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IMPACT OF MUTATION BREEDING IN RICE - A REVIEW

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ABSTRACT

More cultivars have been developed in rice through the use of mutation breeding than in any other crop. Direct releases of mutants as cultivars began some 30 years ago, and now total 198 cultivars. During the last 20 years, increasing use has been made of induced mutants in cross-breeding programs, leading to 80 additional cultivars. Principal improvements through mutation breeding have been earlier maturity, short stature, and grain character modifications. Rice has been a popular subject of mutagenesis because it is the world's leading food crop, has diploid inheritance, and is highly self-pollinated.

Prominent mutation breeding success stories include: Reimei, a mutant semidwarf used to cross-breed 21 additional cultivars in Japan; Calrose 76, a mutant semidwarf used to cross-breed 12 additional cultivars in the USA; Yuanfangzao and Zhefu 802, early maturity mutants, each of which has been grown on over one million hectares annually in China; and the numerous short stature upland rice cultivars developed by IRAT and its cooperators in Africa and South America. As a result of these and other successes induced mutation has been fully integrated by many conventional breeders into their repertoire of breeding procedures.

The most successful semidwarf mutants in rice have been those at the sd_1 locus, which is the same semidwarfing locus present in the tropical semidwarf DGWG that has been the forerunner of the Green Revolution. Because of concerns about potential genetic vulnerability associated with near world-wide use of the sd_1 locus, several non-allelic induced mutant semidwarfs have been examined, but none has been found to be as agronomically suitable as the sd_1 locus. Since the scientific basis for the superiority of sd_1 over other semidwarfs has not been determined, the phenomenon is referred to as "the sd_1 mystique".

In recent years induced mutation has been exploited to develop breeding tool mutants, which are defined as mutants that in themselves may not have direct agronomic application but may be useful genetic tools for crop improvement. Examples include the *eui* gene, hull colour mutants, normal genetic male steriles, and environmentally sensitive genetic male steriles. The environmentally sensitive genetic male steriles, especially those in which male sterility can be turned on or off by different photoperiod lengths, show promise for simplifying hybrid rice seed production both in China and the USA. Future applications of mutation in rice include induction of unusual endosperm starch types, plant types with fewer but more productive tillers, dominant dwarfs, dominant genetic male steriles, extremely early maturing mutants, nutritional mutants, and *in vitro*-derived mutants for tolerance to herbicides or other growth stresses.

INTRODUCTION

General Impact

Perhaps the best measure of the impact of mutation breeding in rice is the fact that 278 cultivars have been released, as noted in the mutant cultivar database recently summarized in the MBNL No. 38 (1991). Of these 278 cultivars 198 were direct releases of mutants and 80 arose from crosses with mutants. The 278 rice cultivars represent a significant portion of the total of 1019 cultivars of all seed propagated crops that have been developed with the help of mutagenesis (MALUSZYNSKI *et al.*, 1991). Reasons why rice has been such a popular mutagenesis subject include: rice, being the world's most important food crop, is being studied by a large number of researchers; it is a diploid species, so mutants are more readily uncovered than in polyploid species; and it is highly self-pollinated, leading to largely homozygous cultivars in which variability induced by mutagenesis is more easily detected than in cross-pollinated crops such as maize where induced variation may be submerged by heterozygosity.

Some 114 of the mutant rice cultivars have been released in China, the world's largest rice growing country, which produces one-fourth of the world's total rice. Other countries in which mutant rice cultivars have been released are Japan with 31, Guyana with 26, Cote d'Ivoire with 26, India with 24, USA with 17, and 18 countries with single-digit numbers of releases. Principal improved characters claimed for these mutation breeding releases have been earliness (70), short culm (63), grain characteristics including waxy endosperm (27), disease resistance (21), and high yield (17) (MBNL No.38, 1991).

Aims and Objectives

The aims and objectives of mutation breeding have been manifold, including hard-to-define attributes such as better adaptation and high yield, but the most successful mutants have arisen when studies have been concentrated on one or a few specific characters. Thus mutant cultivars have been most useful when only one or a few simply inherited traits have been modified, i.e., early maturity, plant height, endosperm starch type. Of course, the same thing can be said of conventional cross-breeding. The literature is replete with plant breeding successes involving single major genes for semidwarfism (the Green Revolution!), early maturity, grain type, disease resistance, etc. Curiously, the real bread and butter issue of conventional plant breeding - disease resistance - has not been particularly well exploited in mutation breeding, although induced mutation for disease resistance was considered promising in early mutation breeding (JORGENSEN, 1991). The lack of success is partly due to heterogeneous starting materials and/or contamination by outcrossing on normal plants or on plants partially sterilized by mutagenic treatment. Also, conventional breeders necessarily have done so much disease resistance breeding that their efforts have overshadowed the efforts of mutation breeders.

The effectiveness of ionizing radiations as mutagens was first noted by (MULLER, 1927) and (STADLER, 1928). Following World War II, mutation breeding began in earnest as national and international agencies sought peaceful uses of atomic energy (FAO/IAEA, 1968; 1970; 1971). The FAO/IAEA has actively supported mutation breeding studies in many crops, including rice, in numerous countries around the world (MALUSZYNSKI *et al.*, 1986, 1991; MICKE *et al.*, 1987). The first mutant rice cultivars appeared in 1957, KT 20-74 and SH 30-21 from China, and by 1963 the first cultivar from cross-breeding with a mutant appeared, Yenhsing-1, also from China (MBNL 38, 1991). The first mutant rice cultivar that became widely known was Reimei, released in Japan in 1966 (FUTSUHARA *et al.*, 1967). Reimei, a short stature mutant, has been used in cross-breeding in Japan to develop 21 additional cultivars (KAWAI and AMANO,

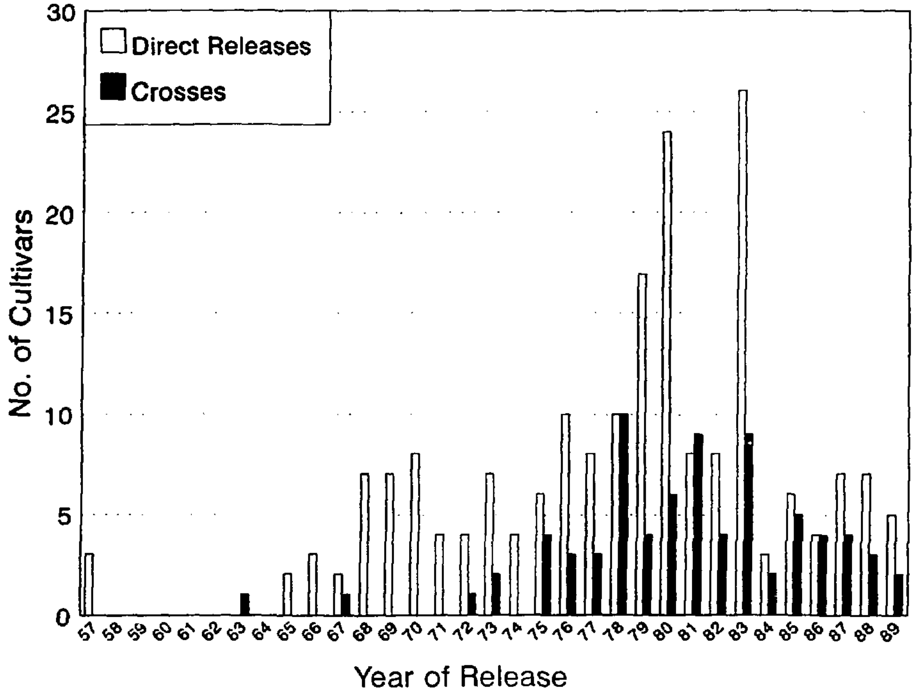


Figure 1. Numbers of directly released rice cultivars (198) and cultivars developed from crosses (80) using mutants.

1991), as well as the cultivar Hangfen in China (MBNL 30, 1987). A similar pattern was followed with the first mutant cultivar in the USA, Calrose 76, a semidwarf cultivar which has appeared in the parentage of 12 cultivars, 9 as a semidwarf donor and 3 in which the source of semidwarfism could have been either Calrose 76 or Deo-Geo-Woo-Gen (DGWG). Both Reimei and Calrose 76 carry a semidwarf gene which is allelic to the sd_l gene in the DGWG-TN1-IR8 source, hereafter referred to as DGWG. Also, both cultivars have become widely cited as examples of the usefulness of induced mutation in plant breeding. The patterns of cultivar development from direct release versus cross-breeding are shown in Figure 1. It is evident from this figure that there has been a lag phase in use of mutants in cross-breeding, with cross-breeding increasing in importance in the last 15 years. Clearly, mutation breeding has been adopted as one of the tools available to all plant breeders.

Mutagenic Agents

The mutagenic agents used to induce the 198 mutant rice cultivars were overwhelmingly ionizing radiations: 159 cultivars from gamma rays, 14 from x-rays, and 12 from various other radiation sources. Effective dosages of gamma rays, the most popular mutagen, generally ranged from 15 to 30 krads. The population sizes have ranged from as few as 2,000 to as many as 100,000 M_1 plants (RUTGER *et al.*, 1976; MESE *et al.*, 1984), and from 5,000 (RUTGER *et al.*, 1976) to 50,000 or more M_2 plants (KAWAI and AMANO, 1991). In recent years the present author usually irradiated 5,000 seeds at 25-30 krads, followed by harvest of 2,000 panicles for panicle-to-row grow-outs in the M_2 generation. This procedure proved effective for identifying early maturity mutants, dwarfs, endosperm mutants, and genetic male steriles.

Only 11 of the 198 mutant cultivars came from chemical mutagens, and 2 came from unspecified mutation. Reasons for the predominant use of ionizing radiation include good penetration, precise dosimetry, and a wide spectrum of mutations (MICKE *et al.*, 1987). Some chemical mutagens give higher mutation rates, but practical problems of using chemicals, which include soaking and re-drying of seeds, and safety of handling and disposal, have limited their use. Genetic variation arising from *in vitro* culture has been frequently reported in recent years, but few if any rice cultivar successes have been published so far.

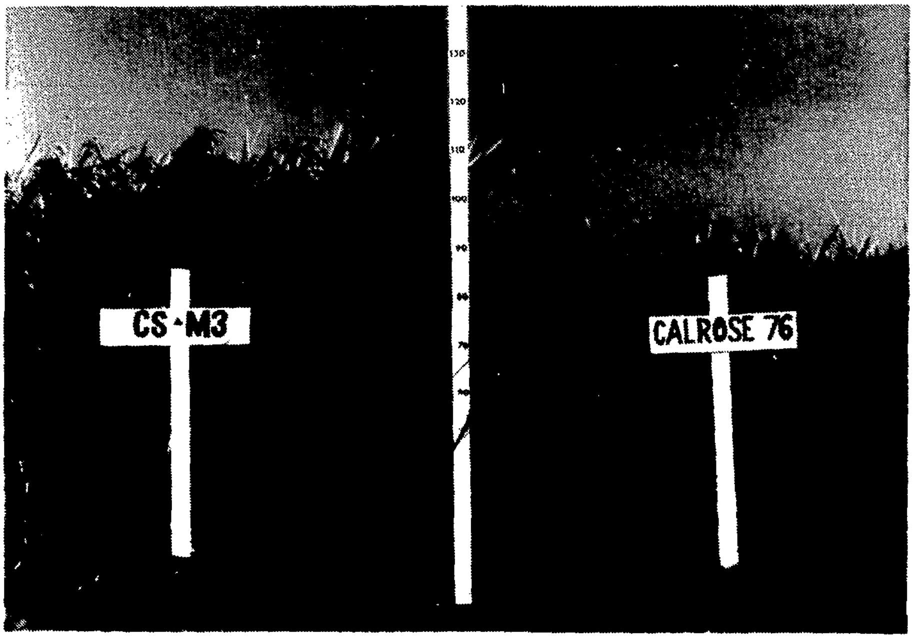


Figure 2. The induced mutant rice cultivar Calrose 76 was about 30 centimeters shorter than comparable tall cultivars such as CS-M3 in California. Because of its short stature, Calrose 76 was lodging resistant and about 13 percent higher yielding than the tall cultivar.

PROMINENT MUTATION BREEDING SUCCESSES

Plant mutation breeding success stories in many crops, including rice, were summarized in Volumes 1 and 2 of 'Plant Mutation Breeding for Crop Improvement' (1991), which are the proceedings of a recent FAO/IAEA Symposium held in Vienna, 1990. Examples of prominent rice mutation breeding successes will be addressed herein on a country and/or program basis.

USA

The USA's experiences with mutation breeding in rice were previously summarized by RUTGER (1983; 1991). Briefly, gamma irradiation was used to induce semidwarfism in locally adapted japonica germplasm, resulting in the direct release of the semidwarf cultivar Calrose 76 (Figure 2; (RUTGER *et al.*, 1977). Calrose 76 was the first US semidwarf cultivar with acceptable grain quality. Another semidwarf cultivar, LA 110, also was released in the USA in 1976, from cross-breeding with TN1, but LA 110 did not have grain quality acceptable for US markets, and soon faded away. Although Calrose 76 itself was grown on only 7% of the California rice hectarage in 1981, probably its peak year, its value in breeding quickly became apparent to California rice breeders. Hence, well before it was released, Calrose 76 or its sister semidwarf selection D51, which also carries the sd_1 gene and is believed to have arisen from the same mutational event (RUTGER, 1983), had been used as a semidwarf donor in crosses with tall California cultivars, mainly by cooperating breeders at the California Cooperative Rice Research Foundation (CCRRF). Thus Calrose 76 was quickly followed by 9 additional semidwarf cultivars, as noted below and in Figure 3:

M7	(CARNAHAN *et al.*, 1978)
M-101	(RUTGER *et al.*, 1979b)
M-301	(JOHNSON *et al.*, 1980)
S-201	(CARNAHAN *et al.*, 1980)
M-302	(JOHNSON *et al.*, 1981)
Calmochi-202	(CARNAHAN *et al.*, 1981b)
Calmochi-101	(CARNAHAN *et al.*, 1986)
M-103	(JOHNSON *et al.*, 1990)
S-301	(JOHNSON *et al.*, 1991)

Three additional semidwarf cultivars have been developed by CCRRF breeders from intercrosses between the induced mutant, Calrose 76, source and the DGWG source (Figure 3), but since both sources carry allelic sd_1 genes, it is no longer possible to identify the exact source:

M-202	(JOHNSON *et al.*, 1986)
M-102	(CARNAHAN *et al.*, 1987)
S-101	(JOHNSON *et al.*, 1989)

All 12 cultivars have the common improvement of semidwarfism, and individually have one or more additional attributes such as glabrous hulls, earlier maturity, altered grain type, or endosperm type.

The CCRRF breeders also have induced and directly released three additional mutant cultivars: Calmochi-201 with waxy endosperm (CARNAHAN *et al.*, 1979), M-401 with semidwarf plant height (CARNAHAN *et al.*, 1981a), and M-203, an early maturity mutant from M-401 (CARNAHAN *et al.*, 1989). The cultivar M-401 carries a semidwarfing allele at the same locus as Calrose 76. The cultivars M-401 and M-203 provide another interesting application of direct mutation, as the original tall, late, parent Terso, was relatively low yielding but had premium quality medium-grain characteristics that were difficult to define. The mutant cultivars descended from Terso had improved lodging resistance because of semidwarfism (M-401), and earlier maturity as well as semidwarfism (M-203), and retained the premium quality medium-grain characteristics.

In summary, in the public breeding sector in California, induced mutation has been used to produce, or is involved in, the parentage of the following numbers of public cultivars:

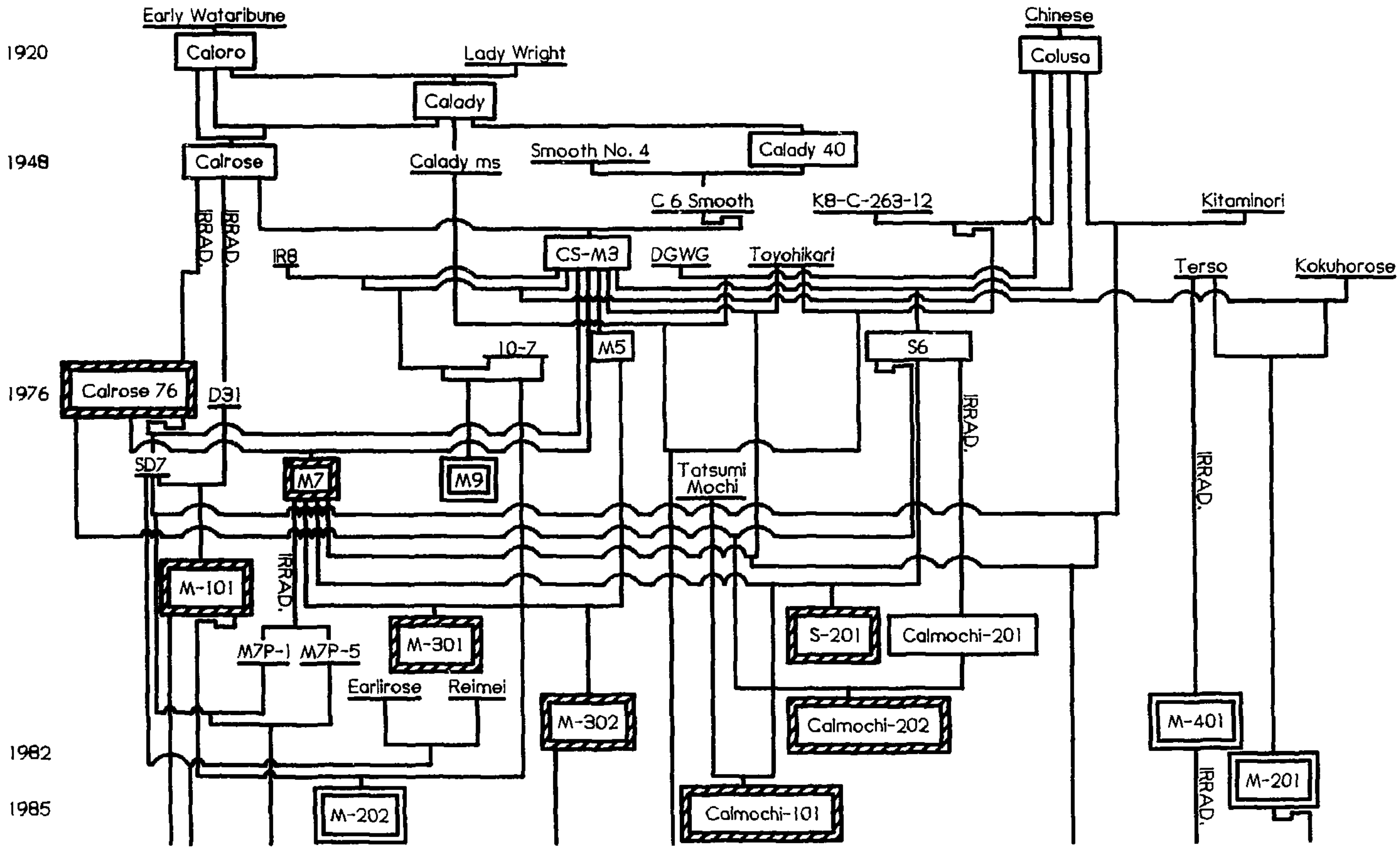
4 direct releases:
- 2 semidwarf mutants, Calrose 76 and M-401
- 1 waxy endosperm mutant, Calmochi-201
- 1 early maturity mutant, M-203

12 cross-bred releases:
- 9 receiving sd_1 from Calrose 76
- 3 receiving sd_1 from either Calrose 76 or DGWG

Numerous additional semidwarf, early maturity, or waxy endosperm, mutants were released as germplasm for use in breeding programs (RUTGER *et al.*, 1979b, 1982, 1987; TSENG *et al.*, 1987).

The above efforts in California were carried out by public-sector breeders, i.e., CCRRF, USDA-ARS, and University of California - Davis. At least one private-sector breeder, Dr. Chao-Hwa Hu, employed by N. F. Davis Drier & Elevator, Inc., Firebaugh, California, has used mutation breeding to develop rice cultivars. One of the original participants in the California public breeding effort, Dr. Hu made the initial selections that subsequently led to Calrose 76 (RUTGER *et al.*, 1976, 1977), during an IAEA-sponsored study leave in Davis, CA in 1971-72. Prior to his study leave, Dr. Hu had attained considerable experience with induced mutation in Taiwan, where he had induced mutants in indica rice (HU, 1973). When his Davis study leave was completed, Dr. Hu returned to Taiwan, and a few years later came back to California to join N. F. Davis Drier & Elevator, Inc. In this latter capacity, Dr. Hu made further use of induced mutation, releasing the cultivar Calpearl from a cross involving Calrose 76 (HU, 1991; MBNL 38, 1991).

Rice breeders in the southern rice states of Arkansas, Louisiana and Texas have examined induced mutation but, to date, induced mutation has not been as useful there as in California. This is at least partially due to the fact that the tropical semidwarfs are moderately adapted to the southern USA growing conditions and can be more readily utilized than in California. Thus, the prevalent source of semidwarfism in the southern USA has been TN1, the ultimate semidwarf donor for Lemont (BOLLICH *et al.*, 1985), the most widely grown semidwarf cultivar in the USA. McKENZIE and RUTGER (1986) induced a semidwarf ("Short Labelle") non-allelic to sd_1 in the long grain cultivar Labelle, and proposed it as an alternative source of semidwarfism for southern USA rice breeding. However, since the Short Labelle mutant is no higher yielding than its tall parent, it has not yet been used in breeding programs. One cultivar in Louisiana, Mercury, also carries an induced semidwarf mutant gene, which is either allelic or identical by descent to the Calrose 76 sd_1 gene source (McKENZIE *et al.*, 1988). Semidwarf mutants of the tall cultivars Saturn, Mars, Nato, and LeBonnet were developed in the Louisiana program. However, these selections did not show significant yield advantages over the best improved breeding materials available in the Southern breeding programs (McKENZIE, K.S., personal communication).



1920
1948
1976
1982
1985
Early Wataribune
Caloro
Lady Wright
Calady
Chinese
Colusa
Calrose
Calady ms
Smooth No. 4
Calady 40
C 6 Smooth
K8-C-263-12
Kitaminori
IRRAD.
IRRAD.
IR8
CS-M3
DGWG
Toyohikari
Terso
Kokuhorose
10-7
M5
S6
Calrose 76
D31
IRRAD.
IRRAD.
SD7
M7
M9
Tatsumi Mochi
M-101
IRRAD.
M-301
S-201
Calmochi-201
M7P-1
M7P-5
Earlirose
Reimei
M-302
Calmochi-202
M-401
M-201
IRRAD.
M-202
Calmochi-101

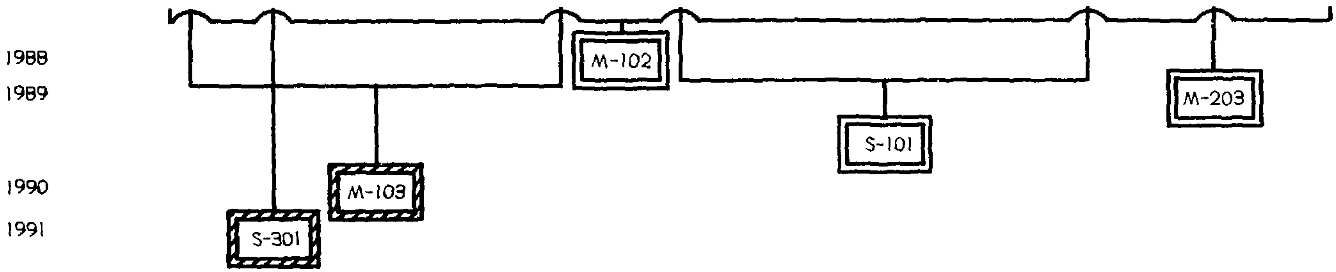


Figure 3. Ancestry of publicly developed medium and short grain rice cultivars in California: an example of the integration of mutation breeding into cultivar development. Semidwarf cultivars carrying the Calrose 76 induced mutant gene are in boxes with cross-hatched borders; other semidwarf cultivars are in double line boxes; tall cultivars are in single line boxes; introductions, breeding lines and proprietary cultivars are underlined.

The economic impact of the mutants peaked in the early 1980s when several cultivars carrying the induced mutant source of semidwarfism were in use. Thus RUTGER (1991) calculated that semidwarf mutant cultivars carrying the induced mutant source of sd_1 occupied over half of the California rice area of 222,000 hectares and earned California growers an additional $20 million per year. These calculations were based on early cultivar x nitrogen rate studies that showed that the two semidwarf cultivars Calrose 76 and M7 averaged 14% more grain yield (and 13% less straw) than the tall check cultivar CS-M3; all indications were that the other semidwarf cultivars similarly outyielded their tall counterparts (BRANDON *et al.*, 1981). In subsequent years, cultivars carrying the DGWG source of sd_1, or developed from crosses between the DGWG source and the mutant source have become more prominent, so the mutant contribution is not readily discernible.

Japan

The principal mutation breeding success story in Japan has been the induction of the mutant short stature cultivar Reimei , from the cultivar Fujiminori (FUTSUHARA *et al.*, 1967) and Reimei's subsequent use in cross-breeding. KAWAI and AMANO (1991), in a thorough summary of mutation breeding in Japan, noted that Reimei has been used in cross-breeding programmes that have led to the release of 21 additional cultivars, and that other mutants have been used in cross-breeding to develop 12 more cultivars, making a total of 33 cultivars that were developed by cross-breeding with mutant lines (Table 1). Reimei itself was grown on 141,000 hectares in Japan in 1969, and one of its descendants, Akihikari, was grown on 120,000 hectares in 1979 (SATO, 1982), as shown in Table 2. Reimei carries a semidwarfing allele that is allelic to sd_1 in DGWG (KIKUCHI *et al.*, 1985).

Selection criteria for other directly-released mutant cultivars have been early maturity, grain size, and glutinous endosperm. Cultivars that apparently have become important include: Miyama-Nishiki, high percentage of grains with white core; Miyuki-mochi, waxy endosperm; Shirankabanishiki, large grain, white core; Shinano-Sakigake, large grain; and Iwate 21, short culm, early maturity, good eating quality (KAWAI and AMANO, 1991).

China

The most widely grown mutant rice cultivars in the world have been Yuanfengzao and Zhefu 802, both in China. Yuanfengzao, a gamma-ray-induced early maturity mutant, from IR8, developed to solve the double- and triple-cropping needs of southern China (ZHAO, 1980; WANG, 1991), was grown on over 1,100,000 hectares in the lower Yangize River region during the early 1980s (WANG, 1991). According to WANG (1991), breeders of Yuanfengzao won the National First Class Invention Prize for their contributions to rice production. Zhefu 802 was also early maturing, had broader disease resistance and higher yield than its parent, and was grown on more than 1,400,000 hectares in China in 1989 (WANG, 1991). Seven other mutant cultivars have been grown on 100,000 or more hectares in China (Table 2).

In a summary of mutation breeding of all crops in China, WANG (1991) noted that 325 cultivars, representing 29 different species, had been developed. Of the total, 110 cultivars were of rice - now grown to 114 (MALUSZYNSKI *et al.*, 1991). Of the 110 cultivars cited by WANG (1991), 94 were direct mutant

Table 1. Notable mutant rice cultivars used in cross-breeding in USA, Japan, China, and at IRAT.

Original cultivar	Induced mutant cultivar	Cross-bred derivatives, No.	Source
USA			This paper, Figure 3
Calrose	Calrose 76	12	
JAPAN			KAWAI and AMANO, 1991
Fujiminori	Reimei	21	
Fujiminori	Fukei 71	2	
Koshihikari	(unnamed)	5	
Norin 8	(unnamed)	4	
Unspecified	(unnamed)	1	
CHINA			WANG, 1991
Nonghu No.6	Funong 709	9	
Zhuyin No.2	Zhuyin C6965	7	
IRAT			CLEMENT and POISSON, 1988
IRAT 2	IRAT 13	Many	

releases and 16 resulted from crosses with mutants. She noted that the number of mutant cultivars resulting from crosses was increasing, and listed 9 cultivars derived from crosses with mutant cultivar Funona 109, and 7 cultivars derived from crosses with mutant cultivar Zhuyin C6965 (Table 1). As in other countries, most mutants arose from ionizing radiation treatment of seeds, particularly gamma rays (WANG, 1991).

IRAT

For about 25 years, scientists at the Institut de Recherches Agronomiques Tropicales (IRAT), Montpellier, France, have been using chronic gamma rays to mutagenize upland rice (JACQUOT, 1986). For upland rice, the semidwarf gene used in lowland rice was considered appropriate only for very favorable upland conditions, hence mutagenesis was applied to traditional tall upland cultivars with the objective of inducing shorter plant height (JACQUOT, 1986). To date 37 cultivars have resulted from direct releases of mutants, and 18 cultivars have been developed by cross-breeding with mutants (MBNL 38, 1991). Reduced plant height has been a major objective, although other characters also are of interest (JACQUOT, 1986). These 55 cultivars have been variously released in several countries in Africa (Cote d'Ivoire, Senegal, Burkina Faso) and South America (Guyana, Brazil) (MBNL 38, 1991). According to CLEMENT and POISSON (1988), all of the IRAT cultivars released or being released (in 1988) have the semidwarf, induced gene of IRAT 13. Whether this gene is allelic to the sd_1 source from DGWG was not specified.

Table 2. Rice cultivars, developed by mutation breeding, that have been grown on 100,000 or more hectares.

Cultivar	Country	Type	Hectares	Year	Main improved attribute	Reference
Yuanfengzao	China	Direct	1,100,000	1980/1985	Early maturity	Wang, 1991
Zhefu 802	China	Direct	1,400,000	1989	Early maturity	Wang, 1991
Qinghuaai 6	China	Songhuaai/ Fuchuerai	240,000	1986	High yield	MBNL No. 37, 1991
Nanjing No. 34	China	Direct	220,000	1981	Short stature	MBNL No. 19, 1982
Reimei	Japan	Direct	141,000	1969	Short stature	Sato, 1982
Akihikari	Japan	Toyonishiki/ Reimei	120,000	1979	Short stature	Sato, 1982
Dongting No. 3	China	Direct	120,000	1982	Short culm	MBNL No. 21, 1983
Wanhua	China	Qinghuaai 6/ Qinglian 32	100,000	1986	Semidwarf	MBNL No. 37, 1991
Aifu No. 9	China	Direct	100,000	?	Short culm	MBNL No. 5, 1975
Wangeng 257	China	Direct	100,000	?	Fertilizer tolerance	MBNL No. 25, 1985
Hongnam	China	Direct	100,000	?	Intermediate maturity	MBNL No. 25, 1985

Other

Of the 24 mutation-derived rice cultivars in India, 21 have been direct releases and 3 have resulted from cross-breeding with mutants (MBNL 38, 1991). A prominent direct release has been the mutant Jagannath, which was released in 1969 and is still in cultivation in the states of Orissa, West Bengal, and Madhya Pradesh (BHATIA, 1991).

Although only 3 cultivars have been released in Pakistan, the Basmati rices of that region are of special interest for mutation breeding. Basmati rices have highly desirable aroma and cooking quality characteristics, but agronomically the cultivars are very tall, late, and low-yielding. AWAN (1991) has undertaken several mutation breeding steps to improve the agronomic attributes. First, an early maturing mutant was selected and released as the cultivar Kashmir Basmati, for cultivation in northerly parts of Pakistan. Then several short stature mutants were induced, and appear promising in yield trials. Cooking quality and aroma characteristics are similar to the parental cultivar Basmati-370, so the mutants may be released soon (AWAN, 1991).

THE sd_1 MYSTIQUE

Genetic studies have revealed that an overwhelming preponderance of the world's semidwarf rices share the same semidwarfing gene locus, sd_1, in spite of different origins. Thus virtually all tropical semidwarf cultivars outside of China received sd_1 by descent from what is commonly referred to as the DGWG source (HARGROVE *et al.*, 1980). In this context, the DGWG source is defined to include the other semidwarf donors widely used at IRRI, which includes Taichung Native 1 (TN1), I-Geo-Tze (IGT), and IR8. Similarly, in China, many indica semidwarf cultivars were derived from the Chinese cultivar Ai-Jio-Nan-Te, which has a semidwarfing gene at the sd_1 locus (OBA *et al.*, 1990).

The two most widely used mutant japonica semidwarfs, Calrose 76 and Reimei, also have a semidwarfing gene at the sd_1 locus (RUTGER, 1983; KIKUCHI *et al.*, 1985). In Japan, the widely used semidwarf cultivar Shiranui and its relatives were derived from a native semidwarf cultivar, Jikkoku, which also has a semidwarfing gene in common with DGWG (KIKUCHI *et al.*, 1985). In California, semidwarfism at the sd_1 locus has been induced not only in the tall cultivars Calrose and Colusa (RUTGER, 1983), but also in the tall cultivar Terso (CARNAHAN *et al.*, 1981b). The allelic relationship to sd_1 of IRAT 13 induced semidwarfness gene has not been specified (CLEMENT and POISSON, 1988).

Numerous additional semidwarf mutants have been induced by researchers around the world. Thus in the early 1980s, FAO/IAEA sponsored two Coordinated Research Programs on semidwarf mutants in cereals. MALUSZYNSKI *et al.*, (1986) summarized the rice semidwarf studies, noting that up to 1983, a total of 53 semidwarf stocks had been reported. Nine stocks were allelic to sd_1; 4 were allelic to sd_2, a locus reported by MACKILL and RUTGER (1979); 3 allelic to sd_4, another locus found by MACKILL and RUTGER (1979); 4 were non-allelic to sd_1, sd_2 and sd_4; and 37 had not yet been investigated. Often the nonallelic semidwarfs have unfavorable pleiotropic effects such as reduced panicle or grain size (MACKILL and RUTGER, 1979; OKUNO and KAWAI, 1977; CHANG *et al.*, 1984; MALUSZYNSKI *et al.*, 1986). However, USA researchers have reported two induced semidwarf mutants which have minimal unfavorable morphological attributes and are phenotypically identical to sd_1, but are non-allelic to sd_1. One of these, CI 11045, induced from the tall cultivar M5, has a tendency to show discolored hulls at harvest, and yields about 5 percent less than its tall parent (RUTGER *et al.,* 1982). The other, Short Labelle, is agronomically very similar to its tall parent - Labelle, but yields 13 percent less (McKENZIE and RUTGER, 1986).

It is obvious that the near-universal use of sd_1, from either the naturally-occurring or induced sources, could lead to genetic vulnerability associated with this locus. Should adverse effects result from this potential genetic vulnerability, additional efforts to "clean up" nonallelic sources such as CI 11045 and Short Labelle by backcrossing to parental lines or other adapted cultivars will undoubtedly be undertaken.

So what is it about sd_1 that makes it the world's most important semidwarf locus? As of now, the answer is not known. Interestingly, a somewhat analogous situation is present in wheat, where the Norin 10 source of semidwarfing genes (*Rht* loci) predominate in world semidwarf cultivars. GALE and YOUSSEFIAN (1985) have noted that the *Rht* genes are insensitive to exogenous gibberellic acid (GA). Apparently this occurs because the *Rht* sources have adequate endogenous GA to achieve high yields. Since these critically important semidwarf genes in wheat are GA-insensitive, it often has been speculated that the important semidwarfing gene in rice would also be GA-insensitive. However, in indica backgrounds the sd_1 gene is associated with increased GA-responsiveness (HARADA and VERGARA, 1971) while in japonica backgrounds there is no association between sd_1 and GA responsiveness (RUTGER and ANDERSON, 1988). Until a scientific basis is determined for the superiority of sd_1, its mystique remains.

BREEDING TOOL MUTANTS

Following the induction of agronomically useful mutants for semidwarfism, early maturity, and endosperm alterations, the present author turned attention to the use of mutants as breeding or genetic tools. This began with the use of the Calrose 76 semidwarf as a donor for cross-breeding (RUTGER *et al.,* 1979a; RUTGER and PETERSON, 1981; RUTGER, 1983), and continued with less obvious mutants such as elongated uppermost internode (eui) (RUTGER and CARNAHAN, 1981), hull color mutants (RUTGER *et al.,* 1986), normal genetic male sterile mutants (HU and RUTGER, 1991, 1992), and environmentally sensitive genetic male steriles (OARD *et al.,* 1991; RUTGER, 1991).

Thus RUTGER and CARNAHAN (1981) reported that the spontaneously occurring eui mutant, which conditions a recessive tall plant type, would be a useful fourth genetic element for facilitating hybrid seed production in cereals. The *eui* gene nearly doubles the length of the uppermost internode, increases panicle length by 12%, and has little effect on other internodes or plant traits. This plant type would be used as a tall pollinator in crossing blocks with semidwarf females, on the premise that a tall male parent would be better for dispersing pollen onto short females. Since tallness is recessively inherited in this case, the F_1 is of the highly desirable semidwarf height. VIRMANI *et al.* (1988) have backcrossed the *eui* gene into the indica fertility restorer cultivar IR50 for distribution to rice breeders in the tropics. In China, a use unanticipated by RUTGER and CARNAHAN (1981) has been made of the *eui* gene, namely, to backcross it into the female lines in order to obtain better panicle exertion from the flag leaf sheath (ZONGTAN and ZUHUA, 1989). This reduces or eliminates the need to treat the female lines with gibberellin to produce panicle exertion.

Three hull colour mutants were proposed as useful cultivar identifiers in breeding programs. These mutants, 'light green panicle', 'yellow-green panicle' and 'goldhull', as well as a waxy endosperm mutant, were controlled by single recessive genes, and were released as the germplasm lines PI 506221, PI 506222, PI 506224 and PI 506223, respectively (RUTGER *et al.*, 1987). Two of the hull colour mutants (light green panicle and yellow-green panicle) were found to have no detrimental effects on yield, and one (goldhull) decreased yield by 11%.

In the 1970s several rice geneticists around the world began to explore the development of genetic male sterile mutants for use in recurrent selection, backcrossing, or population improvement schemes (FUJIMAKI *et al.*, 1977; TREES and RUTGER, 1978; KO and YAMAGATA, 1980; SINGH and IKEHASHI, 1981). A major criterion for successful use of such genetic male steriles is that they show relatively high levels of outcrossing (ca 10 percent or more). Initial mutants studied in California did not meet this criterion (TREES and RUTGER, 1978), so intensive efforts were undertaken to induce useful male steriles in adpated germplasm. Therefore, 10 genetic male sterile mutants were induced by gamma irradiation of the cultivar M-101 (MESE *et al.*, 1984). Later 10 additional male steriles were induced by ethylmethanesulphonate, 1 by ethyleneimine, 1 by streptomycin, 1 was derived from tissue culture, and 3 came from spontaneous mutation (HU and RUTGER, 1992). All behaved as single gene recessive genetic male steriles. Many had undesirable associated features, but two, G1 from irradiation and Np from the streptomycin treatment, showed stable sterility and 18.7 and 34.5% outcrossing, respectively (HU and RUTGER, 1992). These properties should make these two mutants useful in population improvement schemes.

An interesting feature of the Np mutant is that it was induced by streptomycin treatment. This antibiotic is known to induce cytoplasmic male sterility in other crops (BURTON and HANNA, 1982; JAN and RUTGER, 1988), and was employed in rice in anticipation that it would be effective in inducing cytoplasmic male sterility in this crop as well. Although no cytoplasmic male steriles were induced in rice, the potentially useful genetic male sterile, Np, was induced. JAN (1992) has shown that streptomycin was also effective in inducing genetic male steriles in sunflower: seven mutant male steriles represented four loci that differed from existing genetic male steriles in sunflower.

Male sterile mutants also were found which have the unusual and highly desirable features of photosensitive and/or thermosensitive genetic male sterility. The first of these, Calrose ms No. 2, segregated in the normal three fertile one sterile ratio in the California summer nursery (long days, about 15 hours), but showed either no sterile plants or a reduced number in the Hawaii winter nursery (short days, about 12 hours) (RUTGER and SCHAEFFER, 1989). A second line, M-201 ms No. 7, also shows some photoperiod or thermoperiod induced sterility reversal (OARD *et al.*, 1991). Photosensitive genetic male steriles will be extremely useful in hybrid rice production, as they will reduce hybrid rice breeding from a 3-line effort (sterile, maintainer, restorer) to a 2-line effort (sterile, restorer) (Figure 4). In the 2-line effort, the maintainer line is produced by growing the sterile line in an environment that causes it to be fertile, i.e. in short days. Photosensitive genetic male sterile mutants are also under development in China (SHI, 1985; DEMING *et al.*, 1988; YUAN, 1990).

The ultimate hybrid rice mechanism would be the 1-line method or apomixis, which is asexual seed production. In searches in the USA, little evidence of apomixis in rice was found (RUTGER, 1992). Apomixis in rice is also being sought

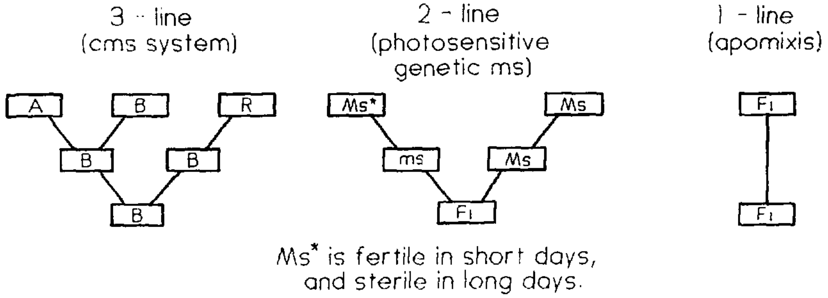


Figure 4. Alternative schemes for hybrid rice breeding include the 3-line or cytoplasmic male sterile (cms) system now in use in China, the 2-line or photosensitive genetic male sterile (ms) system now under development in China and the USA, and the 1-line or apomixis system being sought by several researchers.

in China (JIANSAN *et al.*, 1988). It appears that genetic engineering techniques will be needed to introduce apomixis into rice, although conventional techniques, including induced mutation, should be explored in further detail.

FUTURE APPLICATIONS OF INDUCED MUTATION

Whole-plant mutagenesis

Breeders should continue to look for those special niches where mutation breeding techniques can be readily applied to existing good cultivars needing correction for one or a few simply inherited traits, as in the California situation existing two decades ago, or as in the tall weak-strawed Basmati rice situation, etc. In seeking such opportunities, it should be kept in mind that traits most useful in today's intensive cultivation methods may very well differ from those that have had an evolutionary advantage over the millennia. For example, tall plant height has certainly had an evolutionary advantage in the past, so as to be able to outcompete weeds. But with improved weed control and intensive cultural practices, the semidwarf plant type has become the idiotype of choice in most cereal breeding programs. Similarly, early maturity has become more useful under intensive cultural practices.

Unique grain quality characters, which may or may not have been at a selective disadvantage in the past, such as waxy endosperm or high lysine, may become important. SATOH (1985), noting that the spectrum of rice endosperm mutants was small compared to maize, reported on the use of chemical mutagens to induce not only waxy but also dull, high amylose, floury, white core, sugary, and several shrunken mutants in rice. Such mutants are useful for studying carbohydrate contents in rice (MATSUO *et al.*, 1987), and also may have applications for food and/or industrial uses. KAUSHIK and KHUSH (1991) noted that high amylose mutants are reported to have high fiber content which is desirable in human nutrition.

What will be the next traits to undergo such turnabouts? Perhaps "new rice plant type" recently described by IRRI (ANONYMOUS, 1991) will be one. The ideal new plant type is planned to be an "ultra-high yielding" plant with fewer tillers but almost all bearing panicles, and will be more suitable for direct seeding. The plant may have from 1 to 6 tillers, compared to 20-25 tillers for present modern cultivars. Clearly a high tillering plant type is desirable for widely spaced plants, as in transplanting, but tillering becomes less important as precise direct seeding methods are implemented. Even today, temperate region rice cultivars (japonicas) are recognized to have considerably fewer tillers than tropical cultivars. And the highest rice yields in the world are realized by farmers using these low tillering cultivars in direct seeding cultivation at high latitude areas such as California (average paddy yields 9 tons per hectare in 1991 [ANONYMOUS, 1992]), Australia, Spain, Italy, etc. Low tillering mutants are frequently observed in nurseries. For example, for several years the present author had a line which showed only 1 to 4 tillers under spaced plant conditions, which was noticeably lower than the 10 to 15 tillers usually seen in California. In Japan, TAKAMURE AND KINOSHITA (1985) have also reported a reduced culm number character in rice. Reduced culm number was conditioned by a single recessive gene, with a pleiotropic effect for dwarfness, although seed fertility was not affected. Perhaps it would be worthwhile to seek and evaluate additional low-tillering mutants in other rice growing areas.

Other opportunities may exist for such infrequent mutants as dominant dwarfs, and dominant genetic male steriles. Recessive tall mutants such as eui (RUTGER and CARNAHAN, 1981) are sort of mirror images of dominant dwarfs, but carry an altered plant type which is not desirable for agronomic production per se, i.e., the tall eui plants themselves are lodging susceptible. Dominant dwarfs with phenotypes like sd1 might be useful as females in hybrid rice production schemes with conventional tall males. Dominant genetic male steriles, as described for wheat by JINGYANG AND ZHONGLI (1982), and SORRELS AND FRITZ (1982), have an advantage over recessive genetic male steriles in recurrent selection schemes, since progenies of dominant male sterile plants always segregate 1 fertile : 1 sterile. Thus sterile plants are obtained every generation, thereby halving the number of generations that is needed for exposure of recessive genetic male steriles.

RYDER (1985, 1988) has found partially dominant, extremely early maturity mutants in lettuce, and has demonstrated how these can decrease generation time from 220 days down to 140 days, thereby accelerating backcross transfers of other genes such as disease resistance. Partial dominance for early maturity, rather than complete dominance, is desired so the breeder can identify heterozygous early maturity plants each generation and thus avoid fixing the extremely early maturity, which in itself is agronomically undesirable in the growers' crop. Then, at the conclusion of the backcross transfer, the plants with the desired additional genes, i.e., disease resistance, are selfed for one generation. In the next generation the breeder recovers recombinants with the added gene for disease resistance plus homozygous recessive late maturity. The present author sought, but did not find, extremely early flowering genes in rice. To be useful in rice, it is estimated that the flowering time of such a mutant would need to be in the order of 45-50 days, in situations where present cultivars flower in 90-110 days. Numerous early maturity mutants were found (RUTGER, 1983, 1991), but the difference in flowering time was in the order of 10-20 days, with none less than about 80 days.

A series of nutritional mutants described by Barabas and his colleagues offer fascinating possibilities for hybrid production in a plant with any type of male- or self-sterility system (BARABAS *et al.*, 1989; BARABAS, 1991). Parental lines can be planted together, and the only viable plants produced from harvested seeds will be pure stands of F_1 hybrids. BARABAS (1991) reported that the system works well in tomatoes, and is being studied in barley. No doubt additional opportunities for applications of unusual mutants will occur to perceptive geneticists and breeders.

In vitro Techniques

In the last decade there has been considerable interest in applications of *in vitro* techniques, ranging from somaclonal variation to gametoclonal variation to transformation, for crop plant improvement. To date, examples of successes in rice cultivar development by *in vitro* techniques have been rare, but may increase in the future. Thus in the USA, one rice cultivar, Texmont, developed from anther culture, has been released (C.N. BOLLICH, personal communication). McKENZIE *et al.* (1987) noted that 8 rice cultivars developed in China by anther culture were grown on 170,000 hectares in 1984. Also in China, WANG (1991) noted that the cultivar R462 had been developed from anther culture and released. Much additional work on *in vitro* techniques is underway worldwide, but to date the IAEA has not listed in its databank any rice cultivars arising from *in vitro* procedures in combination with mutagenic treatment (MBNL 38, 1991). NOVAK (1991) has noted that *in vitro* mutation offers the advantage that large populations of individuals, i.e. cells, tissue, can be screened, but inadequate screening and regeneration techniques often limit progress. MAC KEY (1991) has commented that new lines arising from *in vitro* techniques have lower yield and need an adjustment period. KINOSHITA (1991) noted that somaclonal and gametoclonal variation may exhibit genetic instability, a negative aspect if it continues at the whole-plant level. MIN *et al.*, (1989) noted that low dosage (2.5 -5.0 KR) gamma radiation of callus was effective for inducing mutants in rice. The mutants included plants with increased stigma exertion types, early maturity variants, and promising male steriles.

In unpublished studies with rice in California, J.M. CHANDLER and J.N. RUTGER found considerable variation at the whole-plant level from regenerated somaclones of the rice cultivar L-201, for early maturity, plant height, endosperm characteristics and male sterility. However, in parallel seed-mutagenesis studies on the same cultivar, a similar spectrum of mutants was observed. Thus for agronomically-visible traits, it seemed that somaclonal variation did not result in any unique characters that were unattainable through conventional seed mutagenesis.

It does seem likely that *in vitro* selection will be effective in selection for herbicide resistance in rice, as it has been in maize and other crops (SHANER and ANDERSON, 1985). Currently it is becoming politically unpopular in the public sector to select for herbicide resistant crop plants in the USA, but much work apparently is underway in the private sector.

REFERENCES

ANONYMOUS, 1991. IRRI goal: a new rice plant type. The IRRI Reporter 3:1.

ANONYMOUS, 1992. 1991 Rice Breeding Progress Report. In: Ric\ Expt.Sta., Calif.Coop.Rice Res.Found., Biggs, CA.

AWAN, M.A. 1991. Use of induced mutations for crop improvement in Pakistan. In: Plant Mutation Breeding for Crop Improvement. IAEA, Vienna, p. 67-72.

BARABAS, Z., Z. KERTESZ, L. PURNHAUSER, F. SAGI and J. PAUK. 1989. Breeding on a cellular level and research on F_1 hybrid development. In: Current Options for Cereal Improvement. Maluszynski, M. (Ed.) Kluwer Academic Publishers, Dordrecht, p. 11-18.

BARABAS, Z. 1991. Hybrid seed production using nutritional mutants. Euphytica 53:67-72.

BHATIA, C.R. 1991. Economic impact of mutant varieties in India. In: Plant Mutation Breeding for Crop Improvement. IAEA, Vienna, p. 33-45.

BOLLICH, C.N., B.D. WEBB, M.A. MARCHETTI and J.E. SCOTT. 1985. Registration of 'Lemont' rice. Crop Sci. 25:883-885.

BRANDON, D.M., H.L. CARNAHAN, J.N. RUTGER, S.T. TSENG, C.W. JOHNSON, J.F. WILLIAMS, C.M. WICK, W.M. CANEVARI, S.C. SCARDACI and J.E. HILL. 1981. California rice varieties: Description, performance and management. Division of Agricultural Sci., Univ. of Calif., Special Pub. 3271, pp. 39.

BURTON, G.W. and W.W. HANNA. 1982. Stable cytoplasmic male sterile mutants induced in tift 23DB, pearl millet with mitomycin and streptomycin. Crop Sci. 22:651-652.

CARNAHAN, H.L., C.W. JOHNSON and S.T. TSENG. 1978. Registration of M7 rice. Crop Sci. 18:356-357.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG and D.M. BRANDON. 1979. Registration of 'Calmochi-201' rice. Crop Sci. 19:746.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG and D.M. BRANDON. 1980. Registration of 'S-201' rice. Crop Sci. 20:551.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG and D.M. BRANDON. 1981a. Registration of 'M-401' rice. Crop Sci. 21:986-987.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG and J.N. RUTGER. 1981b. Registration of 'Calmochi-202' rice. Crop Sci. 21:985-986.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG and J.E. HILL. 1986. Registration of 'Calmochi-101' rice. Crop Sci. 26:197.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG, J.J. OSTER and J.E. HILL. 1987. Registration of 'M-102' rice. Crop Sci. 27:1311-1312.

CARNAHAN, H.L., C.W. JOHNSON, S.T. TSENG, J.J. OSTER, J.E. HILL and D.M. BRANDON. 1989. Registration of 'M-203' rice. Crop Sci. 29:1089-1090.

CHANG, T.T., C. ZUNO, A. MARCIANO-ROMENA and G.C. LORESTO. 1984. Semidwarfing genes in germplasm collection. RGN 1:94-95.

CLEMENT, G. and C. POISSON. 1988. Genetic determinants of semidwarf characters induced in *Oryza sativa* for upland rice cultivation. MBNL 31:5.

DEMING, J., L. ZEBING and W. JINGMENG. 1988. Use of photoperiod-sensitive genetic male sterility in rice breeding. In: Proc. Int. Symp. Hybrid Rice, Changsha, China. IRRI, Manila, p. 267-268.

FAO/IAEA. 1968. Rice Breeding with Induced Mutations. IAEA, Technical Report Series, No. 86, Vienna, pp. 1-156.

FAO/IAEA. 1970. Rice Breeding with Induced Mutations. II. IAEA, Technical Report Series No. 102, Vienna, pp. 1-124.

FAO/IAEA. 1971. Rice Breeding with Induced Mutations. III. IAEA, Technical report Series No. 131, Vienna, pp. 1-198.
FUJIMAKI, H., K. HIRAIWA, K. KUSHIBUCHI and S. TANAKA. 1977. Artificially induced male sterile mutants and their usage in rice breeding. Jpn. J. Breed. **27**:70-77.
FUTSUHARA, Y., K. TORIYAMA and K. TSUNODA. 1967. Breeding of a new rice variety 'Reimei' by gamma-ray irradiation. Jpn. J. Breed. **17**:13-18.
GALE, M.D. and S. YOUSSEFIAN. 1985. Dwarfing genes in wheat. In: Progress in Plant Breeding. Russell, G.E. (Ed.) Butterworths, London, p. 1-35.
HARADA, J. and B.S. VERGARA. 1971. Response of different rice varieties to gibberellin. Crop Sci. **11**:373-374.
HARGROVE, T.R., W.R. COFFMAN and V.L. CABANILLA. 1980. Ancestry of improved cultivars of Asian rice. Crop Sci. **20**:721-727.
HU, C.H. 1973. Evaluation of breeding semidwarf rice by induced mutation and hybridization. Euphytica **22**:562-574.
HU, C.H. 1991. Use of induced semi-dwarfing gene to alter the rice plant type and cultural breeding practices for sustainable agriculture. In: Plant Mutation Breeding for Crop Improvement. IAEA, Vienna, p. 167-172.
HU, J. and J.N. RUTGER. 1991. A streptomycin induced no-pollen male sterile mutant in rice (*Oryza sativa* L.). J. Genet. Breed. **45**:349-352.
HU, J. and J.N. RUTGER. 1992. Pollen characteristics and genetics of spontaneous genetic male sterile mutants in rice. Plant Breeding **(In Press)**:
JACQUOT, M. 1986. Mutagenesis of upland rice at IRAT. MBNL **28**:10-12.
JAN, C.C 1992. Inheritance and allelism of mitomycin C- and streptomycin-induced recessive genes for male sterility in cultivated sunflower. Crop Sci. **32**:317-319.
JAN, C.C. and J.N. RUTGER. 1988. Mitomycin C-and streptomycin-induced male sterility in cultivated sunflower. Crop Sci. **28**:792-795.
JIANSAN, C., Y. LIN and C. WANJUN. 1988. A study on the apomixis in rice. Genetic Manipulation in Crops Newsletter **4** **(2)**:3-10.
JINGYANG, D. and G. ZHONGLI. 1982. Discovery and determination of a dominant male-sterile gene and its importance in genetics and wheat breeding. Sci. Sin. (Series B) **15**:508-520.
JOHNSON, C.W., H.L. CARNAHAN, S.T. TSENG and D.M. BRANDON. 1980. Registration of 'M-301' rice. Crop Sci. **20**:551.
JOHNSON, C.W., H.L. CARNAHAN, S.T. TSENG and J.E. HILL. 1981. Registration of 'M-302' rice. Crop Sci. **21**:986.
JOHNSON, C.W., H.L. CARNAHAN, S.T. TSENG, J.J. OSTER and J.E. HILL. 1986. Registration of 'M-202' rice. Crop Sci. **26**:198.
JOHNSON, C.W., H.L. CARNAHAN, S.T. TSENG, J.J. OSTER, J.E. HILL, J.N. RUTGER and D.M. BRANDON. 1989. Registration of 'S-101' rice. Crop Sci. **29**:1090-1091.
JOHNSON, C.W., H.L. CARNAHAN, S.T. TSENG, K.S. MCKENZIE, J.E. HILL, J.N. RUTGER and D.M. BRANDON. 1990. Registration of 'M-103' rice. Crop Sci. **30**:960-961.
JOHNSON, C.W., K.S. MCKENZIE, S.T. TSENG, J.J. OSTER, J.E. HILL, D.M. BRANDON and H.L. CARNAHAN. 1991. Registration of 'S-301' rice. Crop Sci. **31**:1090-1091.
JORGENSEN, J.H. 1991. Mutation studies on cereal disease resistance. In: Plant Mutation Breeding for Crop Improvement. Vol.2. IAEA, Vienna, p. 81-91.
KAUSHIK, R.P. and G.S. KHUSH. 1991. Genetic analysis of endosperm mutants in rice *Oryza sativa* L. Theor. Appl. Genet. **83**:146-152.

KAWAI, T. and E. AMANO. 1991. Mutation breeding in Japan. In: Plant Mutation Breeding for Crop Improvement. Vol. 1. IAEA, Vienna, p. 47-66.

KIKUCHI, F., N. ITAKURA, H. IKEHASHI, M. YOKOO, A. NAKANE and K. MARUYUMA. 1985. Genetic analysis of semidwarfism in high yielding rice varieties in Japan. Bull. Nat. Inst. Agric. Sci. **D36**:125-145.

KINOSHITA, T. 1991. Use of high technology by future plant breeders. In: Plant Mutation Breeding for Crop Improvement. Vol. 2. IAEA, Vienna, p. 471.

KO.T, and H. YAMAGATA. 1980. Studies on the utility of artificial mutations in plant breeding, XII. Induction and gene analysis of male-sterile mutants in rice. Jpn. J. Breed. **30**:367-374.

MAC KEY, J.F. 1991. Is plant breeding at the end, or can another breakthrough be expected? In: Plant Mutation Breeding for Crop Improvement. Vol. 2. IAEA, Vienna, p. 466-467.

MACKILL, D.J. and J.N. RUTGER. 1979. Inheritance of induced-mutant semidwarfing genes in rice. J. Hered. **70**:335-341.

MALUSZYNSKI, M., A. MICKE and B. DONINI. 1986. Genes for semidwarfism in rice induced by mutagenesis. In: Rice Genetics. IRRI, Manila, p. 729-737.

MALUSZYNSKI, M., B. SIGURBJORNSSON, E. AMANO, L. SITCH and O. KAMRA. 1991. Mutant varieties - data bank, FAO/IAEA database. MBNL **38**:16-21.

MATSUO, T., M. YANO, H. SATOH and T. OMURA. 1987. Effects of sugary and shrunken mutant genes on carbohydrates in rice endosperm during ripening period. Jpn. J. Breed. **37**:17-21.

McKENZIE, K.S., C.N. BOLLICH, J.N. RUTGER and K.A.K. MOLDENHAUER. 1987. Rice, Principles of Cultivar Development Vol. 2. MacMillian Pub.Co., N.Y., pp. 487-532.

McKENZIE, K.S., C.N. BOLLICH, D.E. GROTH, F. JODARI, J.F. ROBINSON and J.N. RUTGER. 1988. Registration of 'Mercury' rice. Crop Sci. **28**:193-194.

McKENZIE, K.S. and J.N. RUTGER. 1986. A new semidwarf mutant in a long grain rice cultivar. Crop Sci. **26**:81-84.

MESE, M.D., L.E. AZZINI and J.N. RUTGER. 1984. Isolation of genetic male sterile mutants in a semidwarf japonica rice cultivar. Crop Sci. **24**:523-525.

MICKE, A., B. DONINI and M. MALUSZYNSKI. 1987. Induced mutations for crop improvement--a review. Trop. Agric. **64**:259-278.

MIN, S., X. QI, Z. XIONG and C. ZHAO. 1989. Effects of gamma-radiation treatment in somatic cell culture of indica rice Basmati 370 selection. Proc. 6th Int. Congr. SABRAO, p. 793-796.

MULLER, H.J. 1927. Artificial transmutation of the gene. Science **66**:84-87.

MUTATION BREEDING NEWSLETTER (MBNL) No. 5. 1975. IAEA, Vienna. p. 1-8.

MUTATION BREEDING NEWSLETTER (MBNL) No. 19. 1982. IAEA, Vienna. p. 1-22.

MUTATION BREEDING NEWSLETTER (MBNL) No. 21. 1983. IAEA, Vienna. p. 1-20.

MUTATION BREEDING NEWSLETTER (MBNL) No. 25. 1985. IAEA, Vienna. p. 1-28.

MUTATION BREEDING NEWSLETTER (MBNL) No. 30. 1987. IAEA, Vienna. p. 1-32.

MUTATION BREEDING NEWSLETTER (MBNL) No. 37. 1991. IAEA, Vienna. p. 1-48.

MUTATION BREEDING NEWSLETTER (MBNL) No. 38. 1991. IAEA, Vienna. p. 1-56.

NOVAK, F.J. 1991. *In vitro* mutation system for crop improvement. In: Plant Mutation Breeding for Crop Improvement. Vol. 2. IAEA, Vienna, p. 327-342.

OARD, J.H., J. HU and J.N. RUTGER. 1991. Genetic analysis of male sterility in rice mutants with environmentally influenced levels of fertility. Euphytica 55:179-186.

OBA, S., F. KIKUCHI and K. MARUYAMA. 1990. Genetic analysis of semidwarfness and grain shattering of Chinese rice variety 'Ai-Jio-Nan-Te'. Jpn. J. Breed. **40**:13-20.

OKUNO, K. and T. KAWAI. 1977. Induction of short-culm mutants and inheritance of induced short-culm mutants in rice. Gamma Field Symp. **16**:39-62.

RUTGER, J.N. 1983. Applications of induced and spontaneous mutation in rice breeding and genetics. Adv. Agron. **36**:383-413.

RUTGER, J.N. 1991. Mutation breeding of rice in California and the United States of America. In: Plant Mutation Breeding for Crop Improvement. Vol. 1. IAEA, Vienna, p. 155-165.

RUTGER, J.N. 1992. Searching for apomixis in rice. In: Proc. Apomixis Workshop. USDA-ARS, Atlanta, GA., p. 36-39.

RUTGER, J.N. and T.R. ANDERSON. 1988. Evaluation, inheritance, and gibberellin response of induced semidwarf mutants of rice. In: Semi-Dwarf Cereal Mutants and Their Use in Cross-Breeding III. IAEA-TECDOC-455 , Vienna, p. 125-133.

RUTGER, J.N. and H.L. CARNAHAN. 1981. A fourth genetic element for facilitating hybrid seed production in cereals - a recessive tall in rice. Crop Sci. **21**:373-376.

RUTGER, J.N. and M.L. PETERSON. 1981. Research tool uses of rice mutants for increasing crop productivity. In: Induced Mutations - A Tool in Plant Breeding. IAEA, Vienna, p. 457-468.

RUTGER, J.N. and G.W. SCHAEFFER. 1989. An environmentally-sensitive genetic male sterile mutant in rice. Agron. Abstr. 98.

RUTGER, J.N., L.E. AZZINI and P.J. BROOKHOUZEN. 1986. Inheritance of semidwarf and other useful mutant genes in rice. In: Rice Genetics. Proc. International Rice Genetics Symposium. IRRI, Manila, p. 261-271.

RUTGER, J.N., H.L. CARNAHAN and C.W. JOHNSON. 1982. Registration of 10 germplasm lines of rice. Crop Sci. **22**:164-165.

RUTGER, J.N., R.A. FIGONI, R.K. WEBSTER, J.J. OSTER and K.S. McKENZIE. 1987. Registration of early maturing, marker gene, and stem rot resistant germplasm lines of rice. Crop Sci. **27**:1319-1320.

RUTGER, J.N., K.W. FOSTER, K.S. McKENZIE, D.J. MACKILL, M.L. PETERSON and C.H. HU. 1979a. Registration of six germplasm lines of rice. Crop Sci. **19**:299-300.

RUTGER, J.N., M.L. PETERSON, H.L. CARNAHAN and D.M. BRANDON. 1979b. Registration of 'M-101' rice. Crop Sci. **19**:929.

RUTGER, J.N., M.L. PETERSON and C.H. HU. 1977. Registration of 'Calrose 76' rice. Crop Sci. **17**:978.

RUTGER, J.N., M.L. PETERSON, C.H. HU and W.F. LEHMAN. 1976. Induction of useful short stature and early maturing mutants in japonica rice (*Oryza sativa* L.) cultivars. Crop Sci. **16**:631-635.

RYDER, E.J. 1985. Use of early flowering genes to reduce generation time in backcrossing, with specific application to lettuce breeding. J. Am. Soc. Hortic. Sci. **110**:570-573.

RYDER, E.J. 1988. Early flowering in lettuce as influenced by a second flowering time gene and seasonal variation. J. Am. Soc. Hortic. Sci. **113**:456-460.

SATO, H. 1982. Since Reimei: its use for rice breeding. Gamma Field Symp. **21**:1-6.

SATOH, H. 1985. Genetic mutations affecting endosperm properties in rice. Gamma Field Symp. **24**:17-35.

SHANER, D.L. and P.C. ANDERSON. 1985. Mechanism of action of the imidazolinones and cell culture selection of tolerant maize. In: Biotechnology in Plant Science. Zaitlin, M., P. Day, A. Hollaender and C.M. Wilson. (Eds.). Academic Press, New York, p. 287-299.

SHI, M. 1985. The discovery and study of the photosensitive recessive male-sterile rice (*Oryza sativa* L. subsp. *japonica*). Sci. Agri. Sin. **2**:44-48.

SINGH, R.J. and H. IKEHASHI. 1981. Monogenic male sterility in rice: Induction, identification, and inheritance. Crop Sci. **21**:286-289.

SORRELS, M.E. and S.E. FRITZ. 1982. Application of a dominant male-sterile allele to the improvement of self-pollinated crops. Crop Sci. **22**:1033-1035.

STADLER, L.J. 1928. Mutations in barley induced by X-rays and radium. Science **68**:186-187.

TAKAMURE, I. and T. KINOSHITA. 1985. Inheritance and expression of reduced culm number character in rice. Jpn. J. Breed. **35**:17-24.

TREES, S.C. and J.N. RUTGER. 1978. Inheritance of four genetic male steriles in rice. J. Hered. **9**:270-272.

TSENG, S.T., C.W. JOHNSON, A.A. GRIGARICK, J.N. RUTGER and H.L. CARNAHAN. 1987. Registration of short stature, early maturing, and water weevil tolerant germplasm lines of rice. Crop Sci. **27**:1320-1321.

VIRMANI, S.S., R.D. DALMACIO and M.T. LOPEZ. 1988. *eui* gene for elongated uppermost internode transferred to indica rice. IRRN **13 (6)**:6.

WANG, L.Q. 1991. Induced mutation for crop improvement in China. In: Plant Mutation Breeding for Crop Improvement. Vol. 1. IAEA, Vienna, p. 9-32.

YUAN, L.P. 1990. Progress of two-line system hybrid rice breeding. Sci. Agri. Sin. **233**:1-6.

ZHAO, D.J. 1980. Yuanfengzao, a radiation-induced mutant rice cultivar, and its performance. Appl. At. Energy Agric. **4**:1-6.

ZONGTAN, S. and H. ZUHUA. 1989. Transfer *eui* gene to WA-MS line Zhen-Shan 97A (*Oryza sativa* ssp. *indica*) and eliminating its panicle enclosure. IRRN **14 (4)**:8-9.

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