Genetics of fertility restoration of diverse cytosterile sources in rice (Oryza sativa L.)

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Abstract

The availability of stable cytoplasmic male sterility and fertility restoring system is vital for commercial exploitation of heterosis in rice. Inheritance study using four effective fertility restorers (BL-184-AR, IR-54742-22- 19-3, NVSR-20 and Pusa Sugandha-5) and five diverse cytosterile sources (KJTCMS-6A-WA, RTN 2A-ARC, RTN 3A-Mutant of IR 62829B, RTN 13A-Gambiaca and RTN 17A-Dissi), their F₁, F₂ and BC₁ populations revealed that the **fertility restoration was governed by two independent genes, one of which appeared to be stronger in action than other. Crosses KJTCMS-6A X IR-54742-22-19-3, RTN-2A X BL-184-AR and RTN-2A X NVSR-20, RTN-3A X BL-184-AR and RTN-13A X NVSR-20, showed segregating ratio of 12 (fertile) : 3 (partially fertile + partially sterile): 1 (completely sterile plants) and 2 (fertile) : 1 (partial sterile/** fertile) : 1 (sterile) in F₂ and BC₁ generations respectively, **for pollen and spikelet fertility indicating two major genes with dominant epistasis. In case of crosses KJTCMS-6A X BL-184-AR and KJTCMS-6A X NVSR-20, RTN-13A X BL-184-AR, RTN-17A X BL-184-AR segregated in the ratio of** 9:6:1 and 1:2:1 in F₂ and BC₁ generations respectively, for **pollen and spikelet fertility indicating two major genes with epistasis and incomplete dominance. While crosses, KJTCMS-6A X Pusa Sugandha-5, RTN-2A X IR-54742-22- 19-3 and RTN-2A X Pusa Sugandha-5, RTN-3A X IR-54742- 22-19-3, RTN-3A X Pusa Sugandha-5 and RTN-3A X NVSR-20, RTN-13A X IR-54742-22-19-3, RTN-13A X Pusa Sugandha-5 and RTN-17A X IR-54742-22-19-3, RTN-17A X Pusa Sugandha-5, RTN-17A X NVSR-20, exhibited the restoration pattern fitted well in a segregation ratio of 9:3:4** and 1:1:2 in F₂ and BC₁ generations respectively, for pollen **and spikelet fertility displaying an epistasis with recessive interaction. The mode of action of these genes were different in different restorer combinations with five different sources of cytoplasmic genetic male sterility. Change in fertility restoration by same restorer with CMS line of same source and of different source could either due to cytoplasmic genetic interactions of CMS line and** **fertility restoring genes or may be affected by modifier genes.**

Key words: Inheritance, fertility restoration, CMS source, pollen and spikelet fertility, 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 hybrid 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. Hybrids from indica and japonica parents have been reported to show 30-40% yield advantage over the best existing indica/indica hybrid [3].

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 had been shown to follow monogenic [4], digenic [5], digenic with different types of interaction [6-8], trigenic [9, 10], and trigenic interactions [11]. 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

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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.

Knowledge on the nature and mode of gene action for fertility restoration in a CMS system facilitates the transfer of such genes into genetic background of elite lines and their subsequent utilization for the development of high yielding, fully fertile hybrids for commercial use. However, the nature of inheritance is still not well understood. Further, the fertility restorers selected in these studies were not always suitable for commercial exploitation due to either weak restoration ability or lack of good combining ability for developing three line commercial hybrids. In rice, several sources of cytoplasmic genetic male sterility (CGMS) have been reported [12]. However, intensive research work on inheritance of fertility restoration has been done mostly on the WA (Wild abortive) cytoplasmic source but very meagre in other sources. Therefore, the present investigation was undertaken to determine the genetics of fertility restoration of promising varieties/breeding lines of rice with five different cytosterile sources viz., Wild abortive, ARC, Mutant of IR-62829B, Gambiaca and Dissi.

Materials and methods

Twenty crosses were made in line x tester mating design by using five CMS lines from different CMS sources (KJTCMS-6A-WA, RTN 2A-ARC, RTN 3A-Mutant of IR 62829B, RTN 13A-Gambiaca and RTN 17A-Dissi) and four diverse, effective restorers fertility (BL-184-AR, IR-54742-22-19-3, NVSR-20 and Pusa Sugandha-5) by hand pollination at National Agricultural Research Project Farm, Navsari during rabi 2007-2008. Before pollination, sterility of female plants was checked and ensured to have 100 per cent pollen sterility as per procedure. Each CMS line was crossed to each of restorer to obtain 20 cross combinations. A part of resulting 20 F_1 s seed were selfed as well as backcrossed to their respective female parent to generate F_2 and BC₁ populations and the remaining part of the seed was used in the final experiment in subsequent season. The F_1s , F_2s and BC_{1s} of each cross were planted in Randomized Block Design (RBD), replicated thrice at NARP, NAU, Navsari during rabi 2008-2009 at a spacing 20 x 15 cm with 15, 191-313 and 127-161 plants of F_1s , F_2s and BC_{1s} respectively study to genetics of fertility restoration. All the agronomical practices and plant protection measures were followed as per recommendations. Observations were recorded on pollen and spikelet fertility. Genetics of fertility restoration was worked out through pollen and spikelet fertility studies following standard methodologies.

For pollen fertility studies, 5-10 randomly chosen spikelets covering the whole panicle (bottom, middle and top) of the every two panicles of each randomly selected five plants in each of the cross having fully matured anthers (about to dehisce) were collected in a vial containing 70 % alcohol. Two to three anthers from each spikelet were placed together on a glass slide, squashed and pollen grains were stained with 1 % iodine-potassium iodide stain (the stain was prepared by dissolving 1 g iodine and 2 g of potassium iodide in 100 ml of distilled water) and observations for fertile pollen grains were recorded under light microscope in three microscopic fields. Unstained, half stained, shrivelled and empty pollen grains were classified as sterile while well filled, stained and round pollen grains were recorded as fertile and those mixed with both the types were classified as partial fertile [13].

The pollen fertility in per cent was calculated as:

Number of fertile pollen grains

Pollen fertility (%) = --------------------------------------- x 100

Total number of pollen grains examined

Based on the scores recorded for pollen fertility, the genotypes were classified as effective restorers (> 80 pollen fertility), partial restorers (50.1 to 80 pollen fertility), partial maintainers (1.1 to 50 % pollen fertility) and maintainers (0 to 1 pollen fertility) [13].

Five randomly selected emerging panicles from each F_1 hybrid were bagged (to avoid out crossing) before flowering. The spikelet fertility and sterility were calculated on the basis of five randomly selected panicles from each F_1 at the time of maturity. The spikelet fertility was calculated in per cent as:

> Number of fertile spikelets in a panicle (filled)

Spikelet fertility (%) = ----------------------------------- x 100

Total number of spikelets in a panicle (filled and unfilled)

Based on the scores recorded for spikelet fertility, the genotypes were classified as effective restorers (>75 % spikelet fertility), partial restorers (50.1 to 75 spikelet fertility), partial maintainers (0.1 to 50 % spikelet fertility) and maintainers (0% spikelet fertility) [13]. The goodness

of fit for various Mendelian genetic ratios in the F_2 and $BC₁$ generations was tested by Chi square statistic.

Results and discussion

The spikelet fertility data on the parents and hybrids indicated that all the F_1 plants were completely fertile and identical to the restorer line (male parent) (Table 1). The Pollen and spikelet fertility ranged from 81.02 to 92.05 and 80.00 to 89.64 % respectively for parents while in hybrids, the range for pollen and spikelet fertility was from 80.57 to 90.03 and 80.31 to 89.56% respectively. All cross combinations showed more than 80 per cent pollen and spikelet fertility (Table 1). This indicated that restoration of fertility in the F_{1s} was inherited as a dominant trait.

Segregation behaviour for number and nature of genes controlling the fertility restoration using both pollen as well as spikelet fertility analysis in F_2 and BC₁ showed that the fertility restoration in all the lines are governed by two independent dominant genes, one of which is stronger in action than the other. But the mode of interaction of the genes, however, varied among crosses (Table 2). The presence of one of them conferred semi-sterility, although the two genes appeared to have additive effects in imparting the fertility restoration. Similar results were reported earlier using different restorer lines [7, 14]. It could be assumed that R_1 and R_2 were the dominant alleles of the two restorer genes and the plants having dominant alleles of the genes in homozygous or heterozygous condition $(R_1 - R_2)$ R_{2} were fully fertile. The plants having dominant alleles of the stronger gene in homozygous recessive allele of the weaker gene $(R_1-r_1r_2)$ and vice versa $(r_1r_2 R_1)$ were partially fertile, while those having homozygous alleles of both the recessive genes $(r_1r_1 r_2r_2)$ were completely sterile.

The crosses viz., KJTCMS-6A X IR-54742-22-19- 3 (WA cytosterile source), RTN-2A X BL-184-AR and RTN-2A X NVSR-20 (ARC source), RTN-3A X BL-184- AR (mutant source) and RTN-13A X NVSR-20 (Gambiaca source), segregated in F_2 generation in the ratio of 12 fertile: 3 (partially fertile + partially sterile): 1 completely sterile plants (Table 2). The test cross $(BC₁)$ data also confirmed the above results showing the segregation of fertile, partial fertile/sterile and completely sterile in the ratio of 2:1:1. Thus, the results indicated the involvement of two dominant genes in the inheritance of fertility restoration, which exhibited epistasis with dominant interaction. In this case, one of the dominant genes was epistatic to the other dominant

gene for fertility restoration ability. The plants having dominant alleles of the two genes in either homozygous or heterozygous condition (R_1,R_2) and those having dominant allele of one of the two genes in homozygous or heterozygous condition by homozygous for the other gene $(R_1 r_2 r_2$ or $r_1 r_1 R_2$) will be fertile completely, depending on the strength of the gene, thus grouped into one group. This shows the predominance of the stronger gene in its ability to restore fertility. These results have also been confirmed on the studies of earlier workers [5-7,11, 15-20] who reported an epistasis with dominant fertility restoring genes in the inheritance of fertility restoration of WA and Gambiaca CMS system, respectively.

In F₂ progenies crosses viz., KJTCMS-6A X BL-184-AR and KJTCMS-6A X NVSR-20 (WA cytosterile source), RTN-13A X BL-184-AR(Gambiaca source) and RTN-17A X BL-184-AR (Dissi source) segregated in the ratio of 9:6:1 was also confirmed from the segregation behaviour of the test-cross $(BC₁)$ progenies (1:2:1) revealing the role of two dominant independent genes in the inheritance of fertility restoration and displayed epistasis with incomplete dominance interaction. This indicated that two dominant genes are responsible for complete fertility, while only one of the either genes conferred partial fertility (semi-epistatic type of gene interaction). The plants homozygous for the recessive allele of any one of the two genes but homozygous or heterozygous for the dominant alleles of the other gene $(R_1 r_2 r_2$ or $r_1 r_1 R_2$) were sterile depending upon which of the two genes is stronger or weaker. These results are in accordance with the earlier reports of WA CMS lines [14, 16-20].

The segregation pattern of F_2 population in crosses, KJTCMS-6A X Pusa Sugandha-5 (WA source), RTN-2A X IR-54742-22-19-3 and RTN-2A X Pusa Sugandha-5 (ARC source), RTN-3A X IR-54742-22-19- 3, RTN-3A X Pusa Sugandha-5 and RTN-3A X NVSR-20 (mutant source), RTN-13A X IR-54742-22-19-3, RTN-13A X Pusa Sugandha-5 (Gambiaca source) and RTN-17A X IR-54742-22-19-3, RTN-17A X Pusa Sugandha-5, RTN-17A X NVSR-20 (Dissi source) exhibited the restoration pattern fitted well in a segregation ratio of 9:3:4 was also confirmed by the segregation pattern (1:1:2) of the plants for pollen and spikelet fertility in the testcross progeny $(BC₁)$. displaying an epistasis with recessive interaction. This indicated that single recessive gene was epistatic over the other dominant gene for fertility restoration, making the individual plants sterile like the double recessive

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rice **Table 1.** Percent of pollen and spikelet fertility in hybrids and their male parents of rice $\rm \breve{o}$ Percent of pollen and spikelet fertility in hybrids and their male parents Table 1.

condition. The other single dominant gene makes the individual partial fertile, while the presence of both the dominant genes makes the individual plant fertile. The plants where the recessive gene was allelic for any one of the two genes and homozygous or heterozygous for the dominant alleles of the other gene $(R_1 r_2 r_2$ or r_1 r_1R_2) were semi-sterile. Similar results were also reported by several authors [5-11, 14, 17-20] in the inheritance of fertility restoration of WA and Gambiaca CMS system, respectively.

Crosses KJTCMS-6A X IR-54742-22-19-3 (WA cytosterile source), RTN-2A X BL-184-AR and RTN-2A X NVSR-20(ARC source), RTN-3A X BL-184-AR (mutant of IR62829B source) and RTN-13A X NVSR-20 (Gambiaca source), showed segregating ratio of 12 (fertile) : 3 (partially fertile + partially sterile): 1 (completely sterile plants) and 2 (fertile) : 1 (partial sterile/ fertile) : 1 (sterile) in F_2 and BC_1 generations respectively, for pollen and spikelet fertility indicating two major genes with dominant epistasis involved in fertility restoration. In case of crosses KJTCMS-6A X BL-184-AR and KJTCMS-6A X NVSR-20 (WA cytosterile source), RTN-13A X BL-184-AR(Gambiaca source) RTN-17A X BL-184-AR(Dissi source) segregated in the ratio of 9:6:1 and 1:2:1 in F_2 and $BC₁$ generations respectively, for pollen and spikelet fertility indicating two major genes with epistasis and incomplete dominance involved in fertility restoration. While as crosses, KJTCMS-6A X Pusa Sugandha-5 (WA source), RTN-2A X IR-54742-22-19-3 and RTN-2A X Pusa Sugandha-5 (ARC source), RTN-3A X IR-54742-22-19-3, RTN-3A X Pusa Sugandha-5 and RTN-3A X NVSR-20 (mutant of IR62829B source), RTN-13A X IR-54742-22-19-3, RTN-13A X Pusa Sugandha-5 (Gambiaca source) and RTN-17A X IR-54742-22- 19-3, RTN-17A X Pusa Sugandha-5, RTN-17A X NVSR-20 (Dissi source), exhibited the restoration pattern fitted well in a segregation ratio of 9:3:4 and 1:1:2 in F_2 and $BC₁$ generations respectively, for pollen and spikelet fertility displaying an epistasis with recessive interaction**.** The mode of action of these genes were different in different restorer combinations with five different sources of cytoplasmic genetic male sterility, which exhibited three types of gene interactions in $F₂$ and confirmed in their BC_1 generation, epistasis with incomplete dominance (9:6:1and 1:1:2), epistasis with dominance (12:3:1 and 1:2:1) and epistasis with recessive interaction (9:3:4 and 1:1:2). Change in fertility restoration by same restorer with CMS line of same

	S.No. Crosses		Popu- lation	No. of plants intermediate			χ ² value	Genetic ratio (probability)	Popu- lation	No. of plants intermediate			χ ² value	Genetic ratio (probability)
				F	PF PS	CS				$\mathsf F$	PF PS	CS		
	W A source													
1	KJTCMS-6A x BL-184-AR	PF	250	136	69 31 100	14	0.738	9:6:1 (0.75 < P < 0.50)	135	36	33 37 70	29	0.911	1:2:1 (0.75 < P < 50)
			SF 259	156	67 21 88	15	1.674	9:6:1 (0.50 < P 0.25)	145	39	32 43 75	31	1.055	1:2:1 (0.75 < P < 0.50)
$\overline{2}$	KJTCMS-6A x IR-54742-22-19-3	PF	250	178	42 15 57	15	2.693	12:3:1 (0.50 < P < .25)	163	85	22, 15 37	41	0.497	2:1:1 (0.90 < P < 0.75)
			SF 260	189	29 26 55	16	0.990	12:3:1 (0.75 < P < 0.50)	151	78	21 18 39	34	0.497	2:1:1 (0.90 < P < 0.75)
3	KJTCMS-6A x Pusa Sugandha-5	PF	240	136	25 14 39	65	1.224	9:3:4 (0.75 < P < 0.50)	129	32	$12 \quad 16$ 28	69	0.876	1:1:2 (0.75 < P < 0.50)
		SF	209	117	21 16 37	55	0.270	9:3:4 (0.90 < P 0.75)	135	38	11 16 27	70	1.978	1:1:2 (0.50 < P < 0.25)
4	KJTCMS-6A x NVSR-20	PF	200	121	29 36 65	14	2.156	9:6:1 (0.50 < P < 25)	137	31	51 21 72	34	0.489	1:2:1 (0.90 < P < 0.75)
		SF	204	121	54 15 69	14	1.198	9:6:1 (0.50 < P < 25)	133	35	37 32 69	29	0.729	1:2:1 (0.75 < P < 0.50)
	ARC source													
5	RTN-2A x BL-184-AR PF 291			172	66 35 101	18	1.029	12:3:1 (0.75 < P < .50)	145	79	22 13 35	31	1.385	2:1:1 (0.75 < P < 0.50)
		SF	310	182	78 33 111	17	0.862	12:3:1 (0.75 < P < .50)	146	77	19 16 35	34	0.452	2:1:1 (0.90 < P < 0.75)
6	RTN-2A x IR-54742-22-19-3	PF	279	161	35 20 55	63	0.896	9:3:4 (0.75 < P < 0.50)	128	36	12 19 31	61	0.672	1:1:2 (0.75 < P < 0.50)
		SF.	290	166	34 24 58	66	0.875	9:3:4 (0.75 < P < 0.50)	136	37	22 11 33	66	0.353	1:1:2 (0.90 < P < 0.75)
$\overline{7}$	RTN-2A x Pusa Sugandha-5	PF	283	167	37 13 50	66	0.879	9:3:4 (0.75 < P < 0.50)	129	33	$12 \quad 14$ 26	70	1.698	1:1:2 (0.50 < P < 0.25)
		SF	286	168	32 20 52	66	0.788	9:3:4 (0.75 < P < 0.50)	142	35	16 18 34	73	0.127	1:1:2 (0.95 < P < 0.90)

Table 2. Segregation pattern of fertility restoration (pollen fertility (PF) and spikelet fertility (SF)) in F₂ and BC₁ population involving diverse cytosterile sources

Table 2 contd

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source and of different source could either due to cytoplasmic genetic interactions of CMS line and fertility restoring genes or may be affected by modifier genes. The four restorers viz., BL-184-AR, IR-54742-22-19-3, Pusa Sugandha-5, NVSR-20 were able to restore more than 80% fertility with all sources of cytoplasm, the segregation patterns in the CMS lines of said five cytosterile sources were different. The differential gene interaction could presumably be due to the influence of female parent genotype and/or a probable variation expression of the restorer genes in different genetic back ground [5-11, 14-16]. Certain minor or modifier genes could also be responsible for changing the segregation pattern [17-20].This knowledge on mode of action of fertility restoring genes makes us to sculpture the breeding objectives in hybrid rice technology.

In the present investigation, the genetic ratios were worked out by taking fertility/sterility as discrete qualitative traits, though the role of quantitative component can not be ruled out. The frequency distribution of seed set percentage was multimodal and may be influenced by genotype-environmental interactions. The differential mode of action of restorer genes could presumably be due to the interaction of the female parent cytoplasmic genes with restorer genotype, or to the variable expression of the weaker gene in different genetic backgrounds and genotypeenvironmental interactions. The differential segregation behaviour could also be due to the confounding effects of several factors, such as number and effectiveness of restorer genes, association of modifier complexes of varied strength and genetic background of female parent, purity of the male parent and other all environment influence.

The study has revealed the presence of fertility restoration gene(s) for five diverse cytoplasm in the genetical background of several elite lines studied. Four of the restorers are high yielding lines with several desirable traits. These restorer lines should offer much wider choice to plant breeder for direct exploitation in developing different commercial rice hybrids. Further, these restorers would help in breeding for new restorers with better productivity and quality traits by pedigree method. The use of restorers with more than one independent gene for fertility restoration is likely to produce the hybrids with higher fertility restoration and consequently increased yield.

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