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Gene action and fertility restoration behavior of the tropical *japonica/indica, japonica/indica* derived restorers in rice (*Oryza sativa* L.)

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Abstract

To study the gene action and fertility restoration behavior of tropical japonica/indica and *japonica/indica* derived advanced breeding lines, seven testers comprising new plant type i.e. NPT 2-2-694-1, NPT 9, NPT 80-1 and elite testers i.e., ET 1-12, ET 1-13, TOX 981-11-2-3 and R 1244-1246-1-605-1 along with three CMS lines i.e., APMS 6 A, CRMS 31 A and IR 79156 A and their generated 21 F_1 crosses were evaluated for yield and yield attributing traits in a randomized complete block design (RCBD) during wet season, 2010. The phenotypic quantitative data was undertaken as per L x T analysis. The genetic analysis registered the preponderance of positive non-additive gene action for all the traits, whereas negative for flag leaf length. All the seven testers exhibited either minor or additive cytoplasmic gene action which influenced the fertility restoration behavior of different combinations of the same pollen parent. The probability of the potential restorer combination (47.76) was more followed by partial restorers (28.57), potential maintainers (19.04) and partial maintainer (4.00). The high x high allelic reaction was highest in potential restorer combinations (70.00%) followed by partial restorers (16.67%), potential maintainers (0%) and partial maintainer (0.0%).The additive x additive reaction was found for the fertility restoration in 70% restorer combinations.

Key words: *Oryza sativa* L., CMS line, line x tester, variance, gene-action, additive, dominance, fertility restoration

Introduction

Cytoplasmic male sterility (CMS) and nuclear-controlled fertility restoration are wide-spread plant reproductive features that provide useful tools to exploit heterosis in crops [1]. The nature of gene action plays important role on the expression of the fertility restoration behaviour of the restorer in different cross combinations. The fertility restoration, GCA, SCA effects and *per se* performance of the genetic materials decide the true exploitation of potentiality of the heterotic combinations to exploit in practical level. High yield of F_1 hybrids depends largely upon high pollen or spikelet fertility which is determined by the mode of genes prevalent in the restorer lines of the hybrids [2, 3]. The knowledge of the genetic control of male fertility restoration is also useful to transfer fertility restoring genes to promising breeding lines and undertake improved restorer breeding programme. Fertility restorer alleles (*Rfs*) are always tightly evolved with cytoplasmic male sterility (CMS) during plant evolution. Research of *Rfs* inheritance is the precondition for breeders to develop elite restorer lines [4-6]. For studying the inheritance of the fertility of the restorers in general the main three indexes (percent of fertile pollen, bagged seed setting and open seed setting) are often used as the evaluation criteria to evaluate fertility restoration. Of these, the percentage of fertile pollen is thought to be the most reliable criteria for evaluating plant fertility [7]. The study was carried out to understand the nature of gene action and fertility restoration behavior of the advanced breeding lines from different genetic background and with three WA-CMS lines.

Materials and methods

Plant material

The breeding material comprised of three CMS lines *viz.,* APMS 6 A, CRMS 31A and IR 79156 A; seven testers i.e., three new plant type tropical *japonica/indica* derived advanced breeding lines *viz*., NPT 2-2-

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694-1, NPT 9 and NPT 80-1; two elite semi-dwarf *Japonica/indica* advanced breeding lines i.e., ET 1-12 and ET 1-13; other two advanced breeding lines i.e. TOX 981-11-2-3 from WARDA and R 1244-1246-1-605-1 from Raipur, IGKV and generated their twenty-one crosses.

Field experiment

To study the nature of gene action and fertility restoration behavior of the restorers, the crosses were attempted in L x T mating design, the parentages and their crosses were evaluated in randomized complete block design (RCBD) during *kharif* 2009 and *kharif* 2010 in the Research and Instructional Farm, IGKV, Raipur. The characterization was under taken for fifteen major traits including grain yield/per plant. All the genotypes were evaluated at phenotypic level and categorized the fertility restoration as per [8]. The spikelets fertility also influenced by partial pollen fertility. Pollen fertility study was conducted using IKI 1% stain. Anthers were collected from F_1 and their respective pollen parent from five randomly chosen spikelets (top to middle), preserved in 70% alcohol and pollen grains were treezed out of the anther on glass slide. The fertile and sterile pollen grains were counted in five microscopic fields under a compound light microscope. The pollen fertility was calculated as the ratio between the number of fertile (round and darkly stained) and sterile (yellow, sheveal, partially stained or unstained) pollen grain in the microscopic field.

Biometrical analysis

The field and lab evaluated quantitative records were analysed as per Kempthorne [9] for the estimation of genetic components *viz.,* GCA and SCA variance, GCA and SCA effect and gene action.

Results and discussion

Analysis of variance

The analysis of variance due to treatments, parents, hybrids, line x testers exhibited highly significant for all the fifteen traits i.e. days to 50% percent flowering, flag leaf length, flag leaf width, flag leaf area, pollen fertility (%), plant height, productive tillers per plant, panicle length, filled spikelets per panicle, sterile spikelets per panicle, spikelets per panicle, spikelets fertility (%), 1000-seed weight, grain yield per plant and head rice recovery (%) whereas, parents vs. hybrids were significant for all the traits except plant height and panicle length. On the other hand, testers were significant for days to 50% flowering, fertile spikelets per panicle and 1000-seed weight. All the traits under study exhibited the preponderance of non-additive gene action because the SCA variance was higher than the GCA variance. All the traits registered the role of positive non-additive gene action except flag leaf length (Table 1). The present finding also supported by the earlier findings [10, 11].

Gene action in top five per se performing crosses

The SCA effects as *per se* performance of top five crosses and the GCA effects of the respective parentages were screened for major nine traits where allelic reactions registered high x high in 20 crosses (44.44%), high x low in 11 crosses (24.44%) low x high in 10 crosses (22.22%) and low x low in 4 crosses (8.89%) crosses (Table 2). The high yield potential of cross combination with high x low GCA effects was attributed to interactions between positive alleles from good general combiner and negative alleles from poor combiner [12]. The results are getting support from other findings [13, 14] as well.

The cross combinations were categorized into four groups based on the phenotypic performance of pollen fertility (%) and spikelets fertility (%) i.e., potential restorer, partial restorer, potential maintainer and partial maintainer (7). Out of twenty one cross combinations, ten crosses recorded as potential

Table 1. General combining ability and specific combining ability variance

Characters	GCA variance	SCA variance	GCA/SCA ratio
Days to 50% flowering	004.94	028.69	0.172
Flag leaf length (cm)	-000.07	039.86	-1.756
Flag leaf width (cm)	000.00	000.04	0.000
Flag leaf area (cm^2)	012.54	040.68	0.308
Plant height (cm)	005.67	284.66	0.019
Productive tillers/plant	000.13	006.29	0.020
Pollen fertility (%)	036.01	809.58	0.044
Sterile spikelets/panicle	280.62	6647.87	0.042
Fertile spikelets/panicle	865.36	6216.96	0.139
Spikelets/panicle	066.90	3411.12	0.019
Spikelets fertility (%)	043.86	740.39	0.059
Panicle length(cm)	000.53	008.02	0.066
1000-seed weight (g)	000.77	014.86	0.052
Grain yield/plant (g)	3.45	187.29	0.018
Head rice recovery (%)	003.28	119.31	0.027

Table 2. Top five crosses with sca effects, *per se* performance and gca effects of parents for grain yield per plant and its components in rice

Character/cross	Mean performance	SCA effects	GCA effects		GCA status
			Line	Tester	
Days to 50% flowering (early)					
CRMS 31A x ET 1-13	74.50	–7.29**	0.62	–6.64**	H x L
CRMS 31A x ET 1-12	75.50	–2.95**	0.62	–9.98**	H x L
IR 79156A x ET 1-12	77.50	–16.44**	1.26	–9.98**	H x L
APMS 6A x ET 1-12	80.5	4.55**	–1.88	–9.98**	L x L
APMS 6A x NPT 2-2-694-1	80.50	–5.45**	–1.88	0.02	L x H
Flag leaf area (cm^2)					
CRMS 31A x ET 1-12	84.45	8.88**	–6.73**	22.07**	L x H
IR 79156A x ET 1-12	74.77	–18.77**	4.77**	22.07**	H x H
IR 79156A x ET 1-13	72.03	11.02**	4.77**	1.15	H x H
APMS 6A x ET 1-12	71.07	-0.32	1.96	22.07**	H x H
APMS 6A x NPT 2-2-694-1	70.74	10.23**	1.96	2.08**	H x H
Plant height (dwarfness)					
APMS 6A x TOX 981-11-2-3	85.50	–20.24**	–8.77**	–3.25**	L x L
CRMS 31A x ET 1-13	95.10	–18.56**	0.74	–4.85**	H x L
IR 79156A x ET 1-12	110.65	–31.88**	8.03**	–5.23**	H x L
CRMS 31A x ET 1-12	113.45	0.17	0.74	–5.23**	H x L
APMS 6A x ET 1-13	114.25	10.11**	–8.77**	–4.85**	L x L
Productive tillers per plant					
CRMS 31A x R 1244-1246-1-605-1	14.91	2.73**	–0.89	0.01	L x L
IR 79156A x NPT 80-1	13.20	–2.04**	1.99	1.97**	H x H
IR 79156A x NPT 9	10.33	–0.59	1.99	–0.71	H x L
APMS 6A x TOX 981-11-2-3	10.15	2.73**	–1.10	0.12	L x H
IR 79156A x TOX 981-11-2-3	9.86	–2.35**	1.99	0.12	H x L
Spikelets per panicle					
CRMS 31A x ET 1-12	423.00	2.51**	6.17**	30.00**	H x H
CRMS 31A x NPT 80-1	402.50	–3.63**	6.17**	40.33**	H x H
IR 79156A x NPT 80-1	402.50	–2.07**	9.02**	40.33**	H x H
CRMS 31A x R 1244-1246-1-605-1	365.00	–15.39**	6.17**	17.33**	H x H
CRMS 31A x TOX 981-11-2-3	340.00	–15.39**	6.17**	20.17**	H x H
Panicle length (cm)					
CRMS 31A x TOX 981-11-2-3	37.75	5.49**	2.38	1.64**	H x H
CRMS 31A x NPT 80-1	34.30	–0.90**	2.38	–4.47**	H x L
CRMS 31A x ET 1-12	32.87	–0.018	2.38	2.27**	H x H
IR 79156A x ET 1-13	30.12	3.149**	–0.86	0.40	L x H
APMS 6A x ET 1-12	29.73	0.75**	–1.53	2.27**	L x H
1000-seed weight (g)					
IR 79156A x NPT 80-1	34.30	6.06**	–0.61	6.10**	L x H
CRMS 31A x NPT 80-1	30.25	0.01	1.35	6.10**	H x H
CRMS 31A x NPT 9	26.44	3.62**	1.35	-0.83	H x L
IR 79156A x R 1244-1246-1-605-1	24.83	0.42	–0.61	3.21**	L x H
APMS 6A x NPT 9	24.25	3.08**	–0.74	–0.83	L x L
Grain yield per plant (g)					
IR 79156A x NPT 80-1	75.00	10.00**	6.05**	27.36**	H x H
CRMS 31A x NPT 80-1	74.46	12.33**	3.22	27.36**	H x H
APMS 6A x TOX 981-11-2-3	54.86	16.92**	–9.27**	15.62**	L x H
IR 79156A x TOX 981-11-2-3	54.76	1.50**	6.05**	15.62**	H x H
APMS 6A x R 1244-1246-1-605-1	44.45	15.61**	–9.27**	6.51**	L x H
Head rice recovery (%)					
CRMS 31A x R 1244-1246-1-605-1	54.58	–7.00	5.34**	4.11**	H x H
CRMS 31A x ET 1-12	54.21	12.91**	5.34**	–3.39**	H x L
CRMS 31A x ET 1-13	45.50	4.57**	5.34**	–3.77**	H x L
CRMS 31A x TOX 981-11-2-3	41.75	–7.00**	5.34**	4.02**	H x H
IR 79156A x NPT 2-2-694-1	40.85	10.42**	3.33**	8.37**	H x H

restorers (47.61%) followed by six crosses partial restorers (28.57%); four potential maintainers (19.04%); and one partial maintainer (4%) (Table 3). The high and low GCA effect may be due to the additive and non-additive gene action. High GCA indicates the presence of additive gene action and low for the non-additive i.e., dominance or epistasis gene action [11, 13, 16]. The high GCA is reporting to the positively significant GCA effects of the respective parentages and with the respective trait whereas, low GCA is reporting to the negative or negatively significant GCA effects of the respective traits of the parent [10], on the other hand parent having low GCA effects, such a behavior has been attributed to over dominance and epistasis [16].

Allelic reaction in potential restorer combination

The allelic reaction as per GCA effect for spikelets fertility percent was found high x high in eight (70%) among the potential restorer cross combinations i.e. APMS 6 A/ET 1-12, etc. on the other hand two (20%) allelic reaction was registered high x low i.e., in CRMS 31 A/NPT 9 and IR 79156 A/NPT 2-2-694-1 and with low x high in one (10%) cross combination i.e., APMS 6 A/ET 1-12 (Table 4). Therefore, majority of the crosses registered the high x high reaction followed by high x low and low x low for the trait spikelet fertility (%).

Allelic reaction in partial restorer combination

The allelic reaction as per GCA effects for pollen fertility and pollen fertility percent was recorded high x high in one (16.66%) cross combinations i.e., IR 79156 A/ET 1-12; on the other hand high x low in two (33.33%) cross combinations i.e. CRMS 31 A/ET 1-13 and IR 79156 A/ET 1-13; low x low in three (50%) i.e. APMS 6 A/NPT 80-1, APMS 6 A/TOX 981-11-2-3 and APMS 6 A/R 1244-1246-1-605-1 (Table 4).

Allelic reaction in potential maintainer combination

The allelic reaction as per GCA effects for pollen and spikelets fertility percent was recorded high x low in two (50%) cross combinations i.e., CRMS 31 A/NPT 2-2-694-1 and IR 79156 A/NPT 9; on the other hand low x low in two (50%) cross combinations i.e., APMS 6 A/NPT 2-2-694-1 and APMS 6 A/ET 1-13 (Table 4).

Allelic reaction in partial maintainer combination

A single cross combination exhibited as partial maintainers i.e. APMS 6 A/NPT 9 with low x low allelic reaction in pollen fertility and spikelets fertility per cent (Table 4).

The plant having dominant alleles of one of the genes in homozygous recessive or heterozygous condition but homozygous recessive alleles of the other gene (R/-r2r2 or r/r1R2) will behave partially sterile or partially fertile and vice-versa. The plants homozygous for the recessive alleles of both genes (r1r/r2r2) will be completely sterile [13, 17].

Fertility restoration behavior of the pollen parents with different CMS line in different combination

The tester NPT 2-2-694-1 is a potential restorer for IR 79156 A and on the other hand potential maintainer for APMS 6 A and CRMS 31 A. The tester NPT 9 was found potential restorer for CRMS 31 A and on the other hand potential maintainer for IR 79156A and partial maintainer for line APMS 6 A. The tester NPT 80-1 had registered potential restorers for CRMS 31 A and IR 79156 A and on the other hand partial restorer for APMS 6 A. The tester ET 1-12 exhibited as potential restorer for APMS 6 A and CRMS 31 A line whereas, partial restorer for IR 79156 A. The tester ET 1-13 found as partial restorer for CRMS 31 A and IR 79156 A and on the other hand partial maintainer

Table 3. Restorers and maintainers

Reaction lines	Potential restorers	Partial restorers	Potential maintainers	Partial maintainers
APMS 6 A	ET 1-12	NPT 80-1, TOX 981-11-2-3, R 1244-1246-1-605-1	NPT 2-2-694-1, ET 1-13	NPT 9
CRMS 31 A	NPT 9, NPT 80-1, ET 1-12, TOX 981-11-2-3, R 1244-1246-1-605-1	ET 1-13	NPT 2-2-964-1	-
IR 79156 A	NPT 2-2-694-1, NPT 80-1, TOX 981-11-2-3, R 1244-1246-1-605-1	ET 1-12, ET 1-13	NPT 9	-

Table 4. Gene action in potential restorer, partial restorer, potential maintainer and partial maintainer

Cross combination	Mean		SCA effects		GCA effects				GCA status	
					Female		Male			
	PF*	SF	PF	SF	PF	SF	PF	SF	PF	SF
Potential restorers										
APMS 6 A/ET 1-12	93.50	71.43	27.25	16.17	–18.25	–15.42	25.35	11.52	L x H	L x H
CRMS 31 A/NPT 9	82.50	83.97	30.20	42.15	08.96	08.49	–15.81	–30.87	H x L	H x L
CRMS 31 A/ NPT 80-1	77.50	83.97	1.04	-3.63	08.96	08.49	08.35	19.96	H x H	H x H
CRMS 31 A/ET 1-12	94.50	81.67	1.04	2.51	08.96	08.49	25.35	11.52	H x H	H x H
CRMS 31 A/TOX 981-11-2-3	77.00	73.52	–5.80	-15.39	08.96	08.49	14.19	21.27	H x H	H x H
CRMS 31 A/R 1244-1246-1-605-1	96.50	84.24	–5.80	-15.39	08.96	08.49	18.02	20.67	H x H	H x H
IR 79156 A/NPT 2-2-694-1	92.50	78.45	52.25	43.30	09.28	06.93	–28.18	–30.93	H x L	H x L
IR 79156 A/NPT 80-1	77.50	83.97	–2.07	9.28	09.28	06.93	8.35	19.96	H x H	H x H
IR 79156 A/ TOX 981-11-2-3	88.50	88.79	05.88	01.44	09.28	06.93	14.19	21.27	H x H	H x H
IR 79156 A/R 1244-1246-1-605-1	82.50	77.04	05.88	01.44	09.28	06.93	18.02	20.67	H x H	H x H
Potential maintainers										
APMS 6 A/NPT 2-2-694-1	00.01	03.24	–12.57	-9.57	–18.25	–15.42	–28.18	–30.93	L x L	L x L
APMS 6 A/ET-1-13	00.01	01.35	–18.82	-30.81	–18.25	–15.42	–21.93	–11.62	L x L	L x L
CRMS 31 A/NPT 2-2-964-1	00.02	03.00	–39.68	-33.72	08.96	08.49	–28.18	–30.93	H x L	H x L
IR 79156 A/NPT 9	00.10	02.30	–42.62	-32.93	09.28	06.93	–15.81	–30.87	H x L	H x L
Partial maintainer										
APMS 6 A/NPT 9	37.25	3.65	12.41	-9.23	–18.25	–15.42	–15.81	–30.87	L x L	L x L
Partial restorers										
APMS 6 A/NPT 80-1	47.50	69.35	–1.75	5.70	–18.25	–15.42	08.35	19.96	L x H	L x H
APMS 6 A/TOX 981-11-2-3	55.00	79.96	–0.09	13.95	–18.25	–15.42	14.19	21.27	L x H	L x H
APMS 6 A/R 1244-1246-1-605-1	52.50	78.19	–6.42	13.79	–18.25	–15.42	18.02	20.67	L x H	L x H
CRMS 6 A/ET 1-13	49.00	68.18	02.82	12.16	08.96	08.49	–21.93	–11.62	H x L	H x L
IR 79156 A/ET 1-12	65.50	58.93	–39.69	-29.69	09.28	06.93	25.35	11.52	H x H	H x H
IR 79156 A/ET 1-13	62.50	73.12	16.00	18.65	09.28	06.93	–21.93	–11.62	H x L	H x L

*PF : Pollen fertility (%), SF : Spikelet fertility (%).

for APMS 6 A. The tester TOX 981-11-2-3 had been found as potential restorer for CRMS 31 A and IR 79156 A whereas, partial restorer for APMS 6 A. The tester R 1244-1246-1-605-1 recognized as potential restorer for CRMS 31 A and IR 79156 A on the other hand partial restorers for APMS 6 A (Tables 3 & 4). The same pollen parent exhibited different type of fertility restoretation behavior in different CMS line combinations have been found in the material under study [18-22]. Babaeian *et al*. [21] identified fertility restorers from the crosses, Sefidrod x (IR25 x 19A) and (FR25 x R2) x Tarom restoring up to 90% fertility. They also identified partial restorers from a different set of crosses. Such type of results obtained may be due to the minor gene(s) with additive gene action with the cytoplasmic gene of different CMS line. The high and low reactions may be as per allelic status of the respective cross combinations.

Grain yield is a complex character dependent upon the contribution of various characters affecting directly or indirectly. The existence of total genetic variability and magnitude under improvement to a large extent would dictate the choice of breeding methodology. Therefore, the allelic status and the nature of gene action play important role for the expression of the trait of interest and the nature of pollen as well as spikelets fertility control by the similar type of genetic behavior.

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