)	Bangladesh (1992)[b]
Egypt (1987)	
Philippines (1988)	
Japan (1990)	
Sri Lanka (1991)	
Vietnam (1985)	

[a] Collaboration suspended in 1990. [b] Information collaboration.

Table 2. Countries involved in hybrid rice research outside China.

Country	Institution	Year of initiation of research	Collaborators
DPR Korea	Rice Research Institute, Pyongyang	1976	-
Philippines	IRRI	1979	Several NRS
	PhilRice	1988	IRRI
	Cargill Seeds	1981	China
USA	Ring Around	1980	China
	Rice Tec	1988	China
	University of California, Davis	1980	-
India	Several national and state institutes	1981	IRRI
	PHI-Biogene	1988	-
	MAHYCO Seed Company	1990	-
	PROAGRO	1992	-
Indonesia	Food Crops Research Institute, Sukamandi	1982	IRRI
	Cargill Seeds	1986	China
Republic of Korea	C. E. S. Suweon, Honam, Milyang	1982	IRRI
Vietnam	Cuu Long Delta Rice Research Institute. Omon	1985	IRRI
	National Institute of Agricultural Agricultural Research, Hanoi	1992	China (through FAO)
Malaysia	Malaysian Agricultural Research and Development Institute, Bumbong Lima	1985	IRRI
Thailand	Rice Research Institute, Bangkhen	1983	IRRI
Egypt	Rice Research Institute, Sakha	1987	IRRI
Japan	National Agricultural Research Center Tsukuba Zennoh Agricultural	1983	IRRI[a]
	Technical Center, Hiratsuka	1983	
	Mitsui Chemical Company	1989	-
Sri Lanka	Rice Research Station, Batalagoda	1991	IRRI
Colombia	National Rice Growers Federation Bogota	1983	IRRI
Brazil	National Research Center for Rice and Bean, EMBRAPA-CNPAF	1984	IRRI

[a] Collaboration limited to thermosensitive genic male sterility and wide compatibility in rice.

64) for China (Yuan et al 1985); 4) introduction and release of hybrid Wei You 46 (V20 A/Milyang 46 R) developed under the Korea-IRRI collaboration; 5) training of Asian rice researchers in hybrid rice breeding and seed production procedures in China (1980, 1981) and IRRI (1985); 6) training of Chinese rice researchers at IRRI (1980-92); 7) organizing the First International Symposium on Hybrid Rice in China (1986); and 8) study on the economics of hybrid rice production in China (He et al 1984, 1987).

China-IRRI collaboration has benefited other countries working on hybrid rice in many ways. Several countries received Chinese-bred CMS and maintainer lines made available to IRRI to initiate hybrid rice research. Through IRRI, they also gained information and knowledge about hybrid rice seed production technology developed in China. Rice scientists from several countries received training in hybrid rice research and development work in China. About 220 rice scientists from China and 17 other countries attended the First International Symposium on Hybrid Rice, the proceedings of which were published in a book entitled *Hybrid rice,* the first comprehensive publication on the subject.

IRRI's collaboration with countries other than China has led to free exchange of information and germplasm with NARS. IRRI-bred CMS, maintainer, and restorer lines and elite rice hybrids are regularly made available to collaborating NARS as soon as they are developed and seeds are multiplied. CMS lines bred in NARS are also shared with IRRI, from where they are distributed to other countries. Consequently, active hybrid rice research programs are now established in India, Indonesia, Vietnam, Republic of Korea, and the Philippines. Two IRRI-bred rice hybrids have been named for regional adaptability trials in Vietnam (IRRI 1993). In India and the Philippines, some IRRI rice hybrids are in on-farm trials. Our collaboration with Japan has resulted in the development of thermosensitive genic male sterile (TGMS) lines in indica rices to initiate a two-line method of hybrid rice breeding in the tropics. These lines have been shared with some NARS for evaluation. IRRI-NARS collaboration on hybrid rice has also led to training of many hybrid rice scientists at IRRI, through degree and nondegree training courses and postdoctoral fellowships. IRRI has also provided consultancy services to hybrid rice programs in India, Vietnam, Indonesia, Malaysia, the Philippines, and Egypt. The Indian Council of Agricultural Research-United Nations Development Programme project on hybrid rice, initiated in India in 1991, was designed with the help of the author who was hired by the FAO as a consultant. This is the most comprehensive hybrid rice research and development project outside China.

IRRI has provided hybrid rice germplasm to industrialized countries to study the molecular basis of CMS and to transfer CMS systems using protoplast fusion technology. Japan-IRRI collaboration has also resulted in the tagging of gene (S_5^n) with RFLP marker RG213 (IRRI 1993).

Collaboration with private sector

To date, IRRI does not collaborate with the private sector on hybrid rice although it recognizes the role of the private sector in developing and transferring hybrid rice technology. So far, any private company requesting hybrid rice germplasm from IRRI has been advised to ask for the same from the NARS in the country where the company operates. IRRI has recently defined its policy on intellectual property rights and hybrid rice. It has the following clauses:

- IRRI adheres to the policy of free availability of the breeding lines, elite germplasm, and parental lines produced in its breeding program.
- IRRI will not seek intellectual property protection on the breeding lines, elite germplasm, and parental lines emanating from its breeding program.
- IRRI recognizes that the private sector is likely to play an important role in the development of hybrid rice technology.
- IRRI will provide hybrid rice parental lines (and other elite materials) to both public sector institutions and private organizations on the understanding that the material is not intended for exclusive use by a single organization, that IRRI retains the right to distribute the same material to other organizations, and that the use of IRRI materials will be recognized when a hybrid rice variety is released.
- Collaboration with profit-making organizations for the development of hybrid rice technology will proceed after consultation, where appropriate, with the authorities in the respective host country.

With the establishment of these policy guidelines, it should be possible for IRRI to collaborate with private sector companies working on hybrid rice research and development.

A proposal for an international task force on hybrid rice

Although IRRI has bilateral collaboration with several NARS, NARS to NARS collaboration is nonexistent with the present system. Linkages between hybrid rice breeding programs (at the national and international levels) and seed production agencies in public and private sectors are also practically nonexistent. To further expedite the development and wide-scale use of this technology, multidisciplinary and collaborative research and development efforts are needed involving IRRI, NARS, and public and private seed production agencies. IRRI, therefore, proposes to establish an International Task Force on Hybrid Rice which will involve IRRI and national hybrid rice research programs of countries which have strong research programs on hybrid rice and are willing to share their germplasm. The general objective of the task force is to expedite development and utilization of hybrid rice technology. Proposed activities of the task force would include

- exchanging and evaluating breeding materials, including CMS, TGMS, wide compatibility lines, and heterotic rice hybrids;
- conducting strategic, applied, and adaptive research to develop suitable guidelines for agronomic management of F_1 hybrids to attain maximum yield;
- conducting strategic, applied, and adaptive research to develop suitable guidelines for hybrid seed production in member countries of the task force;

- studying the economics of hybrid rice seed production and hybrid rice cultivation in the member countries;
- studying the prospects and problems of sustaining higher yields from hybrid rices;
- identifying target areas for hybrid rice cultivation and hybrid rice seed production and establishing linkages with public and private seed companies in the member countries; and
- exchanging information and experiences of scientists and seed production experts from member countries through workshops, monitoring tours, training, and newsletters.

Responsibilities for the above activities can be shared among IRRI and NARS by utilizing their comparative strengths. The task force will help in developing suitable hybrid rice technology and bringing it to rice farmers faster than the current collaborative arrangements.

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Author's address: S. S. Virmani, International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.

Citation information: Virmani S S, ed. (1994) Hybrid rice technology: new developments and future prospects. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Poster abstracts

Hybrid rice in Guangdong Province, China

Peng Hui Pu

Hybrid rice-growing areas in Guangdong Province have rapidly increased from 29.0% of the total rough rice in 1989 to 50.3% in 1991. Hybrid rice yield is usually about 0.75 t/ha higher than conventional varieties.

Bo-You 64 is the most extensively grown hybrid in Guangdong. It is cultivated over an area of 0.387 million ha. The next two are Shan You 63 and D You 63, each occupying 0.266 million ha. Combinations with 3550, a weak photoperiod-sensitive restorer, can only be planted under short-day conditions as a late-season crop and cover a total area of 0.122 million ha. Other important hybrids are Shan You 64 and Shan You gui 99. Their growing areas have increased from 20,000 to 60,000 ha.

Cong Guang 41 A is a new MS line with Honglien source of cytoplasm. A series of high-yielding hybrids (Guang-You-Qing, Guang-You-Zheng, and Guang-You no. 4) were developed from Guang 41 A.

Mei You 1051 is another recently developed hybrid. It shows high-yielding ability, good grain quality, and resistance to both bacterial blight and blast. It is suitable for the tropics and subtropics. It was extensively accepted by the farmers in the middle, south, and coastal regions in Guangdong.

Author's address: Rice Research Institute, Guangdong Academy of Agricultural Sciences, Guangzhou, China.

Extending cultivation of medium-maturing hybrid indica rice northward through management of cultural practices

Yan Zhen De

Using traditional cultural practices, medium-maturing hybrid indica rices, such as Shan You 63 and Nan You 3, are best suited for central Jiangsu Province (south of 33° N), where the rice - wheat rotation system is practiced. In the mid-l970s, similar hybrids were extended to Xuzhou (34-35° N) and the production area has increased year by year since then.

If the cultural practices used in the south were applied to growing hybrids in Xuzhou, low temperatures would allow only a single-cropped rice system. Local agricultural production is dominated by a double-cropped rice - wheat system. Early and sparse sowing of old hybrid seedlings (with 8-9 leaves) must be adopted to ensure that the heading stage comes before 20 Aug. Grain yields have reached 8.25 t/ha in large areas and 12.75 t/ha in small areas.

Medium-maturing hybrids have been introduced further north, in the Laizhou Bay Region in northern Shandong (37.56° N) following a series of experiments. Local conditions favor a single-cropped rice system. To ensure early heading (mid-August) and harvest before 1 Oct, sowing is done in greenhouses in mid- and late April to produce stronger seedlings. Transplanting is done in early May. The rice yield in commercial production was 9.4 t/ha in 1991; yield potential was 14.25 t/ha. This yield level was higher than that in the south due to simultaneous increases in number of panicles, number of grains per panicle, grain weight, and the rate of filled spikelets resulting from longer growth duration, sufficient sunshine, fewer pests, and a large difference between day and night temperatures.

Author's address: Xu-Zhou Prefecture Agricultural Institute, Jiangsu Province 221000, China.

Heterosis in intersubspecific combinations of rice

J.B. Yang

Research on increasing heterosis beyond the levels currently obtained has shifted from varietal hybrids to intersubspecific hybrids, indica/japonica, indica/javanica, and javanica/japonica, which exhibit very strong heterosis. The F_1 hybrids grow quickly and vigorously throughout the vegetative stage. The plants are bigger and larger and yield potentials are 20% over check hybrids.

Breeding intersubspecific hybrids by the two-line method involves PGMS or TGMS and WC genes. PGMS and TGMS genes have been transferred into some indica varieties with different genetic backgrounds, and some japonicas and javanicas possessing WC genes have been identified. Intersubspecific hybrids Erya No. 1 and Erya No. 2 have been developed in Fujian Province. In 1991, the area of Erya No. 2 under trial was 103 ha, and average yield was 10.6 t/ha. The highest yield recorded was 12.7 t/ha (0.2 ha) in Dahuon countryside. Other high yields included 11.2 t/ha (6.9 ha) in Xianyou County, 11.1 t/ha (3.3 ha) in Nanpin City, and 12.0 t/ha (1.3 ha) in Sha County.

Author's address: Rice and Wheat Institute, Fujian Academy of Agricultural Sciences, China.

Genetic basis of heterosis in two rice hybrids

C. X. Mao and S. S. Virmani

Six basic generations (P_1, P_2, F_1, F_2, B_1, and B_2) and triple testcross families of the heterotic rice hybrids IR46830 B/IR9761-19-1 R and IR54752 B/IR46 R were developed and tested in an experiment using completely randomized design at IRRI in 1991 DS to investigate the genetic basis of heterosis. Nine agronomic traits (grain yield, dry matter weight, 100-grain weight, tiller number, panicle number, spikelet number, plant height, days to heading, and harvest index) were studied and data were analyzed using biometric models (joint scaling test, three- and six- parameter model, perfect fit solution, and triple testcross analysis). In cross II, F_2 was substituted by F_3 because the F_2 mean was found to be lower than the lower parent.

Significant heterosis was observed for grain yield, dry matter weight, and 100-grain weight in the cross IR46830 B/IR9761-19-1 R; and for grain yield, dry matter weight, spikelet number, and days to heading in the cross IR54752 B/IR46 R. Other traits did not show significant heterosis.

The dominance ratio for traits showing heterosis was greater than unity, but it was equal to or smaller than one for traits not showing heterosis.

Traits showing heterosis showed significant additive and dominance effects in the cross IR46830 B/IR9761-19-1 R, and not only significant dominance effects but also significant additive × additive, additive × dominance, and dominance × dominance effects in the cross IR54752 B/IR46 R. Triple testcross analysis showed pronounced additive, dominance, and epistatic variances controlling traits showing heterosis in the cross IR54752 B/IR46 R, and only additive and dominance variances in the cross IR46830 B/IR9761-19-1 R.

Linkages were detected in the traits showing significant epistasis. In the absence of epistasis and linkage, the greater-than-1 dominance ratio in cross I indicated a certain degree of overdominance.

Based on these results, we concluded that heterosis in the two crosses was due to the presence of dominance, or overdominance and epistatic (additive × additive, additive × dominance, and dominance × dominance) variations coupled with linkage effects. Additive and additive × additive variations could be exploited through inbred breeding. Dominance, additive × dominance, and dominance × dominance variations could be exploited through hybrid breeding. The latter would also help to overcome repulsion phase linkages present in the parental lines of the hybrids.

Acknowledgment: The authors acknowledge the guidance and criticism provided by Dr. M.J. Lawrence, School of Biological Sciences, The University of Birmingham, Birmingham, U.K., and Dr. D. Senadhira, Plant Breeding, Genetics, and Biochemistry Division, International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.

Authors' address: International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.

Development of locally adapted CMS lines for India

S.B. Pradhan, S.N. Ratho, and P.J. Jachuck

To develop new CMS lines utilizing popular local high-yielding varieties, 16 CMS lines of WA source from different nuclear backgrounds with resistance to local diseases and pests were developed at the Central Rice Research Institute, Cuttack. Ten of these CMS lines (Sarasa II A, Pusa 33 A, Pragathi A, Annada A, Krishna A, Rajeswari A, Madhuri A, Deepa A, Pusa 4-1-11 A, and Adt. 34 A) were found to be stable over several seasons at Cuttack. Simultaneously, two more CMS lines, Krishna A and Zhunghua-1 A, from two different new cytoplasm sources (Kalinga I and V20 B, respectively) were developed through indica/indica and indica/japonica hybridization. They were both found to be stable. Krishna A (Kalinga I source) was found to be cold-tolerant at the seedling stage (inherited from the cytoplasm of Dunghansali, the female parent of Kalinga I) and had reduced transparent white anthers with more than 90% unstained withered sterile pollen grains. Zhunghua 1 A (V20 B source) had reduced light yellow anthers with more than 50% stained round sterile pollen grains. Of the 13 stable CMS lines from three different sources, 4 were early, 6 were medium, and 3 were of medium-late duration.

The CMS lines V20 A, Krishna A, Kiran A, Madhuri A, Deepa A, and Krishna A were testcrossed with local varieties suitable for irrigated and lowland conditions. Effective maintainers and restorers were identified for these CMS lines. Partial and effective restorers of WA source (V20 A and others), such as Ratna, Aswathi, Punjab Basmati, Anamica, and Bhavani, were found to be effective maintainers of Krishna A. The maintainers were used as recurrent pollen parents in advanced backcross generations to develop new CMS lines for sources other than WA. BC_2 and BC_3 generations were obtained. The lowland varieties BKS64, Moti, Kalashree, Padmini, IET10435, PN56-65, CR644, IET10849, IET11350, and IET10983 were found to be effective maintainers of V20 A and Madhuri A. V20 A and Madhuri A were used as recurrent male parents for advanced backcross generations (BC_1 and BC_2) to develop new CMS lines.

Authors' address: Central Rice Research Institute, Cuttack 753006, Orissa, India.

CMS transfer into japonica varieties with cybrid method

H. Akagi and T. Fujimura

An efficient and reproducible system for transferring CMS character of indica cytoplasm into japonica cultivars with cybrid cell fusion method is presented.

A suspension of cultured cells of japonica cultivars was inactivated with 30 mM iodoacetamide for 15 min. The indica cell culture was inactivated with high dosage of X-ray (125 kr). No calli formed when these treated cells were cultured independently. Protoplasts were isolated from both kinds of treated cells and fused by electric shock. A large number of cells with japonica nucleus and indica cytoplasm formed from the fused protoplasts. Plants were grown from these regenerated calli.

Most of the plants were male sterile and did not set normal pollen and seed after pollination with corresponding fertile, original japonica cultivars. The plants from these seeds were also male sterile. These results show that CMS plants were obtained through cybrid method. Thirty-five japonica cultivars have been converted into CMS. Some japonica cultivars failed to convert into CMS. There may be some restorer gene(s) for this cytoplasm.

Although there are limitations, this cybrid method is a very powerful tool for constructing CMS lines (A lines) more quickly than by conventional methods.

Authors' address: Life Science Laboratory, Mitsui Toatsu Chemicals, Togo, Mobara City, Japan.

CD22 R, an excellent restorer for WA, released in Sichuan, China

Peng Xingfu

Our strategy at Sichuan Academy of Agricultural Sciences is to develop new restorers having good combining ability, resistance to blast, and wide adaptability using IR restorers. CD22 R, derived from IR30 and IR50, is an excellent indica WA restorer. F_1 hybrids yielded up to 9 t/ha and showed a yield superiority of 0.5-16% over checks in yield trials and demonstrations conducted during 1989-91. They also possessed resistance to pests and had good grain and eating quality, acceptability, and wide adaptability. CD22 R produced more pollen, a favorable factor for increasing seed production yield. It is being increased to replace the leading restorer, MH63, in Sichuan, China.

Author's address: Sichuan Academy of Agricultural Sciences, Chendu, Sichuan, China.

Fertility response to photoperiod/ temperature of indica EGMS lines of rice

Zhang Xiang-guang and Lu Xing-gui

The fertility response to photoperiod and temperature in six environment-sensitive genic male sterile (EGMS) lines was studied under artificially controlled photoperiods and natural environmental conditions in Wuhan (30.5° N, 114.3° E) in 1990-91. Tests revealed that the early MS lines W6154 S, W8013 S, and W6111 S, and the midseason lines W7415 S and W6068 S, which all belong to the indica *O. sativa* L. were different from Nongken 58 S, the original japonica photoperiod-sensitive genic male sterile line, and each other in their fertility response to photoperiod and temperature.

W7415 S, a midseason indica, was found to have interactive photoperiod and temperature sensitivity, with fertility expression controlled mostly by photoperiod. All other MS lines show thermosensitive genic male sterility (TGMS), and there was no significant difference between the different photoperiod treatments.

Two critical dates for fertility alteration were found in the indica MS lines, with a basic stable sterile phase lasting for 2 mo or so. This was especially marked in the early-season lines, and helped confirm that, except in W7415 S, fertility induction and its alteration are largely controlled by temperature rather than daylength.

Stepwise regression and correlation analyses showed that fertility could be altered from sterile to fertile or vice versa in indica MS lines between 11 and 16 d before heading. Thus the fertility-inducing thermosensitive stage occurred around pollen mother cell formation and meiosis. High temperatures led to production of sterile pollen and low temperatures led to fertile or partly fertile pollen. Photoperiod had little effect. The critical temperature for fertility induction varied to some extent due to the different genetic backgrounds in the MS lines.

To develop and utilize two-line indica hybrids, further studies are needed on the genetics of the fertility-inducing mechanism and the ecological adaptability of some promising TGMS lines which respond to lower temperatures.

Authors' address: Food Crops Institute, Hubei Academy of Agricultural Sciences, Wuhan 430064, China.

Selection and breeding of indica PGMS lines

Lu Xing-gui, Mo Tong-min, Zhang Xian-guang, Zhou Ji-xian,
Zhou Wen-hua, Li Chum-hai, and Fang Guo-cheng

We began studies in 1982 on selection and breeding of photoperiod-sensitive genic male sterile indica rices (PGMS) by introducing gene(s) from the original japonica PGMS, Nongken 58 S, by crossing, and have achieved much progress since. The main research points are outlined below.

Transforrmbility of the MS genes—introduction of PGMS genes to and their expression in the genetic background of indica rices. By using hybridization (including backcrossing), we have introduced the PGMS genes from Nongken 58 S into indica rice varieties and bred early-season and midseason indica MS lines with obvious and clear-cut fertility alteration, e.g., W6154 S, W6184 S, W7415 S, and W 6068 S. The selected rate of PGMS individual plants is very low.

Ecological characteristics of fertility response to photoperiod and temperature in indica MS lines. Fertility tests and observations of fertility alteration revealed that the fertility response of all these indica MS lines except W7415 S was controlled mainly by temperature rather than by photoperiod.

Breeding and utilization of indica intervarietal two-line hybrid rice combinations. We are evaluating promising indica MS lines. Utilization of promising indica two-line hybrid rice combinations has also begun.

Key points for future breeding and study of PGMS:

- Stability of fertility in indica MS lines;
- Physiological genetics and the relationship between developmental response and reproductive performance (i.e., the fertility response to photoperiod and temperature); and
- Yield potential of indica intervarietal two-line hybrid rice (F_1) and approaches for further breeding improvements.

Authors' address: Food Crops Institute, Hubei Academy of Agricultural Sciences, Wuhan 430064, China.

Wide-compatible indica male sterile lines identified in Sichuan, China

Peng Xingfu

Breeders in Sichuan, China, are developing intersubspecific indica/japonica hybrid rice with three lines. Wide-compatible (WC) japonica 02428 was crossed with indica maintainers, and new A lines CD415 A and CD147A possessing good combining ability were identified. There was normal fertility in the indica/japonica hybrids developed from these CMS lines. The panicles were large, with 75-80% seed set in hybrids. They yielded 18.8-24% more than the best inbreds. Maximum yield was 11.7 t/ha in the 1990-91 trial. It has good grain and eating quality. Replicated yield trials and demonstrations in several locations are being undertaken.

Author's address: Sichuan Academy of Agricultural Sciences, Chengdu, Sichuan, China.

Optimum pollen load and male-female row ratio for hybrid rice seed production

H. L. Sharma and S. S. Virmani

To estimate the optimum ratio between male and female rows for hybrid rice seed production, two CMS lines IR58025 A and IR62829 A, with IR29823 R as restorer, were planted in main plots and with varying female-male row ratios (12:1, 12:2, 12:3, and 12:4 of A and R) in subplots. Pollen load at 15-cm distance from restorer rows was found to be 17.9 (12:4), 15.8 (12:3), 10.9 (12:2), and 8.2 (12:l) airborne pollens/liter, and dropped consistently with increasing distance (*r* = -0.756**) from the pollen source. A highly significant positive correlation (*r* = 0.738**) was found between the number of airborne pollens/liter and outcrossing rate. Extrapolation of the data indicated that a pollen load of more than 10 airborne pollens/liter was necessary for an outcrossing rate of more than 25% at a wind velocity of 3-4 km/h under tropical conditions.

Seed yield was computed for all row ratios, from 1:1 (A and R) to 12:4 (A and R) for both CMS lines. In IR58025 A, row ratios 5:l-11:1, 8:3-12:3, and 10:4-11:4 gave seed yields which were significantly higher than all other row ratios. Yields ranged from 1.77 to 1.95 t/ha and were not significantly different. For IR62829 A, row ratios 4:1-12:1, 6:2-12:2, 7:3-12:3, and 7:4-12:4 gave significantly higher yields (1.14-1.33 t/ha) than all other row ratios.

The highest yield for IR58025 A (1.95 t/ha) was obtained with a row ratio of 11:3, followed by 1.93 t/ha with a row ratio of 10:3. Restorer line yield (from 0.91 t/ha in 12A:lR to 5.91 t/ha in 1A:lR) was higher in 10:3 than in 11:3 by 0.17 t/ha. Therefore we concluded that row ratio 10A:3R was the most economical for hybrid seed production using IR58025 A. Similar results were obtained with IR62829 A. Seed yield was directly proportional to increase in area under female rows (ranging from 16 to 78%) after which it started declining.

Authors' address: Plant Breeding, Genetics, and Biochemistry Division, International Rice Research Institute, P. O. Box 933, Manila 1099, Philippines.

Prospects for hybrid rice seed production technology in Andhra Pradesh

R. Vijaya Kumar, B. Sita Devi, and N.S. Reddy

A trial was conducted in three locations, Maruteru, Warangal, and Palem, during the 1991 wet season to find the best environments for optimum outcrossing and seed yield in CMS lines in Andhra Pradesh. Maruteru is in a humid region, where low wind velocity and high humidity are predominant. The other two locations are in an arid zone with low humidity and high wind velocity.

IRRI CMS line IR62829 and its corresponding maintainer line, IR62829 B, were used in the trial. A row ratio of 4A:2B was adopted, with a spacing of 15 × 15 cm. One seedling was planted per hill. The CMS line was sown first, followed by two sowings of the maintainer line 4 and 8 d after the CMS line. The plantings were done across the wind direction. Flowering synchronization was good in all three sites. Standard seed production techniques, such as flag leaf clipping and supplementary pollination, were used at all sites, while 60 ppm GA_3 was sprayed at Maruteru only.

The mean outcrossing percent was very poor (19.35) in the humid environment of Maruteru. At Warangal and Palem, mean percent outcrossing was very high at 43.94% and 40.23%, respectively. The highest seed yield was 1.2 t/ha, obtained at Warangal, followed closely by 1.0 t/ha at Palem. Yield at Maruteru was 0.4 t/ha.

Further increases in outcrossing rate and seed yield of CMS lines are possible by refining the techniques and applying GA_3 at Warangal and Palem, especially in the dry season.

Authors' address: Andhra Pradesh Agricultural University, Agricultural Research Station, Maruteru, Andhra Pradesh, India.

Commercial hybrid rice seed production

Shong Yi Rhu

Qianyang County Seed Company was established in September 1978. From 1979 to 1991, the company produced and sold 11,447 t of hybrid rice seed to local farmers. The total area under hybrid rice is 0.2016 million ha, with an average grain yield of 5.8 t/ha, 19.2% higher than the best pureline varieties.

Exploiting new hybrid varieties and producing good quality seeds are the two most important factors in competing with other seed companies.

Author's address: Qianyang County Seed Company, Hunan, China.

ISBN 971-22-0053-1