Varietal improvement for rice production in India

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INTRODUCTION

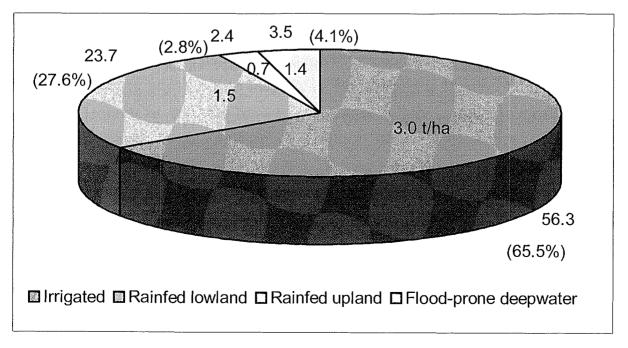
Rice is the most important tropical cereal and it supplies a quarter of the entire calorie intake of the human race. South and Southeast Asia, which support a major part of the world population, account for about 90 percent of rice area and consumption. Rice belongs to the genus *Oryza* and there are two main cultivated species: *sativa* in Asia and *glaberrima* in Africa. The predominant *O. sativa* subspecies grown in Asia are *japonica* (grown mostly in Japan, Korea and northern China), *indica* (mostly in the rest of Asia) and *javanica* (in Indonesia). Rice is a semi-aquatic graminaceous crop with great diversity as it is grown in a complex range of very different environments, from uplands at altitudes of 3 000 m to rainfed lowland, irrigated, tidal swamp and deepwater areas.

Globally, India is first in terms of rice area, second after China in terms of production and it accounts for 24.8 percent of world rice production. Within the country rice occupies 22.8 percent of the total cropped area and 46.3 percent of the area under cereals; it contributes 42 percent of total food grain production and continues to play a vital role in national food security, as it constitutes the staple food for two-thirds of the population supplying about 33 percent of food energy. Despite the low protein content of brown rice, the net protein utilization value of rice is 73.8 percent – the highest amongst cereals. Rice cultivation and processing also form the basic economic activities, either directly or indirectly, for the vast majority of rural households in India.

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Despite the high production growth rate achieved over the years, rice productivity in the country still remains low at around 2.0 t/ha of milled rice (1999-2000), which is much less than many other rice-producing countries, such as China (3.9 t/ha), Japan (4.1 t/ha), Republic of Korea (4.6 t/ha) and Indonesia (2.7 t/ha). This is mainly because rice in India is grown in many different ecosystems and seasons which are not uniformly favourable for high productivity. Irrigated rice is grown on 50 percent of the rice area, contributing 63.5 percent of the total yield with a highest average level of productivity of about 3.0 t/ha. Rainfed shallow water lands (representing about 30 percent of the area) contribute 26.7 percent of production with an average productivity of 1.5 t/ha. Rainfed uplands occupy 15 percent of the area but contribute only 5.8 percent of total production with a least productivity rate of 0.7 t/ha. Floodprone and deepwater rice occupy 5 percent of the total area, contributing 4 percent of production with a productivity of 1.4 t/ha. Ecosystem-wise production and productivity levels are presented in Figure 1. As each of these ecosystems requires a different set of genetic attributes, varietal improvement strategies need to be deployed accordingly. Regional disparity also prevails in terms of productivity (Fig. 2). Southern India – representing predominantly the irrigated

FIGURE 1
Rice production and productivity in different ecologies in India



ecosystem – has the highest productivity (3.7 t/ha). The northern and northwestern region, covering the states of Punjab, Haryana and Himachal Pradesh, has an average productivity of 3.1 t/ha. The predominantly rainfed shallow, semi-deep and deepwater, as well as rainfed, uplands in the eastern region record productivity of 2.4 t/ha. The western region with its hostile environment has the lowest productivity (1.9 t/ha).

RICE IMPROVEMENT IN THE PAST

As a historical backdrop, rice breeding in India began in 1911 in Dacca (now in Bangladesh) and the following year in Coimbatore in the old Madras Province. Recognizing the importance of rice to India's economy, the Imperial (now Indian) Council of Agricultural Research (ICAR) - founded in 1929 - sponsored rice breeding projects in all the major rice-growing states and as a result by 1950 the country had as many as 82 research stations exclusively for rice research. However, rice research in the country was revamped in the late 1940s in the aftermath of the now forgotten holocaust—the famous Bengal Famine of 1943-44, in which an estimated 3.5 to 3.8 million people perished due to starvation. The Indian Government rose to the occasion and set up the National Commission on

FIGURE 2
Rice production and productivity in different regions of India

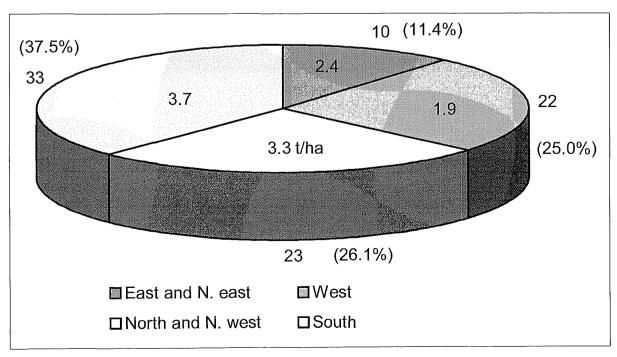


PLATE 3
Irrigated rice field planted with a High Yielding Variety

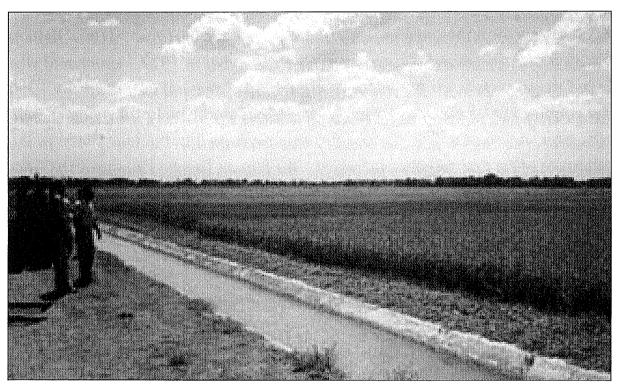


PLATE 4
A deepwater rice field in Bangladesh



Agriculture. The recommendations of the Commission culminated with the setting-up of the Central Rice Research Institute (CRRI) in Cuttack in 1946.

After the Second World War, when food grain supply fell far short of demand and threatened the world community, the Food and Agriculture Organization (FAO) founded the International Rice Commission (IRC) within the FAO framework to find ways of increasing rice production. IRC identified non-lodging habit, fertilizer responsiveness, early maturity and wide adaptability as the important varietal characteristics for achieving higher and more stable yields. Accordingly, FAO launched several regional network projects, including: "Cataloguing and Maintenance of Rice Genetic Stocks", "Indica-Japonica Hybridization, Cooperative Varietal Trials", "Wide Adaptability Test", "Variety-Fertilizer Interaction in Indica Varieties" and "Uniform Blast Nursery and International Training Program in Rice Breeding 1950-59".

Between 1950 and 1967, efforts towards achieving food self-sufficiency in India were not entirely successful. Efforts until 1967 mainly concentrated on expanding the farming area. In a classic case of Malthusian economics, the population was growing at a much faster rate than food production. This called for drastic action to increase yield. The action came in the form of the Green Revolution during the period from 1967 to 1978. Of the factors contributing to the Green Revolution, the credit for the scientific component, consisting of development, testing and release of modern genetically high-yielding varieties of rice and wheat, can be attributed solely to the effective utilization of genetic diversity. A simple comparison between rice production statistics in the country for 1951/52 (total area 30.81 million ha [Mha]; production 20.58 million tonnes [Mt]; productivity 668 kg/ha) and 1999/2000 (44.61 Mha; 88.55 Mt; 1 985 kg/ha) reveals the impact of rice research on food self-sufficiency.

Before the Green Revolution, varietal improvement had largely been confined to pure line selection, resulting in the identification of 445 varieties, such as Manoharsali and Latisail in the rainfed lowlands, Dular and N22 in the rainfed uplands and MTU 15 and GEB 24 in irrigated areas. As early as 1921, varietal improvement programmes were initiated in Uttar Pradesh. Beginning in 1932, research work in Nagina emphasized the development of better quality high-yielding rice varieties. Selection resulted in the production of several improved strains, such as N 105 (selection of Hansraj from Pilibhit), N 12 (selection of

Safeda from Punjab), T 3 (selection of Basmati from Dehradoon), T 9 (selection of Duniapat from Basti), T 1 (selection of Ramjiwain from Saharanpur) and T 23 (selection of Kalasukhdas from Banda). Basmati 370 was also selected at the same time in Kala Shah Kaku (now in Pakistan) in 1933. Varieties, such as Basmati 370, T 3, N 105 and T 9, are still popular and are grown on a sizeable area in the northwestern states.

The first serious research efforts to break the yield barrier of tropical rice were made through the intersubspecific (*indica* x *japonica*) hybridization programme, which combined the non-lodging habit and fertilizer responsiveness of *japonica* varieties with the adaptability and quality of *indica* rice. While the results were not as hoped, the programme did identify Mahsuri in Malaysia and ADT 27 in Tamil Nadu, resulting in significant production advancement in India. This breeding programme convinced breeders that the key to higher yield lay in breeding for non-lodging plants.

The introduction in 1965 of Taichung (Native) 1 was the first of several technological innovations leading to the realization of the potential of semidwarf, photo-insensitive, non-lodging, fertilizer-responsive varieties. A major breakthrough was witnessed in the history of rice breeding in the form of IR 8, which introduced the concept of the dwarf plant type. As information on different components of plant type became available, India recognized new horizons for increasing productivity through the identification of semi-dwarf varieties from introduced materials as well as selections from hybridization programmes. The coordinated research programme aimed to achieve the desired result as rapidly as possible, resulting in the release of IR 8 (from the material introduced from IRRI – International Rice Research Institute, Philippines) in 1966 and Jaya (from the hybridization programme of AICRIP – All India Co-ordinated Rice Improvement Project) in 1968. This was followed by the identification of several varieties combining improved plant type with high yield for different maturity groups. AICRIP's unique mechanism of multidiscipline-based multilocation testing facilitated the rapid development of varietal and production technologies appropriate for varied agro-ecologies. This model – now adopted by several countries and international institutions – helped to evolve more than 640 highyielding varieties (Appendix 2) and enabled the country to boost rice production. While this article focuses on rice development in India during the period 1970-2000, earlier work has been reviewed elsewhere (Muralidharan et al., 1996; Krishnaiah, 1998; Siddiq and Viraktamath, 2001).

BREEDING METHODS AND OBJECTIVES

The thrust in breeding research has varied with changing needs and socioeconomic compulsions. It concentrated on high yield and general adaptability in the first decade. Following the introduction of dwarf varieties, stability of yield by breeding for resistance or tolerance to biotic and abiotic stresses was the priority in the following decade, while raising the genetic yield threshold and the development of varieties suited to rainfed ecologies received increased research attention from the third decade onwards. From the account below of the different breeding methods adopted, it is evident that that choice of method depended on: the breeding objective; the availability of suitable genetic diversity; knowledge of the genetics of the traits of interest; and the development of evaluation methodologies.

Introductions

Introduction is the oldest and simplest method of meeting the varietal needs of a given situation as well as an effective means of enlarging and enriching genetic variability. Varieties found popular for a given set of growing conditions in another country or a state within a country are introduced and evaluated in replicated trials under similar conditions to assess yield performance and adaptability. It is not necessary that all the introduced varieties become acclimatized to the new environment and be acceptable to farmers and consumers in order to justify more systematic investigations into their level of resistance to major pests and diseases and quality features. In the process of evaluation there is often scope for selection under the new environment and such selection may lead to some successful varietal introductions. Table 1 lists 21 rice varieties released as introductions from other countries. Of these, 16 were introduced for irrigated ecology (mostly from IRRI) and two for rainfed ecosystems. Several of the breeding lines developed at IRRI were extensively tested in the country and subsequently released as varieties suited for different purposes. One variety each was introduced for: Basmati quality; salt tolerance; deepwater rice with submergence tolerance; and rainfed lowlands. There are also examples of

TABLE 1
Rice varieties released in India as introductions from other countries

S. no.	Variety name	Year of release	Introduction from
	For irrigated ecology		
1	IR 20	1970	IRRI
2	IR 22	1975	IRRI
3	IR 24 (IR 661-1-1-143-3)	1972	IRRI
4	IR 28 (IR 2061-214-38-2)	1975	IRRI
5	IR 34 (IR 2061-213-217)	1979	IRRI
6	IR 36 `	1981	IRRI
7	IR 50	1982	IRRI
8	IR 64	1989	IRRI
9	IR 64	1992	IRRI
10	Palman 579	1972	IRRI ^a
11	PR 4141	1982	IRRI ^a
12	PR 109	1986	IRRI ^a
13	HKR 126	1992	IRRI ^a
14	PR 103	1976	IRRI ^a
15	PR 106	1978	IRRI ^a
16	Rajendradhan 1	1978	IRRI ^a
	For Basmati quality		
17	Hassan Sarai	2000	Iranian Basmati
18	Munal (C 15310)	1982	USA
	For salt tolerance		
19	Narendra Usar 2	1998	IRRI
	For rainfed ecology		
20	Hemavathi	2000	Bangladesh
21	Intan	1975	Indonesia

^a Breeding line tested locally and released as variety.

successful state-to-state introductions. For example, Swarna (developed in Andhra Pradesh) has become popular in Orissa, Madhya Pradesh and West Bengal. Besides their usefulness as varieties, many of these introductions are being used as parental lines in cross-breeding programmes. Introduced varieties have thus played an important role, not only in enhancing genetic diversity, but in supporting the rice breeding programme.

Pure line breeding

Highly heterogeneous farmer-grown local varieties are purified for uniform height, maturity and other agronomic traits. This simple breeding/selection approach has both strengths and weaknesses. The process of purification begins

either in farmers' fields or with farmers' strains raised on experimental farms. Seeds harvested from promising plants are raised in successive generations as panicle or plant progenies until they become uniform and stable. Following the seed increase, the chosen best line are intensively evaluated in replicated yield trials (where the local variety is the check) for at least 3 to 5 years, in order to ascertain stability of yield performance in the target environment. The best-performing entry, in terms of the breeding objective, is identified for general cultivation after evaluating for consumer quality. Pure line breeding is still relevant, when recombination breeding and other approaches are found to be slow and less effective in special situations, such as breeding for higher yield without compromising the prized quality features of Basmati. The main strength of this approach is that it does not disrupt the combination of characters preserved through generations of selection, while the main limitation is that variability and improvement of the desired character are both limited.

During the last three decades, 35 varieties for rainfed systems and 19 varieties for irrigated ecosystems have been developed through pure line selection (Table 2). Of these, 24 and 6 varieties, respectively, were pure line selections from landraces, while others were selections from elite breeding lines. Even the improved released variety, IR 50, was further selected for specific traits and formed the progenitor of three rice varieties: Sravani for irrigated ecologies in the early duration group; Swathi for rainfed shallow water; and Somasila for upland regions. Nine of the varieties developed for deepwater and nine for semideepwater were from selections from local landraces. Seven of the eight upland varieties developed through pure line breeding originated from local landraces. Likewise, nine varieties for rainfed shallow water lowland were also from pure line selections from both landraces and elite cultures. Six of the selections were from Basmati type locals with aroma and quality traits. Two varieties, namely Shindewahi I (selected from a local landrace) and Vyttila 2 (from the local variety Cheruviruppu), were released for saline/alkaline soils. Some of the earlier varieties developed as pure line selections (and to this day very popular in the country) are: GEB 24, Basmati 370 and Manoharsali, which have quality features; Ptb 18 and Ptb 33 for pest resistance; SR 26B and Vyttila 1 for salt tolerance; and FR 13A for deepwater situations. However, pure line selection also leads to genetic uniformity and erodes the prevailing diversity.

TABLE 2 Rice varieties developed in India as pure line selections

S. no.	Variety	Year of release	Ecology ^a	Selection from
1	ADT 41	1994	IRSCR	Basmati 370
	J.J.92	1993	IRSCR	Dwarf Basmati
2	Basmati 386	1994	IRSCR	Pakistan Basmati
4	Ranabhir Basmati	1994	IRSCR	Basmati 370-90-95
5	Sugandha (T)	1983	IRSCR	Cuttack Basmati
6	Taraori Basmati	1996	IRSCR	Local Basmati
7	T 3 (T)	1973	IRSCR	Local Type 3
8	Jalgoan 5	1978	IRE	Local landrace
9	Sravani	1997	IRE	IR 50
10	Mata Triveni (PTB 45)	1990	IRE	Triveni
11	Terna	1989	IRE	MAU Sel. 9
12	Patel 85	1981	IRM	IR 8
13	Kolhapur	1971	IRM	Local landrace
14	Ambica	1991	IRM	SKL 47-8
15	HMT Sona	2000	IRM	Local landrace
16	T 141 (T)	1988	IRM	Local landrace
17	Kamini (SBR 80-643-14-1-1)	1991	IRM	Katarni Rice
18	Vytilla 2 (Cul. 174)	1980	IRM	Cheruvippu
19	Sindewahi 1	1988	IRSA	Local landrace
20	ADT 32	1972	RSL	Vaigai Samba
21	Swathi	1997	RSL	IR 50
22	Safri 17 (T)	1984	RSL	Safri
23	Seema	1991	RSL	Jagannath
24	BAM 6 (T)	1986	RSL	Ratna Chudi
25	Rajasree (T) (TCA 80-4)	1987	RSL	Local landrace
26	T 90 (T)	1988	RSL	Local landrace
27	T1242 (T)	1988	RSL	Local landrace
28	SR 26 B (T)	1988	RSL	Kalambanka
29	Janaki (T)	1983	SDW	Chenab Rice
30	Amulya	1988	SDW	Local Nagani
31	Nalini	1988	SDW	Sindu Raukhi
32	Vaidehi (T)	1995	SDW	Beldar (TCA 48)
33	Amulya	1988	SDW	Najani -
34	Sabita (T)	1986	SDW	Boyan
35	FR 13A (T)	1988	SDW	Kalambanka
36	Nalini	1989	SDW	Sindhur Mukhi
37	Matangini	1989	SDW	Kajallata

^a IRSCR = irrigated scented rice; IRE = irrigated early duration; IRM = irrigated medium duration; IRSA = irrigated saline/alkaline soils; RSL = rainfed shallow water depth; SDW = rainfed semi-deepwater.

TABLE 2 (contd.)

S. no.	Variety	Year of release	Ecology ^a	Selection from
38	Jalanidhi	1993	DW	Goanath
39	Jalpriya	1993	DW	IET 4060/Jalmagna
40	Jaladhi 1 (T)	1981	DW	Kalakher Sail
41	Jaladhi 2 (T)	1981	DW	Local Baku
42	Jalaprabha (T)	1996	DW	Local landrace
43	Jitendra	1994	DW	Local landrace
44	Jitendra (T)	1994	DW	Local landrace
45	Neeraja	1998	DW	Local landrace
46	Sudha (T) (TCA 72)	1987	DW	Local landrace
47	Suvarnamodan (ARC 11775)	1976	RUP	ARC 11775
48	Somasila	2000	RUP	IR 50
49	Tuljapur-1 (T)	1972	RUP	Lalsal 140-31
50	Imp. Ambemohar	1978	RUP	Local landrace
51	GR 5	1991	RUP	CR 319-344
52	Panke	1989	RUP	Local landrace
53	Birsagora 102 (T)	1992	RUP	Local landrace
54	Maruteru Sannalu	2000	RUP	Oodasannalu

^a DW = rainfed deepwater; RUP = rainfed upland.

Mutation breeding

Mutation breeding is adopted to overcome the limitation of variability in the pure line selection. The original parent line or local landrace is subjected to mutagenesis, either through use of chemical mutagens or by subjecting it to ionizing radiations. Mutation breeding has been successfully exploited to improve many crop plants – including rice – for selective improvement of one or two simply inherited traits. Use of induced mutagenesis for improvement of rice began in India in the 1930s, but it received importance as a potential breeding tool in the late 1960s and 1970s with the active support of the International Atomic Energy Agency (IAEA). A wide range of mutagens were evaluated to induce mutations in rice. The physical mutagens: X-rays, gamma rays and fast neutrons, and the chemical mutagens: ethyl methane sulphonate (EMS), nitroso methyl urea (NMU) and sodium azide, were found to be potent for inducing point mutations. Rice genotypes differ in their response to mutagen since *japonica* varieties are, in general, more sensitive than *indica* and *javanica* types (Sharma, 1985). The sensitivity of genotypes to mutagens is greatly influenced by several

factors, most critically: optimizing conditions to induce point mutations without adverse effects on the plant biology (Mehetre *et al.*, 1993); and post-treatment handling of the early generations to select mutants with desirable features. The mutagen-treated seed is grown as Ml generation to raise M2 generation. M2 and M3 are screened against the trait for which the breeding objective was initially set. Variants which do not show segregation for the desired trait in M3 and M4 are considered mutants.

Mutation breeding in rice was initially targeted at yield improvement, high protein content of seed and resistance to blast and bacterial leaf blight (Mikaelsen, 1979). Some mutants have been either released directly as mutant varieties or used as excellent donor sources for improving specific characters. Two of the mutant lines, namely Orumundakan and Calrose 76, possessed a wide range of gall midge resistance against different biotypes. Jagannath was the first rice variety developed in India through mutation breeding involving the parent line T 141. This variety has been used in the development of six improved varieties for the rainfed ecosystem. Table 3 lists 11 recent rice varieties developed through mutation breeding. One of these, Prabhavati, was developed from the local variety, Ambemohar, through somaclonal variation induced by the tissue culture technique. Two of the varieties were developed from IR 8 through

TABLE 3
Rice varieties of India developed through mutation breeding

S. no.	Variety	Year of release	Ecology	Parental line
1	Biraj	1982	SDW	Co 1393 mutant
2	Padmini	1988	RSL	Mutant of CR 1014
3	Rasmi	1986	RSL	Oorapandy mutant
4	Bipasa	1993	RSL	X-ray mutant of Pankaj
5	Early Samba	2000	IRM	Mutant of BPT 5204
6	AU1	1976	IRE	Sel. from mutant of IR 8
7	Lakshmi (CNM 6)	1982	IRE	Mutant of IR 8
8	Prabhavati	1984	IRE	Mutant of local Ambemohar
9	Remanica	1998	IRM	Mutant of MO1
10	Radhi	1998	IRE	Swarnaprabha mutant
11	Indira (CR MUT 587-4)	1980	IRM	Tainan 3 mutant
12	Gautam	1995	IRME	Rasi, EMS induced mutant

^a IRME = irrigated mid-early duration (others as in Table 2).

mutagenesis. However, no significant progress was made in the improvement of Basmati rice through mutation breeding (Singh *et al.*, 1989). One of the mutant rice lines, HPU8020, had strong blast resistance and was suited for cultivation in low altitude areas of Himachal Pradesh (Sharma *et al.*, 1985). An EMS-induced mutant of Rasi, PSRM1-16-4B-11, was superior in yield and cold tolerance and was released as Gautam for cultivation in high altitude areas of Bihar (Thakur *et al.*, 1994). Two of the varieties developed through mutation breeding in Kerala, namely Rasmi (mutant of Oorapundy) and Radhi (mutant of Swarnaprabha), have resistance to blast and BPH (brown planthopper), respectively. It is evident that mutation breeding has played an important role in enhancing genetic diversity in rice, which in turn has been gainfully exploited for rice improvement.

Recombination breeding

Recombination breeding consists of controlled crossing between parents of choice, followed by pedigree or mass pedigree selection in the segregating generations for targeted trait(s). It is the widely employed approach in rice improvement. Unlike the pureline selection, which is limited to identification of the best in the naturally available variability, recombination breeding is a device for generating variability and recombining desired characters for any given situation. There are different ways of making crosses and procedures for selection of the progeny depending on the breeding goal and the genetics of the trait(s) to be recombined. In breeding for quantitatively inherited traits, such as yield and tolerance to complex abiotic stresses, a straight single cross followed by selection through pedigree or modified pedigree methods is the usual practice. On the other hand, for simply inherited mendelian characters, depending on the agronomic potential of the parents, either single cross or backcross followed by pedigree selection is preferred. If the breeding objective is to combine a set of traits from diverse sources, a "convergent breeding" approach is followed. This involves the stepwise addition of constituent traits. For varieties with multiple pest resistance or diverse quality traits, convergent breeding is adopted.

Backcross breeding is used when a simply inherited trait is to be selectively transferred from a recalcitrant wild donor, e.g. a wild species or poor landrace, to an otherwise good agronomic base. It is necessary to go for several cycles of

backcrossing of the recurrent parent with the recipient variety. This breeding method is effective for breaking tight linkages between desirable and undesirable traits and it is routinely used in hybrid breeding for the development of cytoplasmic male sterile lines. The method is quicker if the donor parent also has good agronomic traits. The successful introduction of bacterial leaf blight resistance genes (*Xa 21* and *Xa 4*) into Pusa 44 is a good example of the potential of backcross breeding.

The selection methodology employed also varies depending on numerous factors: the genetic control of the target trait; field/laboratory facilities; labour requirements and conduciveness of the environment for effective selection. The pedigree method is followed for the improvement of both qualitative and quantitative traits in situations where land/laboratory facilities and manpower are adequate, while the modified pedigree or mass pedigree method of selection becomes inevitable when the selection environment is not appropriate for discriminating desirable genotypes from undesirable ones. In such situations the segregating populations are bulked up to 4 to 5 generations right from F₂ followed by pedigree selection. When the breeding objective is the incorporation of resistance to a particular insect pest of variable incidence under field conditions and no method or facility is available for screening under artificial conditions, bulking of segregating populations is continued until the right screening environment occurs. This practice also holds good for breeding for drought resistance. The whole strategy of early generation bulking is practised when the F₂ population itself is too small or the likelihood of loss of valuable segregants is high under harsh target environments, such as salinity and drought. In the latter case, F_2 is raised under optimal conditions, and F_3 raised from bulked F_2 is screened under the stress.

About 500 of the 633 rice varieties developed for cultivation are through recombination breeding. More than 90 percent of these were developed from single straight crosses involving two parents, while 5 percent are from double cross involving three parents and only 2 percent involved four parents. Table 4 lists the most often used parent lines together with their attributes. IR 8 has been the most extensively used parent in the development of over 80 varieties for both irrigated and rainfed ecologies, followed by TN 1 (40 varieties developed), IR 36 (15), Jaya (14), Basmati 370 (10) and TKM 6 (10).

TABLE 4
Parents most often used in India's recombination rice breeding programme

S. no.	Parent	No. of derived varieties	Genes involved	Attributes involved ^a
Irrigated	ecology			
1	IR 8	58	sd1	Photoperiod insensitive, semi-dwarf plant stature, high yield potential, medium maturity duration and MR to BL, GLH,
2	TN (1)	24	sd1	First semi-dwarf and photoperiod insensitive variety
3	Jaya	14	sd1	Photoperiod insensitive, semi-dwarf plant stature, high yield potential, medium maturity duration
4	IR 36	15		Early-mid early, suitable for intercropping, R to GM
5	Basmati 3 7 0	10		Aromatic, export quality rice
6	TKM 6	10		R to SB
7	Mahsuri	8		Indica/japonica derivative, stable, high yielding, suitable for shallow lowlands and irrigated areas, late duration
8	Sona	8		Fine grain, quality rice, MR to RTV, SB, leafhopper
9	Zinnia 31	7		Quality grain
10	T 90	6		Quality grain
11	IR 50	5		Early duration, high yield potential suitable for multiple cropping system
12	PTB 10	5	Gm4	Good for soil problems, R to GM
13	PTB 33	5		R to BPH, WBPH
14	Vikram	5	Gm2	R to GM, medium duration variety
15	ADT 27	4		Suitable for Kuravai, early monsoon, indica/japonica cross
16	IR 24	4		High yield, early, R to GM, good for saline soils
17	IR 28	4		Earliness, multiple resistance
18	MO 6	4		BPH resistance
19	PR 106	4		Medium maturity, high yield potential, export type non Basmati rice
20	Rasi	4		Indica/japonica derivative, stable, high yielding, suitable for shallow lowlands and irrigated areas, late duration
21	Triveni	4		MR to BL, suitable for direct seeding
22	W 1263	4	Gm1	R to GM, SB
23	W 12708	4	Gm2	R to GM, SB

TABLE 4 (contd.)

S. no	o. Parent	No. of derived varieties	Genes involved	Attributes involved
Raint	ed ecology			
1	Pankaj	24		Late duration, suited for rainfed lowlands, MR to BL, RTV
2	IR 8	21		Photoperiod insensitive, semi-dwarf plant stature, high yield potential; MR to BL, GLH
3	Mahasuri	19		Indica/japonica derivative, stable, high- yielding, suitable for shallow lowlands and irrigated areas, late duration
4	TN (1)	16		First semi-dwarf and photoperiod insensitive variety
5	IR 20	8		High seasonal stability, grain quality, R to RTV
6	Sona	8		Fine grain, quality rice
7	IR 36	7		Early-mid early, suitable to intercropping, R to GM
8	N 22	7		Drought tolerant
9	CR 1014	6		Late maturing, stable widely adaptable, quality rice
10	Jaganath	6		Mutant of T 141, photosensitive, lowland variety good for delayed rain
11	Jaya	6		Photoperiod insensitive, semi-dwarf plant stature, high yield potential
12	Fine Gora	5		Drought tolerant
13	Patnai 23	5		High yield potential, lowland variety
1	Bulk H 9	4		Late, photosensitivity
2	M 63 - 83	4		Drought tolerant
3	Rasi	4		Good for irrigated, rainfed uplands; cropping systems because of early maturity
4	RP 5-32	4		Late maturing, high yield potential
5	Vijaya	4	•	High seasonal stability, R to leaf hopper, Tol. SB

^a T141 = selection from "Saruchinamali"; N22 = selection from "Rajbhog"; R = resistant; MR = moderately resistant; Tol. = tolerant; BL = blast; BPH = brown planthopper; GLH = green leafhopper; GM = gall midge; RTV = rice tungro virus; SB = stem borer; WBPH = white-backed planthopper.

Approaches for accelerated generation advance and selection

One of the major limitations of recombination breeding is the long period required for fixing genotype with desired character combinations. More genetically complex traits need longer to be fixed. It is all the more difficult and time consuming if such traits are to be incorporated in long-duration photosensitive varieties. Various techniques have been developed to reduce the breeding selection cycle.

Rapid generation advance (RGA): Well suited to breeding long-duration photosensitive varieties. Instead of one crop per year (as with long-duration photosensitive varieties under field conditions), three crops can be taken using the RGA strategy. This strategy is invaluable in breeding for lowland and deepwater ecologies.

Shuttle breeding: This involves raising breeding populations alternatively in two agroclimatically diverse environments for two different purposes, namely: practising selection at one centre and advancing generation at another to take advantage of favourable weather; and selection and generation advance at both centres.

Selective diallele mating and recurrent selection

A number of characters cannot be easily bred through single cross/backcross breeding and pedigree/modified pedigree selection approaches, because their expression is governed exclusively by either minor genes or weak major genes in association with strong minor gene complexes. Such characters include resistance to stem borer, leaf folder, sheath blight etc. No strong source of resistance has to date been found against these pests, though sources of moderate resistance (believed to be governed by non-mendelian genes with small effect) are known to exist. Recurrent selection, involving repeated intercrossing among selected source parents and their progenies and practising selection successively, is a proven approach in cross-pollinated crops for selectively pooling desirable genes with little effect. The successive cycles of intermating among the selected recombinants followed by selection facilitate directed accumulation of desirable genes in the segregants, while enhancing

the probability of breaking undesirable linkages. This method has many advantages but the main limitation has been the lack of an easy mechanism for ensuring random intermating. However, genetic male sterility could be effectively used for this purpose.

Heterosis breeding

It was the persistent effort of Chinese scientists that ultimately led to the successful development of hybrid rice technology during the 1970s. The first commercially usable cytoplasmic male sterile (CMS) line was developed in China in 1973 from a spontaneous male sterile plant isolated in a population of the wild rice, O. sativa spontanea, on Hainan Island (Virmani and Edward, 1983). A yield advantage of 15 to 20 percent over the best inbred varieties was the key factor in the wide adoption of the technology. The procedure for developing hybrids is quite different from that employed for conventional breeding. While conventional recombination breeding involves selective accumulation of yield related genes that perform well under homozygous conditions, in hybrid breeding yield genes are assembled and exploited under heterozygous conditions in the first filial F, generation. Heterosis is the phenomenon whereby the F₁ generation expresses quantitative traits better than the best parents. Although the genetic basis of heterosis in rice is not clearly understood, it can result from complete dominance, over dominance, epistasis or a combination of these factors (Virmani, 1996). More recent genetic and molecular studies revealed that differentially expressed DNA fragments occurring in only one parent of the cross were positively correlated with heterosis, while RNA hybridization detected an overall elevated level of gene expression in the hybrid compared with the parents (Zhang et al., 2001). Generally, rice hybrids are developed by using either cytoplasmic male sterility or environment sensitive genic male sterility (EGMS) systems. Of these, the former is widely utilized, while efforts are still underway to utilize photoperiod sensitive and temperature sensitive genic male sterility to develop two-line hybrids.

CMS-based three-line approach: The development of a stable male sterility system is the prerequisite for commercial hybrid seed production. Of the different kinds of male sterility systems known in rice, the cytoplasmic-genic male sterility

based three-line approach has proven most stable and commercially viable, as is the case in traditional hybrid crops. In this system, male sterility results from interaction between the sterility factor present in the cytoplasm and the nucleus. Absence of the sterility-inducing factor (gene) in either the cytoplasm or the nucleus makes a line become male fertile. This system involves a CMS (A line), maintainer (B line) and restorer (R line). A CMS line is maintained by crossing it with its B line. The A and B lines are similar in all respects except that the former is male sterile and the latter male fertile. The restorer line possesses dominant fertility restoring gene(s) and hence when crossed with a CMS line, produces a fertile F_1 hybrid. Since the system involves the use of three lines (A, B and R), hybrids developed using this method are called three-line hybrids.

Three factors are crucial for the commercial success of hybrid rice technology: high standard heterosis, stable male sterile source and efficient package for obtaining high seed yields. Yield heterosis has been reported to be as high as 370 percent, but realizable standard heterosis (yield advantage in comparison to the best standard variety) estimated across countries on the basis of population is only in the range of 18 to 36 percent. In the high-yielding varietal background, even an average standard heterosis of 10 to 15 percent would amount to an additional yield advantage of 1.0 to 1.5 t/ha.

EGMS-based two-line approach: The discovery of environment sensitive genic male sterility (EGMS), wherein alteration of male sterility/fertility is conditioned by environmental factors (e.g. photoperiod or temperature), has led to the development of a two-line breeding system (Virmani and Ahmed, 2001). The lines which respond to day-length changes are called photosensitive genic male sterile (PGMS). The first PGMS source was reported by Shi in 1981 in the japonica cultivar Nong-Ken 58 (Virmani and Edward, 1983). This variant remains male sterile under long day (> 14 hr) conditions and turns male fertile under short day (< 13.75 hr) conditions. PGMS lines are effectively utilized in those regions where day-length differences are quite distinct. The genetic source wherein alteration of male fertility/sterility is controlled by change in temperature, is called thermosensitive genic male sterility system (TGMS). In the tropics, where consistent temperature differences are found at different

altitudes or during different seasons in the same location, the TGMS system is ideal for developing two-line hybrids. Unlike the CMS system, the TGMS system does not require a maintainer line for multiplication of the male sterile line. While a TGMS line in a sterile phase and a male fertile parent are required to produce hybrid seed, the TGMS line is maintained by growing under low temperature conditions and this facilitates its reversion to the fertile phase.

The PGMS/TGMS-based two-line system has the following advantages over the conventional CMS-based three-line system:

- There is no need for a maintainer line for seed multiplication of the male sterile line; hence seed multiplication is less cumbersome
- Any fertile genotype can be used as a male parent and there is no need to have a restorer gene; hence the choice of male parents is wide for developing two-line hybrids.
- The negative effects of sterility-inducing cytoplasm are not encountered.
- The TGMS/PGMS trait can be transferred to any desired genetic background without any restrictions, thus providing wider genetic and cytoplasmic diversity among the male sterile lines.
- The system is ideal for developing intersubspecific hybrids, as there is no need for restorer genes in the male parent.

The recent progress made in the development and adoption of hybrid rice technology in India is described in a separate section.

Cellular and molecular breeding

Advances in cell and molecular biology have opened up new opportunities for rice breeding. The new possibilities in rice breeding through application of biotechnology tools are: anther culture, wide hybridization, genetic engineering and DNA marker technology. Both genetic engineering and wide hybridization are expected to help in enlarging the gene pool by accessing variations beyond cultivated rice genome, while DNA markers and anther culture help, respectively, to increase selection efficiency and compress the breeding cycle.

Tissue culture in rice improvement: Tissue culture is an all-embracing term denoting *in vitro* culture of gametic cells, tissues, organs and isolated protoplasts.

The promising tissue culture techniques relevant to rice breeding are: anther culture for speed and efficiency in breeding a variety; somatic cell culture for efficient screening of large cell populations for variants resistant to biotic and abiotic stresses; and embryo culture to rescue hybrid embryos in interspecific and intergeneric crosses for transfer of useful traits from alien taxa. Another important area of application of tissue culture is the recovery of novel genetic variants – somaclonal variation – in regenerated plants in tissue culture and gametoclonal variation in anther/pollen-derived plants. As mentioned above, one variety, Prabhavati, was developed from the local variety Ambemohar through somaclonal variation induced by tissue culture technique.

Anther culture: Production of doubled haploids (DH) through anther culture is a rapid approach for attaining homozygosity and can shorten the time required to develop a cultivar. It has a potential use in self-pollinated crops, such as rice, because it recovers homozygous lines in the very next generation and has enhanced selection response due to the presence of additive genetic variance alone in dihaploid population. Anther culture as a tool in rice breeding has several other advantages besides providing the quickest method of fixation of homozygous lines: it increases selection efficiency and facilitates early expression of recessive genes; it discriminates genotypes better due to the absence of dominance effects. Compared to the F₂ population, fewer DH plants are sufficient for the selection of desired recombinants. Over the years, the technique of anther culture has been considerably improved, particularly for japonica rice. This approach has also been refined to suit indica rice (Sandhu et al., 1993; Raina et al., 1996; Vijaya Laxmi and Reddy, 1997) and is being employed in breeding for tolerance to cold (Gupta et al., 1996), submergence (Mandal and Gupta, 1997), salinity (Miah et al., 1996) etc. In spite of such unique advantages, the strategy is not widely used, due mainly to the very low frequency of regenerants, especially in indica rices (due to strong genotype influence and media interaction).

Tissue culture and somaclonal variation: Variation induced in in vitro culture provides another option for rice improvement. The basic advantage of somatic cell culture is the ability to screen myriads of cells to increase the

probability of identifying rare variants. The effectiveness of cell selection and exploitation of genetic modifications induced in cell cultures (somaclonal variation) largely depend on the ability to regenerate variants from selected cell variants and the stability of expression of the trait at cellular as well as plant level. A large number of somaclones of the local Basmati rice cultivar, Karnal, were generated and evaluated for semi-dwarf stature, earliness, grain and cooking quality (Raina *et al.*, 1996).

Wide hybridization: Anther culture has potential application in wide crosses to develop substitution and addition lines. In addition to the two cultivated species of rice, O. sativa and O. glaberrima, there are 21 wild species in the genus Oryza. While wild species belonging to the AA genome can be easily crossed with cultivated species, embryo rescue needs to be used for obtaining hybrids between cultivated and distantly related species of other genomes. A number of useful genes have been introgressed into cultivated rice from wild germplasm (Brar and Khush, 1997). Diversification of sources of cytoplasmic male sterility is another important objective in wide hybridization. A gene conferring resistance to the Indian biotype of BPH has been introgressed from O. officinalis and is being used in resistance breeding (Jena et al., 2000). New cytosterile stocks alternative to the widely used WA (Wild Abortive) have been developed using male sterile inducing cytoplasm from O. rufipogon and O. nivara through substitution backcrossing (DRR, 2001).

Genetic transformation: Advances in recombinant DNA technology have provided new means for mobilizing genes within and across the plant and animal kingdom. It is now possible to identify, isolate and transfer genes into rice plants, no matter what the source is. Transformation of rice is done via various techniques, including protoplasm-mediated DNA uptake, microprojectile electroporation and *Agrobacterium*-mediated transfer. The process of genetic transformation accomplishes the same objectives as plant breeding, i.e. transfer of one or a few genes from one organism to another. Genetic engineering techniques are more precise and not limited by sexual compatibility between the donor and recipient variety.

DNA marker technology: Differences in the genomic DNA between potential parents in a genetic cross can be detected by studying variations in the nucleotide sequence polymorphisms. There are several molecular tools, such as restriction fragment length polymorphism (RFLP), simple sequence repeats (SSR) and amplified length polymorphism (AFLP) markers, for detecting such variations. Polymorphism can be used in genetic analysis because at a given allelic locus the markers show mendelian inheritance. This characteristic makes it possible to estimate the genetic distance between each polymorphism and construct genetic maps based on DNA markers.

Progress has been made in tagging and mapping many agriculturally important genes with molecular markers (Mackill and Ni, 2001) which form the basis for marker assisted selection (MAS). DNA markers have enhanced the scope for improving the efficiency of conventional plant breeding through indirect selection for the trait of interest linked to the marker. Of the various molecular markers developed, RFLPs are the most reliable as they are numerous and codominant and distributed all over the genome complement. With the aid of RFLPs, each gene (trait) can be linked to one or more markers, and by following the segregating pattern of the trait and markers in crosses, it is possible to tag the gene(s). Tagging facilitates indirect but precise selection for the gene of interest. Using RFLP markers, genetic maps have been constructed and rice is the most extensively analysed crop species. The availability of comprehensive molecular genetic maps in rice has facilitated tagging of many genes of economic importance with DNA markers. DNA markers have several potential applications in rice improvement. These include germplasm characterization, assessment of genetic diversity, tracking the gene through segregating generation and marker assisted selection (MAS). Pyramiding of genes conferring the same phenotype is important, as gene transfer by MAS is precise and fast, especially when the trait is difficult to select on the basis of phenotype. Similarly, when a number of genes governing the expression of same phenotype-like resistance to a disease or an insect pest are to be pooled, pyramiding is facilitated by the use of markers.

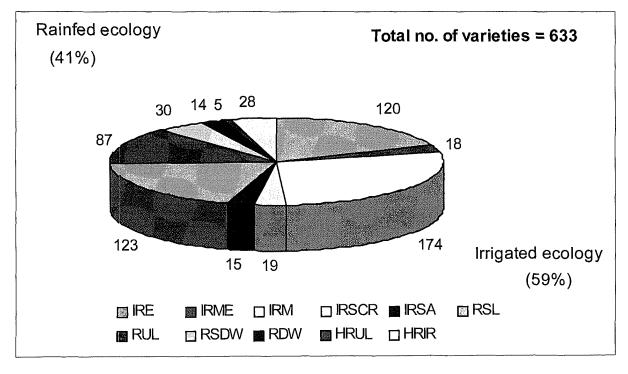
RICE VARIETIES DEVELOPED

The "post-Jaya" period of varietal development in India may broadly be grouped into four phases:

- breeding for yield improvement with different maturity periods and varied grain quality;
- aggressive breeding for resistance to pests and diseases;
- breeding for high-yielding varieties adapted to diverse rainfed ecologies;
 and
- the development and use of hybrid rice technology.

During the last three decades, 633 rice varieties have been developed and released for commercial cultivation by the central and state variety release committees for diverse ecologies (Fig. 3). These varieties have been developed as follows: 374 (59%) for the irrigated ecosystem under early (120, 19%), medium (174, 27.5%) and mid-early (18, 2.8%) duration groups; 15 (2.4%) for irrigated saline/alkaline soils; and 19 (3%) for the Basmati region with aromatic and quality grains. Besides these inbred varieties, 16 rice hybrids have been released mainly for the irrigated system. For rainfed shallowlands 123 (19.4%) varieties have been developed, 87 (13.7%) for rainfed uplands, 30 (4.7%) for rainfed semi-deepwater and 14 (2.2%) for rainfed deepwater. Under

FIGURE 3
Rice varieties released during 1970-2000 in India for different ecosystems



hill ecology, 28 (4.4%) varieties for irrigated areas and 5 (0.8%) for rainfed uplands have been released. Collectively, these high-yielding varieties now occupy over 77 percent of the rice area in the country.

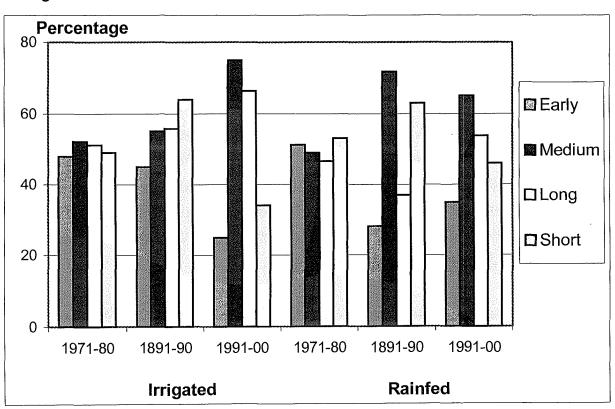
Breeding for yield enhancement

Intersubspecific hybridization: As mentioned earlier, ADT 27 (developed in India) and Mahsuri (Malaysia) became popular in India, thus limiting the adoption of *indica-japonica* hybridization as a breeding strategy to increase the genetic yield level of tropical rices which began in the early 1950s as part of the massive FAO-sponsored programme. The relatively non-lodging habit of *japonica* varieties under higher fertilizer management led to high yields. It seemed that varieties adapted to mild temperate conditions would be more compatible than those adapted to the extremely cold temperate zone. This was proved so when tropical *japonica* varieties from Taiwan - Taichung 65 (introduced in Karnatake), Tainan 3 (Kerala), and Kaohesing 18 and Herunchu (Uttar Pradesh) - were a great success in terms of productivity, although their adoption could not be sustained on account of their poor consumer quality.

Semi-dwarf varieties: The development of short-statured varieties from the spontaneous dwarf mutant Dee-Geo-Woo-Gen (DGWG) with sdl gene is a landmark in the history of rice breeding. Rutger and Mackill (2001) are of the opinion that sd1 gene of rice and Rht gene of wheat are the cornerstone of the Green Revolution. The semi-dwarf varieties are characterized by: non-lodging ability, which results in good response to higher rates of fertilizer in the form of productive growth; photo-insensitivity, which helps breeders select for different growth periods; upright foliage and high leaf area index with delayed senescence enabling good utilization of solar energy; and desired partitioning ability of dry matter resulting in higher harvest index. From the breeder's point of view, the use of DGWG as a source for yield improvement has unique advantages, for example: inheritance of dwarf stature as a simple monogenic recessive trait and facilitated fixation of the plant types. Taichung Native 1 (TN 1), a product from the cross between DGWG and Sai-Yuan-Chung, was released in 1949-1950 and was the first dwarf variety. However, it was IR 8 (developed at IRRI) that heralded the Green Revolution in tropical Asia.

Using largely IR 8, TN 1 and Jaya as the donors for dwarf stature and high yield potential, and several local selected varieties with adaptability and quality traits (Table 4), 633 rice varieties (including 17 released prior to 1970) were developed and released for commercial cultivation by the central and state variety release committees (Appendix 2, Fig. 3). While yield gain was the primary objective in this phase, other goals included the development of short-duration varieties for irrigated areas (enabling farmers to take 2-3 rice crops a year) and rainfed uplands, as well as grain quality. This is evident from the fact that 66 percent of varieties released for irrigated ecology during the period 1991-2000 have long grains compared to 51 percent of the varieties released during 1971-1980 (Fig. 4). Rainfed ecology revealed a similar trend. However, 75 percent of varieties for irrigated area released in the last decade had medium maturity duration, compared to 52 percent for the period 1971-1980. At the outset, genetic uniformity rather than diversity is seen among these semi-dwarf

FIGURE 4
Trend in growth period and grain type among the rice varieties developed in India during the last three decades



rice varieties. Extensive use of *sd1* gene from DGWG source has been a universal phenomenon in rice breeding (Rutger and Mackill, 2001). However, extensive use of varied landraces and improved local varieties has been the strength of rice improvement in India.

New Plant Type: By the early 1990s, it was evident that yield gains through semi-dwarf varieties were plateauing. However, a marginal advantage was posted through the reduction in maturity duration, thereby increasing per day productivity. Breeders are again on the look out for new grounds to break the genetic yield barrier. Plant architecture is being redesigned with a more efficient morphophysiological frame to achieve the next quantum jump in yield. Early attempts to find exploitable variability for physiological components that directly or indirectly contribute to yield were not successful. On the basis of experience and experimental findings, breeders and geneticists believe that the genetic yield level of rice could be further raised by 20 to 25 percent through enhancement of biomass from the present level of 20 t/ha without altering the harvest index. Similar efforts in India at the Indian Agricultural Research Institute (IARI) led to a new plant type capable of breaching yield levels of IR 8 or Jaya. However, no variety has so far been released for commercial cultivation.

Breeding for cooking and nutritive quality

The cooking quality of rice is determined by the physicochemical properties of starch, while the nutritive quality depends on the content and quality of proteins, vitamins and minerals. Nutritive quality is as important as cooking quality for tropical countries, where it is the primary source of dietary protein, vitamins (B10) and minerals. Rice accounts for 40 percent of the average protein consumption in Asia. Except for a few characters, such as aroma, nearly all the indices of quality follow complex polygenic inheritance, making breeding and selection very difficult for evolving varieties.

Varieties of Basmati quality: Ever since the introduction of high-yielding varieties, there has been research to combine Basmati quality into the high-yielding background. Although these efforts led to the release of 23 high-yielding and improved tall traditional Basmati varieties, none gained the acceptance of

either farmer or consumer. Since the 1990s, there has been a concerted effort to breed for quality rice using a network system involving different institutions. This has led to the development of 11 Basmati rice varieties (Pusa Basmati 1, Kasturi, Haryana Basmati 1, Ranbir Basmati, Taroari Basmati, Basmati 385, Basmati 386, Yamini, Vasumati, Pusa Sugandh 2 and Pusa Sugandh 3) after extensive quality testing for the entire range of physicochemical characteristics.

Of the different quality characters of Basmati rice, it is the amylose content of the grain that determines the relative stickiness or dryness of cooked rice. The highly prized Basmati rices have amylose content of around 22 percent. Varieties with high amylose content (> 25%) cook dry and flaky, while those with low amylose content (< 15%) are sticky. The majority of the popular varieties the world over have intermediate amylose content ($\approx 23\%$). Gelatinization temperature (alkali digestion score) determines the resistance to cooking. The soft cooking *japonica* rices have a low gelatinization temperature (GT), while relatively hard cooking indica varieties have high GT. Gel consistency is another important cooking quality index which determines how long cooked rice remains soft. Varieties of medium and low gel consistency (largely associated with medium and low amylose) and medium to low GT are generally preferred, as they remain soft long after cooking. High volume increase and optimum water uptake are other desirable features. Aroma (determined by 2 Acetyl 1-pyrolline) and extra kernel elongation (approximately twice uncooked length) with minimal swelling are the key characteristics qualifying Basmati quality. From the trader's point of view, the percentage of milling out-turn (rice obtainable per unit quantity of paddy milled), head rice recovery (percentage of unbrokens) and colour are important factors. Table 5 lists the quality characteristics of some of the traditional and recently released Basmati varieties.

Development of Basmati hybrids: Pusa RH 10, the world's first hybrid rice with superfine grain and the cooking qualities of aromatic rice, was developed and released recently for cultivation under an ICAR (Indian Council for Agricultural Research)/UNDP/FAO-sponsored project on the development and use of hybrid rice technology. It has a 40 percent yield advantage over Pusa Basmati 1. Being 15 to 20 days early, it escapes infestation by major pests and diseases. It is recommended for areas in the states of Haryana, New Delhi and Uttaranchal.

TABLE 5 Yield, agronomic and grain quality characteristics of traditional and improved Basmati rice varieties developed in India

						Variety			
		Karnal	Pakistani	Basmati	Vasumati	Yamini	Pusa	Pusa	Taroari
S. no	S. no. Character	Local	Basmati	370	(IET 15391)	(IET 14720)	Sugandh 2	Sugandh 3	Basmati
4 ~	Grain yield (t/ha)	2.13	2.12	2.23	3.73	3.27	3.74	375	2.12
7	Plant height (cm)	178	180	165	103	118	102	100	48
က	Duration (days)	155	155	145	135	150	125	131	120
4	Tillers/m ²	285	286	277	327	364	340	350	237
2	Grains/panicle	138	139	140	108	125	124	106	61
9	Lodging score	တ	တ	တ	თ	က	က	က	တ
7	Milling (%)	99	65	62.9	69.7	64.8	64.63	69	61.1
∞	Head rice (%)	38	40	46.2	55.3	58.7	45.9	49.63	49.6
თ	Kernel length								
	. Raw	7.07	7.3	6.93	7.23	7.12	7.66	99.7	7.05
	. Cooked	14.25	14	12.8	13.5	13.1	13.4	13.6	13
10	Elongation ratio	2.01	1.92	1.85	1.86	1.84	1.74	1.77	1.84
1	Alkali spreading value	5.4	4.7	6.2	4.2	4.7	7.7	7	6.2
12	Amylose content	23.21	23.4	22.1	25.1	23.8	22.43	24.39	28.8
13	Aroma	Strong	Strong	Strong	Strong	Strong	Strong	Strong	Strong

Non-Basmati rices: Non-Basmati quality rice has also become a major thrust item for export promotion and foreign exchange earning. Non-Basmati rice of *indica* type constitutes over 80 percent of the world rice trade. Varieties, such as Prakash, PR 106, Kavya, Kamini, White Ponni, Krishna Hamsa, Sona Mahsuri, Ranjit, Krishna Veni, White Ponni, IR 64 and Samba Mashuri, were identified as exportable non-Basmati rices.

Breeding for pest resistance

The second phase of breeding followed the observation that the yield potential of the new high-yielding varieties (HYV) could often not be realized due to severe biotic constraints (diseases and insect pests). In fact, the pest scenario changed rapidly following the widespread adoption of HYVs. The application of high doses of nitrogenous fertilizers leading to luxuriant vegetative growth with closed leaf canopy changed the micro-environment in favour of pest buildup. The introduction of short-duration varieties and the consequent rice-rice production throughout the year facilitated the survival and carry-over of pest populations from one season to the next. During the period 1965 to 1995, the number of insects classified as "major pests" rose from three to thirteen and the number of serious diseases rose from two to eight (Reddy and Bentur, 2000). The Green Revolution pest, brown planthopper (BPH), even threatened rice production in several Southeast Asian countries during the late 1970s and 1980s. As for diseases, besides the age-old problem of blast and brown spot, several viral (rice tungro virus, grassy stunt virus, ragged stunt virus etc.) and bacterial (bacterial leaf blight and bacterial leaf streak), as well as a few fungal (sheath blight and sheath rot) diseases came to prominence. Strain variation established in bacterial leaf blight (BLB) and grassy stunt virus (GSV), in addition to the known races of blast pathogen, made disease management increasingly difficult. Biotypic variation in gall midge and BPH also increased the insect pest problems. The second phase of rice development focused on breeding for disease and insect resistance.

Resistance to diseases

In the case of blast, resistance is required: during the seedling and vegetative phases against leaf blast; and in the reproductive phase against neck blast. High

correlation between resistance to leaf and neck blasts, however, suggests that they may be governed by the same gene(s). Breeding for blast resistance in India dates back to the 1920s when resistance donor sources, such as CO4, TKM9 and GEB24, were used (Manibhushanrao, 1994) leading to the development of improved varieties, such as CO25, CO26 and Ratna. However, by the late 1930s these donors were reported to be susceptible. Subsequently, other cultivars, such as Tetep, Tadukan, Zenith, BJ1, CR905 and CR906, showed promise against the disease. Several popular rice varieties cultivated have blast resistance (Table 6). However, the population of the causative pathogen, *Pyricularia grisea*, adapts to resistant varieties and resistance breaks down

TABLE 6
Popular rice varieties resistant to blast

S. no.	Variety	Parentage	Source of resistance	Year of release	50% flowering duration	Ecology	Grain type
1	IR 20	IR 262-24-3 /TKM 6		1970	105	IRM	
2	IR 36	IR 1561-228-1-2/IR 1737//CR 94-13		1981	84	IRE	LS
3	IR 64	IR 5657-33-2-1/IR 2061-465-1-5-5		1992	84	IRE	LS
4	IR 8	Peta/Dee-Geo-Woo- Gen		1966	105	IRM	LB
5	Pantdhan 10	IR 32/Mahsuri//IR 28		1992	90	IRM	LS
6	Pinakini	Bulk H 9/Millek Kuening		1987	130	RSL	MS
7	Rasi	TN1/Co.29		1977	84	IRE	MS
8	Swarnadhan	RPW 6-13/Sona		1979	125	RSL	SB
9	Tikkana	RP 31-49-2/BCP 2		1988	120	RSL	SB
10	VL Dhan 221	IR 2053-521-1-1- 1/CH 1039		1991	85	HRUR	MS
11	VLK Dhan 39 (K39-96-31- 1-1-9)	China 1039/IR 580- 19-2-3-1		1980	85	HRIR	MS
12	Rasmi	Oorapandy mutant		1986	120	RSL	SB
13	Himadhan	R 575/TN 1		1978	105	HRIR	SB
14	Himalaya 1	IR 8/Tadukan	Tadukan	1982	95	HRIR	LB
15	Himalaya 2 (Pusa 33-C- 30)	Imp. Sabarmati/Ratna		1982	95	HRIR	LS

rapidly. For example, rice varieties NLR 9672, Intan and Tellahamsa are no longer effective against the local races of the pathogen.

Earlier studies on the genetics of blast resistance in India by Padmanabhan and associates pointed to the presence of dominant genes in Zenith, Tetep and Tadukan (Manibhushanrao, 1994). They also suggested combining a high degree of resistance to hyphal penetration (polygenic trait) with resistance to the spread of the disease inside the tissue (conferred by major genes) for effective resistance against blast. Studies carried out elsewhere identified over 16 resistance genes. The racial spectrum of the pathogen varied from region to region, as revealed in studies using the molecular approach and covering several blast isolates from south India (Sivaraj et al., 1996) and from the Himalayan region (Kumar et al., 1996). While 29 distinct clonal lineages were identified from the former collection, 46 lineages were found in the latter. As many as 14 pathotypes were recognized in the south Indian collection based on the reaction against a set of national and international differentials. These pathotypes were grouped into four race groups: IA, IB, IC and ID. This study revealed a partial relationship between virulence and phylogeny. Recent field monitoring of virulence has shown a broad range of resistance in varieties, such as Tadukan, Tetep and IR 64 (DRR, 2001). Six varieties (Archana, Deepa, Bhagya, Himalaya 1, Rajendradhan 201 and IR 22) derived from Tadukan, one from Tetep (Swarnamukhi) and one from IR 64 (Cottondora sannalu) have been released for cultivation.

In the case of bacterial leaf blight (BLB) caused by *Xanthomonas oryzae* pv. *oryzae*, as many as 77 of the released rice varieties have been claimed to possess some degree of resistance. As for blast, variability in the pathogen population has been the main obstacle to the development of resistant varieties. HKR 120 possessing *Xa4* gene was the first variety released in 1987 in Haryana for the pest endemic area (Panwar *et al.*, 1989). Ajaya, developed from the cross IET 4141 and CR 98-7216, was released during 1992. On the basis of the genetics study in Punjab using the local isolate of the pathogen, it is suggested that Ajaya (IET 8585) has two dominant genes conferring resistance (Saini *et al.*, 1996). Thus, Ajaya appears to be a naturally bred gene pyramid with a wide range of resistance across test locations (DRR, 2001). Following BLB epidemics in Punjab during 1980, concerted efforts were made to incorporate

resistance into local popular rice varieties (e.g. PR 106) by incorporating disease resistance from different sources, such as Patong 32 (in PR 110, PR 114, PR 116), IR 54 (PR 111) and RP 2151-sister selections of Ajaya (PR 113, PR115), in addition to the direct introduction (PR 4141). Of these, PR 116 now occupies a quarter of the rice area in the state.

While more than 20 genes conferring BLB resistance have been characterized mainly on the basis of genetic studies carried out in countries such as Japan and the Philippines, the availability of Near Isogenic Lines carrying each of these genes has helped to establish the allelic relationship of the resistance genes identified in Indian cultivars (Goel and Singh, 1999). Field monitoring of virulence among pathogen populations on test locations suggested a prevalence of pathotype Ia at Titabar, Ib at Ludhiana and of pathotype II at Faizabad (DRR, 2001). A subpopulation of the pathogen in Kerala is reported to have overcome the resistance conferred by *Xa21* gene – introgressed from wild rice, *O. longistaminata*, and known to confer a wide range of resistance across races of India and the Philippines.

In view of the frequent breakdown of blast and BLB resistance, various gene deployment strategies are proposed to effectively manage/contain the disease. Sequential release of R genes is the widely employed strategy. Varietal mosaic – i.e. planting varieties carrying diversely different resistance genes – is another approach. With the development of markers for 16 blast and 8 BLB resistance genes (Mackill and Ni, 2001), the development of gene pyramids appears to be a more feasible and effective strategy. For example, two-gene pyramids with Pil + Pi4, Pil + Pi2 and Pi2 + Pi4 gene combinations were susceptible to the disease at Titabar and Hazaribagh, while a three-gene pyramid with Pil + Pi2 + Pi4 was resistant on all 19 test sites (Kumar *et al.*, 1999). On the contrary, a two-gene pyramid with Pil + Pi2 genes has shown consistent resistance on test sites in Kerala (Gnanamanickam *et al.*, 1999). A molecular breeding approach for combined resistance to both blast and BLB is being followed (Babujee *et al.*, 2000).

The first rice tungro-resistant variety, Vikramarya, was developed from the cross between Vikram and Ptb 2 and released for cultivation during 1986. It possesses resistance to both the vector and the virus. Another variety, Nidhi, developed from the cross Sona/IET 14529, also has resistance to tungro disease.

Resistance to insect pests

Significant impact has been made in the development and adoption of insectresistant rice varieties. Though breeding for resistance to rice gall midge (GM), Orseolia oryzae, was initiated in the 1950s, the first high-yielding resistant variety Kakatiya was not released until 1974, since when over 50 GM-resistant rice varieties have been released. The prevalence of three distinct biotypes prior to 1988 (Kalode and Bentur, 1989) and subsequent reports of the evolution of three more virulent biotypes in response to the widespread cultivation of resistant varieties hindered the task of resistance breeding. The virulence pattern and distribution of gall midge biotypes in India is provided in Table 7. While over 250 primary sources of GM resistance have been identified through greenhouse and field evaluation of germplasm, genetic studies covering some of these donors have characterized at least 11 distinct genes. As a result, 88 percent of released resistant varieties are derivatives of three-gene sources only (Fig. 5). Breeding for GM resistance at Warangal in Andhra Pradesh and Raipur in Madhya Pradesh has mainly used resistance sources containing Gm1 gene, while at DRR Gm2 gene sources (e.g. Siam 29) have been extensively used. Varieties released for cultivation by the latter programme include Phalguna, Vikram and Surekha.

TABLE 7
Virulence pattern and distribution of rice gall midge biotypes in India

Biotype	Biotype Reaction against differential group ^a		Distribution		
	1	2	3	4	
1	R	R	R	S	Andhra Pradesh (Hyderabad), Madhya Pradesh (Raipur), Orissa (Sambalpur)
2	S	R	R	S	Orissa (Cuttack)
3	R	\$	R	S	Andhra Pradesh (Jagtiyal), Bihar (Ranchi)
4	S	S	R	S	Andhra Pradesh (Srikakulam), Maharastra (Sakoli)
5	R	R	S	S	Kerala (Moncompu)
6	R	S	S	S	Manipur (Wangbal)

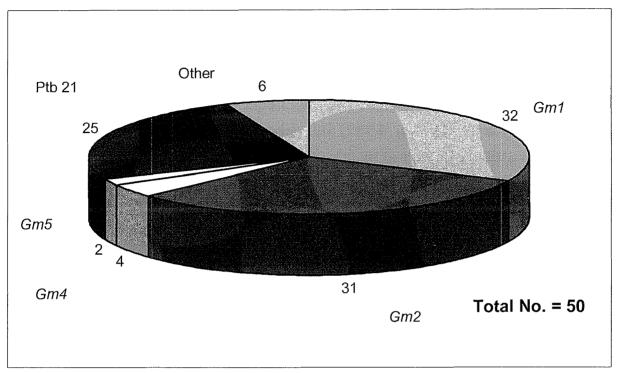
^a Group 1 with differentials W1263 (having gene *Gm1*) and ARC 6605 (to be confirmed).

Group 2 with Phalguna (Gm2) and ARC 5984 (Gm5).

Group 3 with Abhaya (Gm4), RP 2068-18-5 (Gm3) and others.

Group 4 with susceptible check TN 1.





Phalguna proved very popular, covering over 80 percent of the rice area in the pest endemic regions of Andhra Pradesh and Maharastra. This extensive cultivation was probably responsible for: the 1986 epidemics of the new virulent GM biotype 4 in the northeastern coastal region of Andhra Pradesh; the 1989 epidemics in the Vidarbha region of Maharastra; and the evolution of biotype 3 in the Karimnagar region of Andhra Pradesh in 1993. Subsequently, new sources of resistance, such as Ptb 21 (leading to the development of Suraksha), Velluthacheera and CR309, have been used in the local breeding programme. A similar epidemic in the Kattanad area of Kerala State in 1993 (the population was later identified as biotype 5) rendered all the earlier varieties susceptible. A re-oriented breeding programme using *Gm1* and *Gm2* gene sources led to the development of Panchami and Pavithra, respectively. The development of specific gene markers (Mackill and Ni, 2001) is now paving the way for the adoption of the gene pyramiding strategy through marker aided selection.

Extensive damage by BPH during the late 1970s triggered an active breeding programme aimed at planthopper resistance. Efforts at DRR led to the release

of Mansarovar in 1983, with resistance derived from the donor source Leb Mue Nahng. Of the various breeding lines field-evaluated in Kerala, M11-57-5-1 (from IR 8 and Ptb 20) withstood the severe BPH outbreak during 1975-77. This culture was later released as the BPH-resistant variety Bhadra (Joseph *et al.*, 1990). To date, about 23 resistant varieties have been released with diverse genetic sources of resistance, including Manoharsali, ARC 6650 and ARC 5984, and some of these varieties are also resistant to white-backed planthopper (WBPH) (Table 8). While four varieties each have been developed from Manoharsali and ARC 6650, it is not certain whether or not these two donors carry the same gene. Although the presence of a more virulent biotype of BPH in northern India was suspected during the 1980s, subsequent monitoring of virulence did not confirm these observations. However, the introduction of

TABLE 8
Rice varieties with resistance against BPH

S. no.	Name	Donor	Gene/nature
1	Chaitanya ^a	ARC 5984	bph4/wbph4
2	Cottondora Sannalu ^a	ARC 5984	bph4/wbph5
3	Deepti	ARC 6650	bph3
4	Vajram	ARC 6650	bph3
5	Pratibha	ARC 6650	bph3
6	Triguna ^a	ARC 6650	bph3
7	Suraksha ^a	CR 57 (Ptb 18, Ptb 21)	2 recessive
8	Neela	CR 94 (Ptb 21)	2 recessive
9	Manasarovar	Leb Muey Nahng	Single recessive
10	Nagarjuna	Manoharsali	Single dominant
11	IET 7575	Manoharsali	Single dominant
12	Sonatali	Manoharsali	Single dominant
13	Ch'andana	Manoharsali	Single dominant
14	Aruna	PTB 33	3 complimentary/bph3
15	Kanakam	PTB 33	3 complimentary/bph3
16	8116°	Andrewsali	3 complimentary
17	Bhadra (MO 4)	Ptb 20	?
18	Asha (MO 5)	Kochuvithu	?
19	Pavizham (MO 6)	Karivennel	? ?
20	Kartika (MÒ 7)	Triveni	
21	Radhi	Swarnaprabha Mutant	?
22	Vijetha ^a	MTU 5249/MTU 7014	?
23	ADT 42°	AD 9246/ADT 29	?

^a Also resistant to WBPH.

varieties with resistance to BPH alone resulted in an outbreak of WBPH in some parts of the country, which meant that varieties had to be developed with resistance against both BPH and WBPH. Rice varieties now available have this combination. While genetic studies reveal a wide genetic diversity in sources of resistance, fewer than a dozen sources of resistance have been used in breeding planthopper-resistant varieties. Furthermore, wild rice accessions have been an additional source of BPH resistance (Jena *et al.*, 2000).

Given that single pest-specific resistance does little to reduce crop losses in multi-pest-prone rice-growing areas, the emphasis of breeding strategies has shifted from specific to multiple resistance over the last two decades and many of the varieties under cultivation today are resistant to more than one pest or biotype (Table 9).

Breeding for tolerance to abiotic stresses

Rainfed rice – accounting for about 50 percent of rice area with varied moisture regimes (uplands, lowlands and deepwater), injurious soils (due to acidity/alkalinity and salinity across ecologies) and subject to extreme temperatures – is generally grown in the less favourable environments. Each of these environments is complex in nature and is characterized by more than one constraint. Upland problems are: moisture stress, impoverished soil, weed infestation and P deficiency, while lowland problems are: continuous anoxic conditions due to stagnant flood water, submergence, intermittent drought and low light. In the coastal areas and irrigation commands, on the other hand,

TABLE 9
Rice varieties possessing multiple pest resistance

Variety	Resistance
IR 36, Rasi	Blast, brown spot
Vikramarya	Blast, RTV
Swarnadhan, Pankaj, Radha	Blast, sheath blight
CNM 539	Blast, brown spot and RTV
Suraksha, Shaktiman	GM, BPH, WBPH, blast
Lalat	GM, BPH, GLH
Rasmi	GM, BPH
Daya, Smalei	GM, BPH, GLH
Kshira	GM, BPH, WBPH, GLH, RTV

salinity and sodicity are the constraints, while low temperature is the problem in high altitude areas.

Finding a varietal solution to such harsh environments is quite challenging. Rice improvement in the third phase concentrated on breeding for abiotic stresses. As a short-term approach, the pure line selection method was adopted, involving native varieties well adapted to a given stress environment. Thanks to the availability of diverse genetic sources and an understanding of the genetic basis of tolerance to specific stresses, together with national and international collaborative efforts, more targeted breeding was initiated as a long-term strategy. The breeding efforts for tolerance to salinity, drought and submergence are briefly presented below.

Salinity tolerance

Salt stress is a major yield-destabilizing factor in coastal areas and irrigation commands. Unlike coastal salinity, which remains almost static in terms of area, inland salinity is on the increase due to poor water management in canalirrigated areas. Salt stress in coastal areas is not the same as in irrigation commands and waterlogged lowlands. The former is saline, due largely to chloride and sodium sulphate, while the latter is alkaline (sodic). The composition and level of severity vary, depending on the salts involved and their proportions. Tolerance in plants to salinity is growth-stage specific. Recent breeding efforts for salt tolerance have been very encouraging; indeed, over 30 rice varieties with varying levels of tolerance to salinity and alkalinity have been developed (Table 10) (Mishra, 1999). The screening methodology has been improved to detect salt tolerance at the reproductive stage, while the selection criteria and breeding methodology have been standardized. A wide spectrum of rice germplasm (both indigenous and exotic) have been evaluated for salt tolerance and suitable donors have been identified. Basic studies indicate no significant correlation between the score of salinity tolerance during vegetative stage and reproductive stage and/or grain yield. K+ content exhibited strong positive correlation with grain yield while the ratio of Na+/K+ revealed significant negative correlation with grain yield. Genetic studies suggested both additive and non-additive gene effects for salt tolerance. Studies under controlled conditions in lysimeters further confirmed the involvement of a few major genes

TABLE 10
Rice varieties with salt tolerance

S. no. Variety		Parentage	Stress adaptation	
			pH	ECe (dSm ⁻¹)
1	CSR1 (Damodar)	Local selection of Sunderban area	9.8-10.4	6.11
2	CSR2 (Dasal)	Local selection of Sunderban area	9.8-10.4	6.11
3	CSR3 (Getu)	Local selection of Sunderban area	9.8-10.4	6.11
4	CSR5	TKM6/IR 8	9.0-9.5	<6.0
5	CSR8	CSR1 mutant	9.0-9.6	<7.0
6	CSR9	CSR1/Basmati 370//CSR5	>9.7	<9.0
7	CSR10	M40-431-24-114/Jaya	9.8-10.2	6-11.0
8	CSR11	M40-431-24-114/Basmati 370	9.8-10.2	6-11.0
9	CSR12	CSR1/Basmati 370//CSR5	9.2-9.8	<9.0
10	CSR13	CSR1/Basmati 370//CSR5	9.2-10	<9.0
11	CSR14	Milyang 23/Milang 30	9.2-9.8	<8
12	CSR15	Sipi 661044/Sipi 651202	9.2-9.8	<8
13	CSR16	CSR1 mutant	9.2-9.8	<8
14	CSR17	IR19661-131-1-2/IR9129-209-2-2-2-1	9.2-9.8	<8
15	CSR18	RPA 5829/CSR5	9.2-9.8	<8
16	CSR19	CSR1/Basmati 370//CSR5	9.2-9.8	<8
17	CSR20	CSR5/Palaman 579	9.2-9.8	<8
18	CSR21	IR 5657-33-2/IR 4630-22-2-5-1-3	9.8-10	<9
19	CSR22	IR 64//IR4630-22-2-5-1-3/IR 9764-45-2-2	9.6-9.9	<10
20	CSR23	IR 64//IR 4630-22-2-5-1-3/IR 9764-45-2-2	9.8-10	<10
21	CSR24	IR 8/Chettivirippu	9.6-9.9	<10
22	CSR25	IR 17494-32-3-1-1-3/IR 4432-52-6-4	9.8-10	<10
23	CSR26	Nona Bokra/IR5657-33-2	9.8-10	<9
24	CSR27	Nona Bokra/IR5657-33-2	9.8-9.9	<10
25 .	CSR28	IR 42/IR 4630-22-2-5-1-3	9.8-9.9	<9
26	CSR29	IR 14632-22-3/IR 19799-17-3-1-1	>10	6-10.0
27	CSR30	BR4-10/Pakistan Basmati	>9.7	6.7
28	Panvel 1	IR 8/ BR4-10	NA	NA
29	Panvel 2	BR4-10/IR 8	NA	NA
30	Panvel 3	Damodar/Pankaj	NA	NA
31	Vyttila 1	Selection from Pokkali	NA	NA
32	Vyttila 2	Selection from Chettivirippu	NA	NA
33	Vyttila 3	Vytilla 1/TN1	NA	NA
34	Vyttila 4	-	NA	NA
35	Karishma	MO1/MO6	NA	NA
36	Uma	MO6/Pokkali	NA	NA

along with numerous minor genes for salinity tolerance, but there was a lack of maternal influence (Mishra et al., 1998).

Tolerance to NaCl salinity in the majority of donor sources is due to the relatively high retention of Na and Cl in roots compared to shoots. In salt-

tolerant SR26B and PVRI, the regulation of accumulation of Na and K during tillering appeared to be the physiological basis of tolerance (Balasubramanian and Rao, 1977). In the salt-tolerant variety, Pokkali, tolerance is partly due to the compartmentation of Na in leafsheath sparing the leaf blades, while the mitigation of high Na content in shoots is due to the faster growth rate. In tolerant sources (e.g. Taipei 309), tolerance appears to be through higher tissue tolerance of Na content in the shoot due to either osmotic adjustment or compartmentation. By and large, a plant's ability to regulate either Na uptake or selective accumulation of K, the translocation of salts from root to shoot and the ionic balance (ratio of Na to macro-/micronutrients) – rather than just absorbed Na content – determine the level of tolerance (Siddiq *et al.*, 1999).

Initial breeding attempts at the Central Soil Salinity Research Institute, Karnal, involved pure line selections from the local traditional cultivars collected in the Sunderban region of West Bengal leading to the development of Damodar (CSR1), Dasal (CSR2) and Getu (CSR3). Varieties adapted to salinity stress were later identified as also possessing sodic tolerance. A later stage of the hybridization programme involved CSR1 as a promising source of tolerance. This led to the release of as many as 24 varieties that not only are tolerant to salt and sodic stress but also possess quality features. Through the shuttle breeding programme under the ICAR-IRRI collaborative project, more than a dozen promising breeding lines have been identified and they are undergoing advanced field testing. Furthermore, anther culture derivative lines generated at IRRI led to the identification of additional salt-tolerant rice varieties, such as CSR 21 and CSR 28 (Singh and Mishra, 1995). Nona Bokra, Damodar (West Bengal), BR 4-10 (Bangladesh), Chettiviruppu (MO1) and Pokkali (Kerala) have also been extensively used in breeding for salt stress in other parts of the country, leading to the release of varieties, such as Panvel 1, Panvel 2 and Panvel 3 in Maharastra, and Vittyla 1, Vyttila 2, Vyttila 3, Vyttila 4, Uma and Karishma in Kerala. For the acid-saline soils (pH 3.5, ECe 4.5 dS/m) of coastal West Bengal, Thailand rice varieties, such as Khao Dawk Mali and RD 19, were found promising (Bandyopadhyay, 1986).

Drought tolerance

Moisture stress at any stage of crop growth causes significant yield reduction.

Escape, avoidance and tolerance are the three mechanisms by which rice copes with a drought environment. Upland varieties generally survive through either the escape mechanism (facilitated by early maturity) or the avoidance mechanism (by stress-induced root elongation to reach moisture zones). The tolerance mechanism operates by curtailing transpiration losses via leaf-rolling, early stomatal closure and cuticular resistance. Another important mechanism is rapid recovering ability, when moisture is replenished after a prolonged drought. Since most of the indices of stress resistance are independently inherited, there is good scope for recombining them through convergent breeding. The absence of leaf-rolling under drought has been used as an index of reduced drought sensitivity. A major dominant gene controlled leaf-rolling under drought stress in some of the varieties studied. While genetic variability for drought resistance at the reproductive stage is meagre, concerted efforts are needed to screen germplasm for reproductive-stage drought resistance, as it is directly related to productivity under drought.

The breeding programme for developing early-duration rice varieties with drought tolerance for the rainfed upland areas initiated at DRR in 1975 led to the identification of several superior cultivars (Prasada Rao, 1984). Of the 85 varieties released for this specific ecosystem, 42 (49.6%) have growth duration of 100 days or less. Of the varieties so far developed, Sattari has the shortest growth period of 70 days and has been dubbed "super fast rice". While the grain yields of these varieties are understandably low, they are nevertheless important for sustenance farming by poor farmers with small landholdings. Further yield improvement under this harsh ecology has been achieved with the utilization of local landraces, such as N22 (7 varieties developed), Fine gora (5), M63-83 (4), Black gora (1) and Brown gora (1), which are moderately drought tolerant. Of these donors, local "gora" landraces from Bihar are known for drought avoidance thanks to their good root system, while M63-83 has a rapid recovery mechanism and N22 escapes drought through early maturity. Some of the developed varieties and breeding lines, such as Rasi, Ratna, UPLR 5, IR 4575 and IR 6023-10-1-1, also have good recovering ability and have been used for yield improvement. Salt tolerance donors, such as Tadukan (2) and SR26 B (1), have also been used as sources of drought tolerance.

Submergence tolerance

Submergence is as serious and important a physical constraint as drought in rainfed lowland ecologies. Submergence tolerance is defined as the ability of rice crop to survive under complete submergence for as long as 10 days. Submergence due to flash floods or excessive rain causes inundation without effective drainage in low-lying areas and may occur at any stage of crop growth. The underlying mechanisms of tolerance to submergence are: i) an ability to survive without any growth under water until after drainage; and ii) escape from submergence by growing along with the rising water level and remaining above the flood waters by stem or leaf elongation. A set of morphophysiological traits confer submergence tolerance, for example, by building up or conserving carbohydrate reserves before or during flooding and or by maintaining physical structure during submergence and/or avoiding submergence by emerging above the water.

There is a lack of initiative for targeted breeding for submergence tolerance. Breeding efforts in Bihar prior to 1970 were pure line selections leading to the identification of improved varieties, such as BR 14, BR 15 and BR 46 (Saran, 1977). Of the 14 varieties subsequently identified for deep water and the 28 for semi-deep water, 9 and 8 varieties, respectively, are pure line selections. In the limited hybridization programme, Patnai 23 has been the most extensively used donor for submergence tolerance through stem elongation. Pankaj is another common donor well suited to poorly drained shallow-water lands.

Besides the above-listed abiotic stresses, varietal improvement has been attempted for several other constraints, such as P-, Zn- and iron-deficient soils, iron and aluminium toxic soils and low light intensity (Singh, 2000).

Development of hybrid rice technology

Though research efforts into hybrid rice in India were initiated during the 1970s, they were mostly of an academic nature. There was no coordinated, applied and result-oriented programme aimed at the development, evaluation and release of the hybrids, or at the development of seed production technology and technology transfer activities for the popularization of hybrids. Hence, in the project initiated in 1989, a national network approach was adopted, bringing together research institutions, public and private seed agencies and departments of agriculture of

the target states. International organizations were also involved for consultancy and training purposes. Effective linkages were established among the agencies and the project was implemented involving all the partners in a coordinated and mission mode approach.

The hybrid rice research network comprises 12 centres across the country in the target states, with the Directorate of Rice Research (DRR), Hyderabad the coordinating centre. Each centre in the network has a specific responsibility, for example, development of: the Basmati hybrid (New Delhi centre); hybrids for shallow lowland (Cuttack); long-duration hybrids for the coastal region (Maruteru); two-line hybrids (DRR, Hyderabad, Coimbatore, Pantnagar); or intersubspecific *indica* x tropical *japonica* hybrids (DRR, Hyderabad, Maruteru, Delhi, Kapurthala, Coimbatore and Pantnagar). Other centres are developing region-specific hybrids well adapted to their state/region. Hybrids developed by various centres and those nominated by the private seed sector and IRRI are pooled together and shared by all the centres and private seed companies for critical evaluation.

Development, evaluation and release of hybrids

The development of high-yielding hybrids is one of the project's main objectives. During the last 10 years, over 1 000 experimental hybrids developed by different network centres, IRRI and private sector seed companies have been evaluated in multilocation trials. To date, 16 hybrids showing consistent yield superiority over local inbred check varieties have been released for commercial cultivation in different regions by the respective state variety release committees (Table 11). Of these, three privately bred hybrids, namely PHB-71 (Pioneer Overseas Corporation) and 6201 and HRI 120 (Hybrid Rice International), have been released by the Central Variety Release Committee (CVRC), and another six to eight hybrids are being marketed by private seed companies. Pusa RH 10 is the first Basmati rice hybrid in the world which has been developed and released through the national network on hybrid rice. All these hybrids possess a mean grain yield of 6 to 8 t/ha with 15 to 20 percent yield superiority over corresponding high-yielding inbred check varieties.

Out of the 16 hybrids released so far, large-scale seed production of five hybrids, namely DRRH-1, KRH-2, Sahyadri, PHB-71 and PA 6201, has been

TABLE 11 Rice hybrids released in India

S. no.	S. no. Hybrid	Year of release	Duration (days)	Yield of hybrid (t/ha)	Yield of check (t/ha)	Yield adv. over check (%)	Released for the state of
- 0	APHR-1 APHR-2	1994 1994	130-135 120-125	7.14	5.27 (Chaitanya) 5.21 (Chaitanya)	35.4	Andhra Pradesh Andhra Pradesh
თ -	MGR-1 KPH-1	1994	110-115 120-125	6.08	5.23 (IR 50)	16.2	Tamil Nadu
γ 1	CNRH-3	1995	125-130	7.49	5.45 (Khitish)	37.4	Mest Bengal
9	DRRH-1	1996	125-130	7.3	5.50 (Teliahamsa)	32.7	Andhra Pradesh
7	KRH-2	1996	130-135	7.4	6.10 (Jaya)	21.3	Karnataka
o	Pant Sankar	1007	1111 100	o u	() (C) (C)	7	
o თ	CORH-2	1997	120-125	6.0 6.25	5.20 (ADT 39)	9.7 20.0	Ottar Pradesh Tamil Nadu
10	ADTRH-1	1998	115-120	7.1	4.90 (ASD-18)	44.9	Tamij Nadu
7	Sahyadri	1998	125-130	6.64	4.89 (Jaya)	35.8	Maharashtra
12	Narendra Sankar Dhan-2	1098	125_130	A 7.	4 94 (Sarion, 52)	7 VC	Har Dradoch
<u> 6</u>	PHB 71	1997	130-135	7.86	6.14 (PR 106)	28	Haryana, UP, TN
14	PA 6201 ^a	2000	125-130	6.18	5.03 (Jaya)	22.9	Eastern and some parts of
15	HRI 120 ^a	2001	105				southern India Southern, eastern, western
16	Pusa RH 10	2001	95				regions Haryana, Delhi, Uttranchal

^a Developed by the private sector.

PLATE 5 **Hybrid rice variety 6021**



PLATE 6
An upland rice variety in East Timor



taken up by public and private sector seed agencies. Hence, seed of the above-mentioned hybrids is available to the rice farmers for undertaking large-scale cultivation. At present, hybrid rice is reported to be grown on approximately 200 000 ha. The area under hybrid rice will further increase once heterotic hybrids suitable for the high productivity areas of Punjab, Haryana, the coastal region of Andhra Pradesh and shallow lowland areas have been identified and an effective transfer of technology programme has been initiated in the target states.

Genetic diversity in hybrid rice breeding

Use of genetically diverse material is the prerequisite for the success of heterosis breeding. At present, the Wild Abortive (WA) source of cytoplasmic male sterility is the widely used source for developing hybrids in many countries, including India. Such over-dependence on a single source may prove disastrous if it becomes vulnerable to any serious pest or disease (as with maize). Concerted efforts are therefore made to diversify the CMS source at DRR and CRRI. Six CMS lines have been developed in the background of *O. nivara* and *O. rufipogan* at DRR. Efforts are underway to identify restorers to these new CMS sources (DRR, 2001). Similarly, at CRRI, CMS lines in the background of Kalinga have been developed.

In order to widen the genetic basis of parental lines, specific breeding programmes involving cross breeding and male sterility-facilitated recurrent selection approaches were followed to improve the restorers and maintainers. Crosses between *indica* and tropical *japonica* were made and more than 2 500 diverse derivatives isolated. These diverse materials are now being utilized in hybrid rice breeding.

Quality considerations

Rice quality means different things to different people and it is region-specific. The best quality type in one region may not be liked at all in another region. Therefore, breeding for better quality hybrids depending upon the local requirement assumes added significance. The acceptance of hybrids by consumers is primarily determined by the cooking and eating quality characteristics. The price which the farmers get for their produce is also

determined by quality traits. The Chinese hybrids which were introduced earlier, besides being poorly adaptable to Indian conditions, had very poor grain quality. At present, hybrids are developed using the locally developed parental lines and those introduced from IRRI. All the released hybrids in India and the promising pre-released hybrids have moderate acceptable quality, but they cannot be compared with high quality varieties, such as Samba Mahsuri in Andhra Pradesh, White Ponni in Tamil Nadu and the Basmati varieties of northern India. Separate breeding programmes must be initiated to develop hybrids of very high quality.

Hybrids have been evaluated for quality characteristics. Some of the hybrids, namely ADTRH-1 and DRRH-1, possess good quality characters. With the availability of a large number of CMS lines and the pollen parents, it would be possible to develop hybrids with desired quality characters.

Resistance to major pests and diseases

For large-scale adoption of hybrid rice technology, the released hybrids should possess a fair degree of resistance to some of the major diseases/pests in the target areas, in addition to the distinct yield advantage over the existing varieties. Promising hybrids are, therefore, being regularly evaluated for resistance to major pests and diseases, both in glass houses and under field conditions. Promising hybrids and some parental lines with resistance to major pests and diseases have been identified

INTERNATIONAL COLLABORATION

Genetic diversity in rice germplasm is nature's gift to mankind. Were it not for the extensive international collaboration in identifying this diversity, preserving and sharing it, the benefits of the Green Revolution would not have spread globally. The role of International Rice Research Institute, and specifically its International Rice Testing Program (IRTP) initiated in 1975, is most commendable. India has been a major partner in this endeavour. So far, over 30 000 germplasm accessions and breeding lines have been tested in India under diverse environments. Of these lines, 3 500 have been contributed by India. More than 250 varieties (40% of the total) developed in India have derived benefit from the genetic potential of this shared material. Reciprocally, several

germplasm and breeding lines from India have been utilized in breeding programmes in many rice-growing countries across the continents. Table 12 lists 46 rice varieties of Indian origin adopted and released in over 27 countries.

POTENTIAL AND CONSTRAINTS

The large collection of rice germplasm maintained within the country is a rich source of genetic diversity yet to be fully characterized and utilized. A recent network project undertook the evaluation of about 16 000 accessions of germplasm against biotic stresses and identified several new sources of resistance (DRR, 2000). Detailed genetic studies must follow to characterize these sources and utilize them in the breeding programme for biotic stresses. A better understanding of pest-host interactions has helped to develop strategies for the development of durable resistance. Marker aided selection has been a reality in tracking and pyramiding genes in any desired combination. Recent advances in DNA markers and mapping of several quantitative trait loci (QTLs) has provided breeders with new tools while dealing with quantitative traits, such as tolerance for abiotic stresses. The genetic engineering approach has pulled down the taxonomic barrier for transferring genes of desirable traits. Thus there is great potential for enhanced utilization of genetic diversity for rice improvement in the years to come. However, with WTO conventions and Trade Related Intellectual Property Rights (TRIPS), genetic resources and tools to harness these are becoming ever less available for the public cause. Even the free exchange of germplasm among researchers is becoming a difficult proposition. While some of the toughest technical hurdles in harnessing genetic diversity have been overcome, we are entering a new era of socio-legal and environmental issues. A new order must evolve to ensure the equitable distribution of what mother nature has provided for the benefit of present and future generations.

A critical analysis of the parentage of released varieties in India indicates that the genetic base is narrowing and this is a matter of concern. Recent studies have shown that landraces and even wild species could contribute genes for yield enhancement. Rice breeders should make a concerted effort to utilize the genetic diversity in the development of varieties so as to achieve the expected outputs and maintain the natural balance.

TABLE 12
Rice varieties developed in India and released in other countries

Country where released	Designation	Year released	Ecosystem
Afghanistan	CR 44-11	1975	Irrigated
Afghanistan	Cauvery	1975	Upland
Afghanistan	Padma	1975	Irrigated
Benin	CO 38	-	Irrigated
Benin	RAU 4072-13	1991	Upland
Bhutan	Barkat (K 78-13)	1992	Irrigated
Brazil	Seshu	1984	Upland
Burkina Faso	Rp 4-2	1979	Irrigated
Burkina Faso	Vijaya	1997	Rainfed
Burkina Faso	RP 6-13 (Vikram)	1979	Irrigated
Burundi	CR 1009	-	Irrigated
Cambodia	OR 142-99	1992	Rainfed
Cameroon	Jaya	1977	Irrigated
Côte d' Ivoire	Jaya	-	Irrigated
Dominican Republic	IR 2153-276-1-10-PR 509	1986	Irrigated
Ghana .	RP 6-13 (Vikram)	1982	Irrigated
Iran	Sona	1982	Irrigated
Iraq	RP 2095-5-8-31	-	Rainfed
Kenya	Basmati 217	-	Irrigated
Kenya	AD 9246	-	Irrigated
Malawai	CR 156-5021-207 (Kitish)	1993	Irrigated
Mali	RPCB-28-849 (Rasi)	1984	Rainfed
Mali	Vijaya	1978	Irrigated
Mali	Jaya	-	Irrigated
Mauritiana	Jaya	-	Irrigated
Mynmar	Mahsuri mutant 3628	1977	Irrigated
Nepal	CR 123-23	1978	Upland
Nepal	RPCB-28-849 (Rasi)	1981	Upland
Nepal	IR 2298-PLPB-3-2-1-1B	1982	Irrigated
Nepal	IR 3941-4-PLP2B	1982	Irrigated
Nepal	K 39-96-1-1-1-2	-	Irrigated
P.R. China	M 114	1981	Irrigated
Pakistan	CR 156-5021-207 (Kitish)	1984	Irrigated
Paraguay	CR 156-5021-207 (Kitish)	1989	Irrigated
Paraguay	R 22-2-10-1	1989	Irrigated
Senegal	RPCB-28-849 (Rasi)	1981	Upland
Senegal	Jaya	-	Irrigated
Tanzania	BIET 360	1986	Irrigated
Tanzania	RPCB-28-849 (Rasi)	1984	Upland
Tanzania	RP 143-4	1984	Rainfed
Tanzania	L 5P23	-	Irrigated
Tanzania	Sabarmati BC 5/55	-	Rainfed
Togo	RPCB-28-849 (Rasi)	1978	Upland
Venezula	PR 106	1984	Irrigated
Viet Nam	Jaya	-	Irrigated
Zambia	RTN 500-5-1	<u>-</u>	Irrigated

REFERENCES

- Babujee, L., Venkateshan, B., Kavitha, S., Gnanamanickam, S.S., Leenakumari, S., McCouch, S.R. & Leong, S.A. 2000. Molecular breeding of rice for resistance to Magnaporthe grisea and Xanthomonas oryzae pv. oryzae in southern India. Abstracts, p. 85. Fourth International Rice Genetics Symposium, 22-27 Oct. 2000, IRRI, Manila, Philippines.
- **Balasubramanian**, V. & Rao, S. 1977. Physiological basis of salt tolerance in rice. *Il Riso*, 26: 291-294.
- **Bandyopadhyay, A.K.** 1986. Varieties screened for acid saline soils. *Intl Rice Res. Newsl.*, 11(6): 14.
- Brar, D.S. & Khsuh, G.S. 1997. Alien introgression in rice. *Plant Molecular Biology*, 35: 35-47.
- **DRR** (Directorate of Rice Research). 2000. Evaluation of rice germplasm for biotic stresses: Final report. Hyderabad, India, DRR. 341 pp.
- **DRR.** 2001. Annual report 2000-2001. Hyderabad, India, DDR. 107 pp.
- Gnanamanickam, S.S., Dayakar, B.V., Babujee, L., Leenakumari, S., Levy, M., Leong, S. & McCouch, S.R. 1999. Lineage exclusion resistance breeding and marker assisted selection for management of rice blast in India. Abstracts, General meeting of the International Program on Rice Biotechnology, 20-24 Sept., Phuket, Thailand. 80 pp.
- Goel, R.K. & Singh, O. 1999. Genetic basis of resistance against bacterial blight caused by *Xanthomonas oryzae* Ishiyama pv. *oryzae* (Swings *et al.*) in three breeding lines of rice (*Oryza sativa*). *J. of Genetics and Breeding*, 53: 87-91.
- Gupta, H.S., Bhuyan, R.N., Pattanayak, A. & Pandey, D.K. 1996. Development of cold-tolerant rice through anther culture. *Intl Rice Res. Notes*, 21(1): 20.
- Jena, K.K., Pasalu, I.C., Varalaxmi, Y., Kondal Rao, Y., Krishnaiah, K., Kochert, G. & Khush, G.S. 2000. Molecular mapping and marker aided selection (MAS) of a gene conferring resistance to Indian biotype of brown planthopper in rice. Abstracts. Fourth International Rice Genetics Symposium, 22-27 Oct. 2000, IRRI, Manila, Philippines. 77 pp.
- Joseph, C.J., Remabai, N., Devika, R., Regina, A. & Radha Devi, D.S. 1990. Rice Breeding. In *Five decades of rice research in Kuttanad*, p. 9-26.

- Kerala Agricultural University, Thrissue, Kerala.
- **Kalode, M.B. & Bentur, J.S.** 1989. Characterization of Indian biotypes of the rice gall midge, Orseolia oryzae (Wood-Mason) (Diptera: Cecidomyiidae). *Insect Sci. and its Application*, 10: 219-224.
- Krishnaiah, K. 1998. Rice (*Oryza sativa*) research in India. *Indian J. Agric. Sci.*, 68: 385-395.
- **Kawai, T.** 1980. Current rice mutation breeding in Japan. *Intl Rice Commission Newsl.*, 29: 19-21.
- Kumar, J., Nelson, R.J. & Zeigler, R.S. 1996. Population structure of Magnaporthe grisea in the traditional Himalayan rice system. *In* Khush, G.S. (ed.) *Rice genetics III*, p. 963-969. Manila, Philippines, IRRI. 1011 pp.
- Kumar, J., Ramos, M.S., Leuing, H. & Zeigler, R.S. 1999. Analyzing Himalayan rice blast populations: I. Genetic diversity, virulence and migration. Abstracts, General Meeting of the International Program on Rice Biotechnology, 20-24 Sept., Phuket, Thailand. 247 pp.
- Mackill, D.J. & Ni, J. 2001. Molecular mapping and marker assisted selection for major-gene traits in rice. *In* Khush, G.S., Brar, D.S. & Hardy, B. (eds) *Rice genetics IV*, p. 137-151. New Delhi, Science Publishers, Inc. and Philippines, IRRI. 488 pp.
- Mandal, N. & Gupta, S. 1997. Anther culture of an interspecific rice hybrid and selection of fine grain type with submergence tolerance. *Plant Cell, Tissue and Organ Culture*, 51: 79-82.
- **Manibhushanrao, K.** 1994. *Rice blast disease*. Delhi, India, Daya Publishing House. 180 pp.
- Mehetre, S.S., Patil, P.A., Machajan, C.R. & Dhumal, P.M. 1993. Effect of different doses of gamma rays on germination and survival of upland rice varieties. *Intl Rice Res. Notes*, 18(4): 23.
- Miah, M.A.A., Pathan, M.S. & Quayum, H.A. 1996. Production of salt tolerant rice breeding line via doubled haploid. *Euphytica*, 91: 285-288.
- Mikaelsen, K. 1979. Mutation breeding in rice. IRC Newsl., 28: 1-6.
- Mishra, B. 1999. Recent advances and breeding strategies for salt tolerance in rice. J. of Indian Soc. for Coastal Agric. Res., 171: 109-116.
- Mishra, B., Singh, R.K. & Jetly, V. 1998. Inheritance pattern of salinity tolerance in rice.

- Muralidharan, K., Prasad, G.S.V. & Rao, C.S. 1996. Breeding for rice improvement: where do we stand? *Current Sci.*, 71: 438-448.
- **Panwar, D.V.S., Gupta, K.R. & Battan, K.R.** 1989. Resistance breeding against bacterial blight of rice in Haryana, India. In *Bacterial blight of rice*, Manila, IRRI. 235 pp.
- **Prasada Rao, U.** 1984. Breeding of rice varieties for rainfed upland areas. *Indian J. of Genetics and Plant Breeding*, 44: 42-48.
- Raina, S.K., Khanna, H., Bisht, M.S., Kumar, K., Kumar, U., Irfan, S.T. & Singh, V.P. 1996. Haploid, somaclone, and transformation studies in basmati rice. *In* Khush, G.S. (ed.) *Rice genetics III*, p. 487-491. Philippines, IRRI.
- **Reddy, A.P.K. & Bentur, J.S.** 2000. Insect and Disease Resistance in Rice. *In* Nanda, J.S. (ed.) *Rice breeding and genetics*, p. 143-167. New Delhi, Oxford & IBH Publishing. 382 pp.
- Rutger, J.N. & Mackill, D.J. 2001. Application of mandelian genetics in rice breeding. *In* Khush, G.S., Brar, D.S. & Hardy, B. (eds) *Rice genetics IV*, p. 27-38. New Delhi, Science Publishers, Inc and Philippines, IRRI. 488 pp.
- Saini, R.S., Goel, K.K. & Sharma, S.C. 1996. Genetic analysis of resistance to bacterial blight (Xanthomonas oryzae pv. oryzae Ishiyama) in some rice (Oryza sativa L.) lines. *Indian J. of Genetics*, 56: 178-181.
- Sandhu, J.S., Gill, M.S. & Gosal, S.S. 1993. Callus induction and plant regeneration from cultured anthers of indica rice varieties. *Plant and tissue culture*, 3: 17-21.
- **Saran, S.** 1977. Progress of deep-water rice research in Bihar, India. In *Deep-water rice*, p. 145-150. Manila, Philippines, IRRI. 239 pp.
- **Sharma, K.D.** 1985. *Induced mutagenesis in rice*. Rice Genetics Symposium II: Abstracts, p. 27-31. IRRI, Philippines.
- Sharma, K.D., Kaushik, R.P. & Sharma, S.L. 1985. HPU8020, a promising mutant rice. *Intl Rice Res. Newsl.*, 10(5): 5.
- **Siddiq, E.A., Garg, A.K. & Ali, J.** 1999. Breeding for salt tolerance in rice. Paper presented at the Indo-UK Soil Salinity Project: End of Project Workshop, 12-14 Oct. 1999. 12 pp.
- **Siddiq, E.A. & Viraktamath, B.C.** 2001. Rice. *In* Chopra, V.L. (ed.) *Breeding field crops*, p. 2-85. New Delhi, India, Oxford and IBH Publishers.

- **Singh, B.N.** 2000. Breeding for adverse soil problems in rice. *In* Nanda, J.S. (ed.) *Rice breeding and genetics*, p. 219-240. New Delhi, Oxford & IBH Publishing. 382 pp.
- **Singh, R.K. & Mishra, B.** 1995. Screening anther culture derivatives of rice for salt tolerance. *In* Sharma *et al.* (eds) *Genetic research and education: Current trends and the next fifty years*, p. 501-513. New Delhi, India, Indian Society of Genetics and Plant Breeding.
- Singh, V.P., Siddiq, E.A., Zaman, F.U. & Sadananda, A.R. 1989. Induced variation in aromatic rice cultivars. *Intl Rice Res. Newsl.*, 14: 14.
- **Sivaraj, R., Gnanamanickam & Levy, M.** 1996. Studies on genetic diversity of Pyricularia grisea: a molecular approach for management of rice blast. *In* Khush, G.S. (ed.) *Rice genetics III*, p. 958-962. Manila, Philippines, IRRI. 1011 pp.
- Thakur, R., Sahu, S.P., Mishra, S.B., Singh, U.K., Mishra, M. & Rai, J.N. 1994. Gautam, an improved rice variety for winter (boro) season in Bihar, India. *Intl Rice Res. Notes*, 19(2): 19.
- **Vijaya Laxmi, G. & Reddy, G.M.** 1997. Anther culture of indica rice. Technical improvements in callus induction and green plant regeneration (*Oryza sativa* L.). *J. of Genetics and Breeding*, 51: 295-301.
- **Virmani, S.S. & Ahmed, M.I.** 2001. Environment sensitive genic male sterility (EGMS) in crops. *Advances in Agronomy*, 72: 139-195.
- **Virmani, S.S. & Edward, I.B.** 1983. Current status and future prospects for breeding hybrid rice and wheat. *Advances in Agronomy*, 36: 145-214.
- Virmani, S.S. 1996. Hybrid rice. Advances in Agronomy, 57: 377-462.
- **Zhang, Q., Hua, J., Yu, S., Xiong, L. & Xu, C.** 2001. Genetic and molecular basis of heterosis in rice. *In* Khush, G.S., Brar, D.S. & Hardy, B. (eds) *Rice genetics IV*, p. 173-185. New Delhi, Science Publishers, Inc. and Philippines, IRRI. 488 pp.