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Genetics of fertility restoration of 'WA'-based cytoplasmic male sterility system in rice (*Oryza sativa*) using *indica/japonica* derivative restorers

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ABSTRACT: Exploitation of the higher degree of heterosis manifested in inter sub-specific (*indica* and *indica/japonica*) derivatives is one of the current trends in hybrid rice breeding. The success in developing *indica/japonica* hybrids using new plant type restorers developed from *indica/japonica* derivatives largely depends on the availability of effective restorers and knowledge of the genetics of fertility restoration of such derivative lines. A study using three *indica/japonica* restorers (P1277-100, P1266-89, and P1266-8) and three 'WA'-type cytoplasmic male sterile lines (Pusa 3A, Pusa 5A, and Pusa 6A) revealed that two or three major genes govern the fertility restoration, with epistatic interactions that differed from cross to cross. Crosses Pusa 6A/P1277-100 and Pusa 3A/P1266-89 showed a segregation ratio of 12:3:1 and 2:1:1 in F_2 and BC_1 generations, respectively, for pollen fertility, indicating two major genes with dominant epistasis involved in fertility restoration. The restorer P1266-89, when crossed with Pusa 5A, segregated in different digenic ratios of 9:3:4 and 1:1:2 in F_2 and BC_1 generations, respectively, for pollen fertility, indicating two major genes with recessive epistasis involved in fertility restoration. The same restorer P1266-89 when crossed with Pusa 6A, segregated in ratios of 27:30:7 and 1:2:1 in F_2 and BC_1 generations, respectively, indicating three major genes governing fertility restoration. Restorer P1266-8 when crossed with Pusa 5A and Pusa 6A, gave the same segregation ratios of 27:30:7 in F_2 and 1:2:1 in BC_1 generation, indicating that fertility restoration is also governed by three major genes.

KEYWORDS: *indica/japonica* hybrids, NPT restorers

INTRODUCTION

Among the various approaches for improving the yield threshold of rice, exploitation of hybrid vigour is considered to be the most feasible and readily practicable. China pioneered hybrid rice research in the 1970's and demonstrated 20–30% yield advantage over conventional varieties [1,2]. The hybrids grown in China, India, Vietnam, Bangladesh, and other countries are based on *indica* rice sources which on average show a standard heterosis of 15–20% in commercial cultivation mainly due to the narrow genetic diversity in the *indica* source material.

With the availability of wide compatibility genes allowing normal spikelet fertility in *indica/japonica* hybrids, exploitation of heterosis between two subspecific groups has become possible. Hybrids from *indica* and *japonica* parents have been reported to show 30–40% yield advantage over the best existing *indica/indica* hybrid [3]. Although the level of heterosis in *indica/japonica* hybrids is quite high, their parental lines being too diverse for grain characteristics, they suffer from serious problems of grain quality. To overcome such problems, efforts are being made to develop the hybrids using *indica/japonica* derived lines with improved grain quality.

Genetics of fertility restoration in WA-CMS lines has already been investigated. However, conclusions regarding the number of nuclear genes controlling fertility restoration depend on the materials and methods used. The genetics of fertility restoration in WA-CMS lines has been shown to follow monogenic [4,5], digenic [6], digenic with different types of interaction [7–10], trigenic [10–12], and trigenic interactions [13]. Nevertheless, most of the investigations tend to indicate that fertility restoration of the WA cytosterility system is controlled by two nuclear genes. Even though attempts have been made to understand the nature of inheritance of fertility restoration, most of the information available in this aspect is based

on *indica/indica* or *japonica/japonica* crosses. Not much information is available on genetic behaviour of fertility restoration in the *indica/japonica* genetic background, on which the success of hybrids would depend. This necessitates a study on the genetics of fertility restoration of *indica/japonica* derived restorer lines for improving the restoring ability and breeding of new plant type (NPT) restorer lines to use in developing rice hybrids with enhanced level of heterosis.

MATERIALS AND METHODS

The three restorers, P1277-100, P1266-89, and P1266-8, from *indica/japonica* derived lines were crossed with cytoplasmic male sterile (CMS) lines Pusa 3A, Pusa 5A, and Pusa 6A possessing 'WA' cytoplasm for the study of genetics of fertility restoration. The crosses were made between Pusa 3A, Pusa 5A, Pusa 6A, and the three new plant type restorers to produce F_1 seeds at IARI, New Delhi during the autumn harvest 2002 (June–November). The plants of F_1, their respective pollinators, and CMS lines were raised during the off-season 2002–2003 (December–May) at RBGRC, Aduthurai, Tamil Nadu using single seedling per hill at a spacing of 20×20 cm. Each F_1 and the corresponding pollen parent were grown in 2 m long rows side by side and CMS lines were grown in isolation. Uniform agronomic practices were followed while raising the crop. The crosses were made at Aduthurai to produce F_1 ($A \times PP$) and sufficient test cross seeds ($A \times F_1$'s) for raising an appropriate plant population of each combination for genetic study. Seeds were harvested from each F_1 plant as F_2 and from respective A lines as F_1 and BC_1F_1 for growing in the next season.

The F_1, F_2, and BC_1F_1 seeds of each cross were planted at IARI, New Delhi during the autumn harvest 2003, at a spacing of 20×15 cm and having a plant population of 20, 250–300, and 100–150 plants per cross in the respective generations. Since a sufficient number of seedlings could not be obtained in the case of the test cross progenies (Pusa 3A/Pusa 3A/SPS89), only observations of F_2 populations were recorded. The data were recorded on both pollen and spikelet fertility. Since spikelet fertility data did not give any convincing pattern as it is influenced by several physiological and environmental factors, the data on pollen fertility were considered reliable for the study. The spikelet fertility is also influenced by pollen of partial stainability. Pollen fertility studies were conducted using 0.5% iodine and 2% potassium iodide solution, where due care was taken about the proper sampling from F_1, BC_1, and F_2 populations. Anthers were collected from three randomly chosen spikelets (top and middle) and pollen grains were teezed out of the anther on a glass slide. The fertile and sterile pollen grains were counted in three microscopic fields under a binocular microscope. Pollen fertility was calculated as the ratio between the number of fertile pollen grains (stained round) and the total number of pollen grains in the microscopic field (i.e., fertile and sterile).

Plants were classified into different fertility-sterility groups as was done by Chaudhary et al[14]. Plants with more than 60% fertile pollen were grouped as fully fertile (FF), those with 30–60% fertile partial fertile (PF), those having 1–30% fertile pollen as partial sterile (PS) and those which had 0% were grouped as completely sterile (CS). The goodness of fit for various Mendelian genetic ratios in F_2s and test cross progenies ($CMS \times F_1$s) was tested using the χ^2 statistic.

RESULTS AND DISCUSSION

Pollen fertility ranged between 63% in P 5A/P1266-8 to 79% in P 3A/P1266-89 (Table 1). The restorer P1266-89 showed varying levels of pollen fertility (75–79%) with different CMS lines. Similar trends of pollen fertility (63–71%) were observed in the case of restorer P1266-8. The results revealed that fertility restoration is under dominant gene control and the degree of restoration varied with the CMS lines. The pollen fertility results (Table 2) suggested that relatively few genes were involved in fertility restoration in the crosses studied.

Some of the recent reports clearly show that two independent dominant genes with sporophytic mode control the fertility restoration of WA cytoplasm[15,16]. Mapping and genetic analysis using molecular markers (restriction fragment length polymorphism markers) have revealed that the fertility restorer loci in WA CMS system are located on chromosomes 1 and 10 and that both loci have major effects on almost complete dominance on fertility restoration with the chromosome 10 locus having larger effect than its counterpart. It was also stated that the two loci acted as a pair of classical duplicate genes; a single

Table 1 Pollen fertility scores in F_1 hybrids.

Cross combination	Pollen fertility (%)
Pusa 6A/P1277-100	77
Pusa 3A/P1266-89	79
Pusa 5A/P1266-89	78
Pusa 6A/P1266-89	75
Pusa 5A/P1266-8	63
Pusa 6A/P1266-8	71

Table 2 Segregation for pollen fertility restoration in F_2 populations and test cross progenies.

Cross combination	Generation	Total no. of plants scored	Segregation pattern: No. of plants with pollen fertility reaction					Genetic ratio (FF:SF:CS)	p-value
			FF	PF	PS	SF	CS		
P 6A × P1277-100	F_2	150	113	21	11	32	5	12:3:1	0.28
P 6A × (P 6A × P1277-100)	BC_1	51	23	6	9	15	13	2:1:1	0.72
P 3A × P1266-89	F_2	150	106	29	9	38	6	12:3:1	0.08
P 5A × P1266-89	F_2	150	82	16	17	33	35	9:3:4	0.60
P 5A × (P 5A × P1266-89)	BC_1	77	23	9	10	19	34	1:1:2	0.54
P 6A × P1266-89	F_2	150	61	33	38	71	18	27:30:7	0.89
P 6A × (P 6A × P1266-89)	BC_1	76	17	10	28	38	21	1:2:1	0.81
P 5A × P1266-8	F_2	150	65	29	42	71	14	27:30:7	0.82
P 5A × (P 5A × P1266-8)	BC_1	57	12	6	27	33	12	1:2:1	0.49
P 6A × P1266-8	F_2	150	65	27	45	72	13	27:30:7	0.68
P 6A × (P 6A × P1266-8)	BC_1	53	12	5	22	27	14	1:2:1	0.76

FF = Fully fertile, PF = Partial fertile, PS = Partial sterile, PF + PS = SF (semi fertile), CS = Complete sterile, P = Pusa
Data for one test cross (P3A//P3a × P1266-89) were unavailable. Observations were recorded on only the F_2 population.

dominant allele at one of the two loci would suffice to restore the fertility to normal or nearly normal[17].

In the present study, the inheritance of fertility restoration in the cross Pusa 6A/P1266-100 reveals an F_2 segregation ratio of 12:3:1 (FF:SF:CS), indicating the involvement of two dominant genes which exhibit dominant epistasis (Table 2). This suggests that two dominant genes Rf_3 and Rf_4 seem to control the fertility restoration. The effect of one of the two dominant genes (Rf_3) in restoring fertility appears to be strong and as good as the two together while the other gene (Rf_4) showed weak restoration. The homozygous or heterozygous plants for both the dominant genes (Rf_3— Rf_4—) and those having homozygous or heterozygous dominant gene (Rf_3—) and homozygous recessive gene (rf_4rf_4) were fully fertile. This indicated that the strong dominant gene Rf_3 alone could control the fertility restoration. While the plants homozygous for rf_3rf_3 and homozygous dominant (Rf_4Rf_4) or heterozygous dominant (Rf_4rf_4) at Rf_4 locus were semi fertile. The plants homozygous for recessive alleles of both the genes (rf_3rf_3 rf_4rf_4) were completely sterile. The F_2 population of the cross Pusa 3A/P1266-89 exhibited a similar trend of segregation ratio of 12:3:1 of FF:SF:CS type of plants, also indicating the epistasis with dominant type gene action controlled by two dominant genes. The segregation behaviour of F_2 population was further confirmed by the ratio of 1:1:2 in the test cross but the BC_1 generation of the cross Pusa 3A/P1266-89 could not be confirmed due to insufficient plant population. An epistasis with dominant type gene action in the inheritance of fertility restoration of WA-CMS system has also been reported by earlier workers[7,8,18–21].

When the CMS line Pusa 5A was crossed with the restorer line P1266-89, the F_2 segregation for pollen fertility fell into the digenic ratio 9FF:3SF:4CS (Table 2). The results indicated the involvement of the digenic supplementary or an epistasis with recessive gene action. Assuming that Rf_3 and Rf_4 were the dominant alleles of the two restorer genes, the fertility restoring action of Rf_3 seemed to be stronger than Rf_4. The segregation pattern in the cross combination indicated that when both dominant genes were present together in heterozygous or homozygous condition (Rf_3— Rf_4—) the plants were fully fertile. The homozygous rf_4rf_4 plants with homozygous dominant (Rf_3Rf_3) or heterozygous dominant (Rf_3rf_3) for the Rf_3 gene fell in the semi-fertile group. The homozygous rf_3rf_3 plants with homozygous dominant (Rf_4Rf_4) or heterozygous dominant (Rf_4rf_4) for Rf_4 locus were completely sterile. The dominant allele of Rf_4 gene did not show any effect of fertility restoration in the absence of the other dominant allele of the Rf_3 gene. Thus, the two genes appeared to have additive effects in imparting full fertility restoration. The plants homozygous for recessive alleles of both the genes (rf_3rf_3 rf_4rf_4) were completely sterile. The F_2 ratio of 9:3:4 involving supplementary or epistasis with recessive gene action has been reported earlier by Shoud and Phul[8] in the crosses Yar-Al-Zhao A, a CMS line carrying WA cytoplasm with restorer lines IR-36, IR-9761, PAU-164 and PR-106. However, when these restorer lines were crossed with another CMS line V 20A carrying the WA cytoplasm, the different F_2 ratios of 9:6:1, 12:3:1, 12:3:1 and 12:3:1

were obtained in that order. Zhou[19] claimed that genetics of fertility restoration is likely to vary with CMS-restorer combination and the number of gene(s) controlling fertility restoration is not a fixed concept. Similarly, other researchers also showed the mode of inheritance of fertility restoration of WA-CMS lines to be under control of an epistasis with recessive gene action[7,10,19,21,22].

When the CMS line Pusa 6A was crossed with restorer P1266-89, the F_2 segregation ratio for pollen fertility was somewhat puzzling. The F_2 ratio of this cross did not fit any expected digenic ratio but fitted well to the trigenic ratio of 27:30:7 (FF:SF:CS), indicating the involvement of three dominant genes in the inheritance of fertility restoration. The results of the pollen fertility analysis in BC_1 generation with segregation ratio of 1:2:1 for FF, SF and CS plants were in agreement with the F_2 segregants. Assuming that two dominant genes, one with strong (Rf_3) and the other with weak effect (Rf_4), confer fertility in the plants and one dominant gene (Rf_e') enables or enhances the expression of weak restorer gene; the restoration pattern is expected to segregate into a 27:30:7 F_2 ratio. The observed segregation pattern (Table 2) showed a close correspondence with the segregation ratio expected on the basis of the proposed hypothesis. The segregation pattern in the cross combination indicated that when three dominant genes were present together in heterozygous or homozygous condition (Rf_3— Rf_4— Rf_e'—), the plants were fully fertile. The plants homozygous dominant (Rf_3Rf_3) or heterozygous dominant (Rf_3rf_3) for the Rf_3 gene or the homozygous rf_3rf_3 plants, which were homozygous dominant or heterozygous dominant (Rf_4— Rf_e'—) for Rf_4 and Rf_e' genes were in the semi-fertile group. From the segregation ratio as noticed in BC_1 generation of these crosses, it was evident that the gene which enables or enhances the expression of the weak restorer gene is contributed to by the genetic background of the CMS lines. Thus, it appears that the plants homozygous for the recessive allele of the gene ($rf_e'rf_e'$) which enables the expression of weak restorer gene will be completely sterile even with the homozygous or heterozygous condition for the weak restorer gene (rf_3rf_3 Rf_2— $rf_e'rf_e'$).

The crosses of Pusa 5A/P1266-8 and Pusa 6A/P1266-8 also showed the same trigenic ratio of 27:30:7 (FF:SF:CS) as in the F_2 population which was confirmed by the 1:2:1 segregation ratio of their BC_1 populations (Table 2). Through RFLP analysis, three loci (one major and two minor) conferring significant effects on fertility restoration have been identified[23]. The segregation pattern of crosses showing trigenic epistatic interaction has also been reported by many workers[8,11–13].

The digenic and trigenic pattern of fertility restoration observed in the present crosses is in accordance with the earlier reports. The common restorer line PRR78, when crossed with the CMS lines Pusa 3A and IR58025A, showed monogenic and digenic patterns of fertility restoration[22]. The explanation of obtaining different ratios of the same restorer is that the two F_1 hybrids differ from each other in respect of nuclear genetic contribution from CMS lines which are obviously different. After one cycle of meiosis the genomic contribution from the CMS and restorer lines is randomly distributed to different F_2 plants and, unlike the F_1 plants, the F_2 plants are likely to have the different genetic constitution. This change in genetic background as a result of recombination is likely to have an influence on the genetics of fertility restoration.

The differential mode of action of restorer genes could presumably be due to the influence of the female parent genotype or to the variable expression of the weaker gene in different genetic backgrounds. The differential segregation behaviour could also be due to the existence of certain modifiers influencing the penetrance and expressivity of the fertility-restorer genes. The trigenic epistatic ratio obtained during the present study in three crosses may partly account for complicated genetics of fertility restoration in inter-subspecific crosses.

A clear mode of the genetics of fertility restoration can be established by developing isogenic lines differing for the *Rf* locus and developing segregating population from such near isogenic lines. This approach could eliminate the influence of the genetic background of the CMS line on restoration of fertility. For example, if the Pusa 6A CMS lines are crossed with restorer PRR-78, the genotype of F_1 hybrids will be *Rf rf* with the CMS source of Pusa 6A. After 6–7 generations of repeated backcrossing, the F_1 plants (iso-cytoplasmic) to the Pusa 6A near isogenic lines will be generated having the genotype of *Rf rf*. On selfing and progeny testing, Pusa 6R (*Rf Rf*) will be generated. The cross between Pusa 6A with Pusa 6R will produce an F_2 population having all the plants genetically similar which will be ideal for the study of genetics of fertility restoration without the influence of the undesirable genetic effect of a CMS line on restoration of fertility. On the basis of the above results, the proposed genetic constitution of CMS lines, NPT restorer lines, and their F_2 segregants is presented in Table 3.

Table 3 Proposed genetic constitution of CMS lines, restorer lines and their F_2 segregants.

Sl No.	Cross combination	Genetic constitution				
		CMS	Restorer	F_2 segregants		
				FF	SF	CS
1	P6A/P1277-100	rf_3rf_3 rf_4rf_4	Rf_3Rf_3 Rf_4Rf_4	9 Rf_3— Rf_3— 3 Rf_3— rf_4rf_4	3 rf_3rf_3 Rf_4—	1 rf_3rf_3 rf_4rf_4
2	P3A/P1266-89	rf_3rf_3 rf_4rf_4- $Rf_e'Rf_e'$	Rf_3Rf_3 Rf_4Rf_4- $Rf_e'Rf_e'$	9 Rf_3— Rf_4— 3 Rf_3— rf_4rf_4	3 rf_3rf_3 Rf_4—	1 rf_3rf_3 rf_4rf_4
3	P5A/P1266-89	rf_3rf_3 rf_4rf_4- $Rf_e'Rf_e'$	Rf_3Rf_3 Rf_4Rf_4- $Rf_e'Rf_e'$	9 Rf_3— Rf_3—	3 Rf_3— rf_4rf_4	3 rf_3rf_3 Rf_4— 1 rf_3rf_3 rf_4rf_4
4	P6A/P1266-89	rf_3rf_3 rf_4rf_4- $rf_e'rf_e'$	Rf_3Rf_3 Rf_4Rf_4- $Rf_e'Rf_e'$	27 Rf_3— Rf_4— Rf_e'—	9 Rf_3— Rf_4— $rf_e'rf_e'$ 9 Rf_3— rf_4rf_4— Rf_e'— 3 Rf_3— rf_4rf_4— $rf_e'rf_e'$ 9 rf_3rf_3 Rf_4— Rf_e'—	3 rf_3rf_3 Rf_4— $rf_e'rf_e'$ 3 rf_3rf_3 rf_4rf_4 Rf_e'— 1 rf_3rf_3 rf_4rf_3 $rf_e'rf_e'$
5	P5A/P1266-8	rf_3rf_3 rf_4rf_4- $rf_e'rf_e'$	Rf_3Rf_3 Rf_4Rf_4- $Rf_e'Rf_e'$	27 Rf_3— Rf_4— Rf_e'—	9 Rf_3— Rf_4— $rf_e'rf_e'$ 9 Rf_3— rf_4rf_4— Rf_e'— 3 Rf_3— rf_4rf_4— $rf_e'rf_e'$ 9 rf_3rf_3 Rf_4— Rf_e'—	3 rf_3rf_3 Rf_4— $rf_e'rf_e'$ 3 rf_3rf_3 rf_4rf_4 Rf_e'— 1 rf_3rf_3 rf_4rf_4 $rf_e'rf_e'$
6	P6A/P1266-8	rf_3rf_3 rf_4rf_4- $rf_e'rf_e'$	Rf_3Rf_3 Rf_4Rf_4- $Rf_e'Rf_e'$	27 Rf_3— Rf_4— Rf_e'—	9 Rf_3— Rf_4— $rf_e'rf_e'$ 9 Rf_3— rf_4rf_4— Rf_e'— 3 Rf_3— rf_4rf_4— $rf_e'rf_e'$ 9 rf_3rf_3 Rf_4— Rf_e'—	3 rf_3rf_3 Rf_4— $rf_e'rf_e'$ 3 rf_3rf_3 rf_4rf_4 Rf_e'— 1 rf_3rf_3 rf_4rf_4 $rf_e'rf_e'$

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