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Research Article

Studies on gene action and combining ability in rice (*Oryza sativa*. L) hybrids

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Abstract
The study was carried out to learn about the nature of gene action and combining ability in rice hybrids for grain yield and its component traits. For this, eight lines were crossed with four testers in an L x T mating design. The analysis of variance revealed significant variance for all the characters studied among the parents and hybrids. GCA variances were higher than SCA variances for most of the characters, indicating the predominance of additive gene action, while SCA variances were higher than GCA variances for number of productive tillers per plant, pollen fertility, hulling, milling, head rice recovery and grain yield per plant, indicating the predominance of non-additive gene action. The testers JMS 13A (3.91) and CMS 59A (2.46), as well as the lines MTU 1153 (9.52), RNR 28355 (3.26) and RNR 26085 (3.09), were the best combiners for grain yield and important yield components due to positive GCA effects. Based on SCA effects and corresponding mean performance for grain yield and its component traits, the hybrids CMS 59Ax RNR 26015, CMS 23A x JGL 25960, CMS 64Ax RNR 26015 and JMS 13Ax MTU 1153 were identified as the best specific combiners. These hybrids could be tested in multi-environment trials for commercial use.

Keywords: CMS lines, Gene action, Combining ability, GCA, SCA, Line x Tester

INTRODUCTION

India has the largest rice acreage at 45 million ha (24 percent of cropped area), with an annual production of 124.3MT in 2020-21 as per indiastat. Since the 1960s, the adoption of semi-dwarf varieties, combined with the green revolution, has resulted in spectacular growth in rice production, with the country becoming self-sufficient in rice during the 1980s. India was one of the first countries to launch an applied strategic research programme on hybrid rice. The hybrid rice programme in India was launched in 1989 through a systematic, goal-oriented and time-bound network project funded by the Indian Council of Agricultural Research (ICAR).

The availability of stable male sterile lines is critical for the successful development of rice hybrids using the cytoplasmic genetic male sterility and fertility restoration system. The selection of suitable parents with favourable alleles on cross, which could result in heterotic hybrids, is also critical. The ability of the parents to combine provides useful information on their selection for better hybrid performance, as well as elucidating the nature and magnitude of gene action in the inheritance of a specific character. Kempthorne's (1957) Line x Tester analysis of combining ability is the most widely used method for determining general and specific combiners and studying the nature of gene action governing the inheritance of different characters.

MATERIALS AND METHODS

The material for the current study, which included 44 genotypes (4 'B' lines of corresponding male sterile lines, 8 restorer lines, 32 hybrids and two hybrid and two varietal checks (JGL H1, JKRH 3333 and RNR 15048, MTU 1001), was evaluated in two replications in a randomized block design with a plot size of 20m² during the *kharif* season of 2018 at the Rice Research Centre in Rajendranagar, Hyderabad.

To raise and maintain a healthy crop, all recommended practices were followed. Plant height, panicle length, panicle weight, number of productive tillers per plant, spikelet fertility percent, number of grains per panicle, grain yield per plant, 1000 grain weight, grain length, grain breadth and length-breadth ratio were all observed. The mean data of various traits were analyzed using standard statistical and biometrical methods for combining ability.

RESULTS AND DISCUSSION

The analysis of variance for combining ability (**Table 1**) revealed significant variance for all of the characters studied for parents and hybrids. For each character, the variance due to hybrids was divided into variance due to lines, testers and lines x testers. Except for spikelet fertility percent, the variance due to lines was significant for all of the characters. Variance due to testers was significant for all traits except pollen fertility percent, hulling and head rice recovery percent. Except for plant height, spikelet fertility percent, grain yield and milling percentage, the variance due to lines x testers was significant for all characters studied. Parents and hybrids showed significant variance for twelve characters, indicating hybrid superiority and the presence of heterosis for nearly all of the traits studied.

These findings highlighted the significance of combining ability studies in indicating variability in the material studied and there is a good opportunity for identifying promising parents and hybrid combinations for improving yield through its components.

Table 1. Analysis of variance for different characters in rice in Line x Tester mating

Source of variations	Degrees of freedom	Days to 50% flowering	Plant height (cm)	Number of productive tillers per plant	Panicle length (cm)	Panicle weight (g)	Number of grains per panicle	Pollen fertility (%)	Spikelet fertility (%)
Replicates	1	1.13	10.57	1.89	0.08	0.08	125.2	22	20.61
Treatments	43	92.44**	94.86**	13.66**	8.05**	1.88**	3167.2**	852.83**	91.95**
Parents	11	132.6	111.4	19.98	11.22	0.84	4531.4	85.73	67.6
Lines	7	101.1**	159.8**	6.55**	7.99**	0.90**	3077.8**	78.71**	7.45
Testers	3	83.45**	30.16**	11.30**	17.16**	0.78**	4922.4**	40.45	221.58**
L x T	1	500.5**	17.16	140.08**	15.98**	0.66**	13534.08**	270.7**	27.0
Crosses	31	81.16**	89.98	10.79**	7.14**	1.92**	2479.8**	895.6**	86.48**
Parents vs Crosses	1	0.12	63.28**	32.80**	1.24	12.12**	9469.1**	7963.1**	529.4**
Error	43	2.46	4.51	1.383	0.89	0.12	333.86	19.06	13.66
Total	87	46.91	49.24	7.45	4.42	0.99	1731.8	431.1	52.43

Source of variations	Degrees of freedom	1000 grain weight (g)	Hulling (%)	Milling (%)	Head rice recovery (%)	Kernel length (mm)	Kernel breadth (mm)	Kernel length breadth ratio	Grain yield per plant (g)
Replicates	1	0.95	1.205	61.05*	14.89	0.02	0.00	0.002	20.85
Treatments	43	21.95**	31.54**	37.14**	41.95**	0.45**	0.07**	0.31**	181.01**
Parents	11	33.99	21.11	38.42	43.65	0.64	0.18	0.71	35.46
Lines	7	28.93**	23.73**	50.27**	55.33**	0.90**	0.12**	0.72**	42.18**
Testers	3	28.22**	5.17	20.89**	11.8	0.17**	0.13**	0.23**	30.05**
L x T	1	86.69**	50.63**	8.08	57.42**	0.20**	0.75**	2.06**	4.69
Crosses	31	17.8**	33.7**	28.82**	42.63**	0.39**	0.04**	0.18**	172.2**
Parents vs Crosses	1	18.14**	79.47**	281.09**	1.96	0.03	0.03**	0.14**	2054.5**
Error	43	0.66	2.51	4.55	5.80	0.032	0.006	0.01	9.96
Total	87	11.19	16.84	21.31	23.77	0.23	0.04	0.16	94.63

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The variance estimates for GCA and SCA, as well as their ratios, are presented in the (**Table 2**). In the current study, it was observed that GCA variances were greater than SCA variances for the majority of the characters, indicating the predominance of additive gene action for the traits like Plant height, panicle length, panicle weight, number of grains per panicle, spikelet fertility percent, 1000 grain weight, kernel length, kernel breadth and kernel length-breadth ratio. The findings of Pratap *et al.,* (2013); Samrath and Deepak, 2014 and Ramesh *et al.,* (2018) support the present results of predominance of additive positive gene action for majority of traits. The SCA variances were greater than the GCA variances for the number of productive tillers per plant, pollen fertility percent, hulling percentage, milling percentage, head rice recovery and grain yield per plant, indicating predominance of non-additive gene action. Various studies in rice by other researchers show that non-additive gene action predominates over additive gene action, which is ideal for exploitation via heterosis breeding (Bhadru *et al.,* 2013; Devi *et al.,* 2017 and Sudeepthi *et al.,* 2018).

The GCA effects of the parents (**Table 3**) revealed that the *gca* effect was significant and positive for MTU 1153 (9.52), RNR 28355 (3.26) and RNR 26085 among lines (3.09). Two lines, JMS 13A (3.91) and CMS 59A (2.46), demonstrated significant and positive *gca* effects. For grain yield per plant SCA effects ranged from -12.86 (CMS 64A x RNR 26015) to 15.61 (CMS 59A x RNR 26015). Nine hybrids out of 32 showed significant positive SCA effects (**Table 4**). CMS 23A x JGL 25960 (12.20), CMS 64A x RNR 26085 (7.71), JMS 13A MTU 1153 (7.18), CMS 59A x IET 27253 (6.73) and CMS 64A x JAYA (6.65) were selected as desirable hybrids for higher grain yield. CMS 59A x RNR 26015 (15.61) and CMS 23A x JGL 25960 (12.20) had the high significant positive *sca* effect for increased grain yield. Hybrids demonstrated significant positive SCA effects, making such hybrids desirable. Similar findings have been reported by Raju *et al.,* 2014; Parimala *et al.,* 2018 and Yadav *et al.,* 2020). CMS 59A was a good general combiner among the testers for the traits grain yield per plant, spikelet fertility percent, 1000 grain weight, panicle length and head rice recovery percent, while JMS 13A was a good general combiner for grain yield per plant, panicle weight and number of grains per panicle.

MTU 1153 was the best general combiner among the lines for traits such as days to 50% flowering, number of grains per panicle, grain yield per plant, pollen fertility percentage, 1000 grain weight, milling percentage and head rice recovery percentage. RNR 28355 (3.26) was the best general combiner for characters such as days to 50% flowering, number of productive tillers per plant, number of grains per panicle, spikelet fertility and grain yield per plant, while RNR 26085 (3.09) was the best general combiner for plant height, number of productive tillers per plant, panicle length, kernel length and kernel breadth. These findings were supported by Satheeshkumar *et al*. (2016) and Azad *et al*. (2022).

Table 2. Estimates of general and specific combining ability variances and proportionate gene action in rice for the characters under study

Character	Source of variation			Degree of Dominance (σ^2sca/ σ^2gca)$^{1/2}$	Nature of gene action
	σ^2gca	σ^2sca	σ^2gca/ σ^2sca		
Days to 50% flowering	47.33	12.74	3.71	0.51	Additive
Plant height (cm)	36.93	9.09	4.06	0.49	Additive
Number of productive tillers per plant	1.696	3.97	0.42	1.53	Non additive
Panicle length (cm)	2.23	0.69	3.21	0.55	additive
Panicle weight (g)	0.67	0.17	3.91	0.5	Additive
Number of grains per panicle	1309.1	142.4	9.19	0.33	Additive
Pollen fertility (%)	217.18	298.6	0.72	1.17	Non additive
Spikelet fertility (%)	28.27	22.61	1.25	0.89	Additive
1000 grain weight (g)	9.72	0.18	51.91	0.13	Additive
Hulling per cent	5.72	15.13	0.37	1.62	Non additive
Milling per cent	3.12	14.31	0.21	2.14	Non-additive
Head Rice Recovery (%)	6.38	15.16	0.42	1.54	Non additive
Kernel length (mm)	0.13	0.09	1.48	0.82	Additive
Kernel breadth (mm)	0.01	0.008	2.48	0.63	Additive
Kernel length breadth ratio	0.09	0.02	4.26	0.48	additive
Grain yield per plant (g)	42.31	61.99	0.68	1.21	Non additive

Table 3. Estimates of general combining ability effects of lines and testers for yield and yield contributing characters in rice

Parents	Days to 50% flowering	Plant height	Number of productive tillers per plant	Panicle length	Panicle weight	Number of grains per panicle	Pollen fertility %	Spikelet fertility %
LINES								
MTU 1153	-3.250 **	-1.375	-0.088	0.263	0.333 *	33.125 **	16.734 **	1.032
RNR 26015	-2.125 **	5.975 **	2.050 **	0.813 *	-0.381 **	-3.750	-1.391	0.329
RNR 28355	-0.750	-5.288 **	1.288 **	-1.888 **	-0.827 **	17.500 *	-5.141 **	2.866 *
JGL 25960	3.375 **	-3.525 **	0.625	-1.625 **	-0.904 **	-16.000 *	3.984 *	0.535
MTU 1010	-0.750	9.200 **	-0.475	-0.288	-0.349 **	-4.500	17.484 **	5.484 **
IET 27253	4.250 **	-2.413 **	-0.363	1.688 **	0.778 **	-30.000 **	-28.891 **	-3.654 **
RNR 26085	-0.375	3.037 **	-2.925 **	2.625 **	1.679 **	19.500 **	2.984	-3.838 **
JAYA	-0.375	-5.612 **	-0.113	-1.588 **	-0.329 *	-15.875 *	-5.766 **	-2.754 *
TESTERS								
CMS 23A	-8.375 **	-5.375 **	-0.850 **	-0.431	-0.221 *	-27.438 **	10.484 **	2.755 **
CMS 59A	1.938 **	2.113 **	0.056	0.762 **	-0.099	-7.563	-2.516 *	4.007 **
CMS 64A	2.000 **	0.825	0.538	0.281	-0.224 *	-4.375	-7.516 **	-5.124 **
JMS 13A	4.438 **	2.438 **	0.256	-0.613 *	0.544 **	39.375 **	-0.453	-1.638

Table 3. Continued...

Parents	1000 grain weight	Hulling %	Milling %	Head rice recovery	Kernel length	Kernel breadth	Kernel length breadth ratio	Grain yield per plant
LINES								
MTU 1153	-0.783 *	-1.380 *	-1.217	1.277	-0.115	0.035	-0.105 *	9.520 **
RNR 26015	-1.447 **	-0.167	0.058	-6.073 **	0.460 **	-0.084 **	0.360 **	-0.908
RNR 28355	-4.265 **	-1.905 **	0.183	1.202	-0.369 **	-0.103 **	-0.039	3.261 **
JGL 25960	0.030	-3.217 **	-1.230	3.127 **	-0.165 *	-0.024	-0.049	-4.495 **
MTU 1010	-0.043	2.695 **	1.320	1.489	0.180 **	0.031	0.026	1.451
IET 27253	3.685 **	1.370 *	0.658	1.039	0.051	0.076 *	-0.077	-5.195 **
RNR 26085	1.255 **	0.558	-1.780 *	-3.273 **	0.287 **	-0.007	0.131 **	3.094 **
JAYA	1.568 **	2.045 **	2.008 *	1.214	-0.327 **	0.076 *	-0.247 **	-6.728 **
TESTERS								
CMS 23A	1.802 **	1.489 **	1.377 *	-0.617	-0.181 **	0.167 **	-0.305 **	-5.740 **
CMS 59A	1.085 **	-2.142 **	-1.930 **	-0.961	0.306 **	-0.065 **	0.227 **	2.462 **
CMS 64A	0.182	-0.161	-0.117	0.889	0.089	-0.069 **	0.138 **	-0.640
JMS 13A	-3.068 **	0.814 *	0.670	0.689	-0.214 **	-0.033	-0.060	3.917 **

CMS 59A x RNR 26015 was discovered to be a good specific combiner for traits such as Days to 50% flowering, plant height, number of productive tillers per plant, grain yield per plant and 1000 grain weight in hybrids and CMS 23A x JGL 25960 for number of productive tillers per plant, kernel length and grain yield per plant. Previously, (Priyanka *et al.,* 2014, Mallikarjuna *et al*., 2016, Saravanan *et al*., 2018 and Manivelan *et al*., 2022) reported similar findings.

According to the study, the testers JMS 13A (3.91) and CMS 59A (2.46), as well as the lines MTU 1153 (9.52),

Table 4. Estimates of specific combining ability effects of crosses for yield and yield contributing characters in rice

Hybrids	Days to 50% flowering	Plant height	Number of productive tillers/plant	Panicle length	Panicle weight	Number of grains per panicle	Pollen fertility (%)	Spikelet fertility (%)
CMS 23A X MTU 1153	3.625 **	1.500	-0.813	-0.194	-0.163	12.063	-6.734 *	-0.138
CMS 59A X MTU 1153	-3.188 **	0.912	-0.719	0.413	-0.355	-21.313	2.766	-3.529
CMS 64A X MTU 1153	-4.750 **	-1.650	0.800	-0.406	-0.384	-11.500	7.266 *	3.521
JMS 13A X MTU 1153	4.313 **	-0.762	0.731	0.187	0.902 **	20.750	-3.297	0.146
CMS 23A X RNR 26015	-1.500	6.050 **	-2.950 **	0.856	0.871 **	10.938	8.891 **	6.966 *
CMS 59A X RNR 26015	-5.313 **	-3.238 *	5.094 **	0.563	-0.086	-3.938	-8.109 *	-1.580
CMS 64A X RNR 26015	3.625 **	-0.300	-0.737	-1.256	-0.466	4.875	-13.109 **	-6.585 *
JMS 13A X RNR 26015	3.188 **	-2.513	-1.406	-0.162	-0.319	-11.875	12.328 **	1.200
CMS 23A X RNR 28355	2.625 *	2.362	0.213	-0.244	-0.188	0.688	7.641 *	-6.057 *
CMS 59A X RNR 28355	1.313	-1.925	-2.144 *	2.163 **	0.505	-8.188	-14.359 **	0.992
CMS 64A X RNR 28355	0.250	1.763	0.075	-0.956	0.041	-3.875	-19.359 **	4.473
JMS 13A X RNR 28355	-4.188 **	-2.200	1.856 *	-0.963	-0.358	11.375	26.078 **	0.592
CMS 23A X JGL 25960	1.000	-3.600 *	0.475	0.094	0.495	14.688	-1.484	-3.850
CMS 59A X JGL 25960	2.188	3.012	-1.481	0.200	-0.213	20.313	14.516 **	1.588
CMS 64A X JGL 25960	0.125	3.750 *	-1.163	-0.469	0.103	-2.375	16.516 **	3.324
JMS 13A X JGL 25960	-3.313 **	-3.163 *	2.169 *	0.175	-0.386	-32.625 *	-29.547 **	-1.062
CMS 23A X MTU 1010	-2.875 *	-2.725	2.225 *	-0.994	-0.045	1.188	-4.984	4.361
CMS 59A X MTU 1010	-0.188	2.338	-2.181 *	0.613	0.257	-12.188	2.016	-7.205 **
CMS 64A X MTU 1010	-0.750	0.225	-1.163	0.144	0.108	8.125	3.016	1.805
JMS 13A X MTU 1010	3.813 **	0.163	1.119	0.237	-0.321	2.875	-0.047	1.040
CMS 23A X IET 27253	-1.375	0.638	2.113 *	0.531	0.162	-7.813	-21.109 **	0.413
CMS 59A X IET 27253	4.313 **	-2.100	2.206 *	-1.813 *	-0.420	-1.688	9.391 **	11.722 **
CMS 64A X IET 27253	1.250	-3.063	-1.175	0.119	-0.139	-2.375	4.391	-10.287 **
JMS 13A X IET 27253	-4.188 **	4.525 **	-3.144 **	1.163	0.397	11.875	7.328 *	-1.848
CMS 23A X RNR 26085	4.250 **	1.038	-0.325	0.444	-0.279	1.688	-0.484	-4.983
CMS 59A X RNR 26085	-1.063	-1.250	0.119	-0.950	0.069	11.313	12.516 **	-0.454
CMS 64A X RNR 26085	-2.125	-3.413 *	1.288	0.831	0.449	-19.375	-22.484 **	0.946
JMS 13A X RNR 26085	-1.063	3.625 *	-1.081	-0.325	-0.239	6.375	10.453 **	4.491
CMS 23A X JAYA	-5.750 **	-5.262 **	-0.938	-0.494	-0.855 **	-33.438 *	18.266 **	3.288
CMS 59A X JAYA	1.938	2.250	-0.894	-1.188	0.242	15.688	-18.734 **	-1.533
CMS 64A X JAYA	2.375 *	2.687	2.075 *	1.994 **	0.288	26.500 *	23.766 **	2.803
JMS 13A X JAYA	1.438	0.325	-0.244	-0.313	0.324	-8.750	-23.297 **	-4.558

*Significant at 5% level, **Significant at 1% level

Table 4. Continued.

Hybrids	1000 grain weight	Hulling percent	Milling per cent	Head rice recovery %	Kernel length	Kernel breadth	Kernel length breadth ratio (L/B ratio)	Grain yield per plant
CMS 23A X MTU 1153	-0.690	0.273	0.536	2.517	0.160	-0.080	0.178	-2.649
CMS 59A X MTU 1153	0.686	2.505 *	-1.208	-4.539 *	0.082	-0.044	0.102	-4.825 *
CMS 64A X MTU 1153	0.455	1.673	2.480	2.761	-0.095	0.110	-0.195 *	0.286
JMS 13A X MTU 1153	-0.450	-4.452 **	-1.808	-0.739	-0.147	0.014	-0.086	7.189 **
CMS 23A X RNR 26015	0.198	-10.989 **	-9.389 **	-7.133 **	-0.055	0.188 **	-0.317 **	-2.182
CMS 59A X RNR 26015	1.175	2.542 *	0.317	-1.339	0.357 **	-0.025	0.212 *	15.612 **
CMS 64A X RNR 26015	-0.747	7.161 **	9.655 **	5.211 **	0.155	-0.101	0.250 **	-12.862 **
JMS 13A X RNR 26015	-0.627	1.286	-0.583	3.261	-0.457 **	-0.062	-0.146	-0.569
CMS 23A X RNR 28355	-0.023	1.698	0.536	1.542	-0.241	-0.043	-0.063	-8.345 **
CMS 59A X RNR 28355	-0.762	-1.670	-1.558	2.536	0.266 *	0.078	0.021	1.663
CMS 64A X RNR 28355	-0.303	1.498	1.680	-0.764	0.144	0.103	-0.081	5.215 *
JMS 13A X RNR 28355	1.087	-1.527	-0.658	-3.314	-0.168	-0.138 *	0.123	1.468
CMS 23A X JGL 25960	0.602	1.261	2.298	0.617	0.295 *	0.053	0.067	12.206 **
CMS 59A X JGL 25960	-0.117	-2.658 *	-3.145 *	-0.289	-0.533 **	-0.005	-0.244 **	-6.285 **
CMS 64A X JGL 25960	-0.388	-5.239 **	-5.308 **	-2.289	-0.565 **	-0.196 **	0.019	1.526
JMS 13A X JGL 25960	-0.098	6.636 **	6.155 **	1.961	0.803 **	0.148 *	0.158	-7.446 **
CMS 23A X MTU 1010	-0.850	1.898	3.198 *	-5.395 **	-0.035	-0.072	0.082	-5.365 *
CMS 59A X MTU 1010	0.301	-0.970	2.105	0.548	0.037	0.045	-0.049	-1.032
CMS 64A X MTU 1010	0.480	-0.702	-3.558 *	0.748	0.100	0.104	-0.101	4.145
JMS 13A X MTU 1010	0.070	-0.227	-1.745	4.098 *	-0.102	-0.077	0.068	2.253
CMS 23A X IET 27253	0.697	3.023 *	2.961	-2.095	-0.201	-0.007	-0.060	5.261 *
CMS 59A X IET 27253	-0.107	-1.545	1.417	5.398 **	-0.249	0.060	-0.207 *	6.730 **
CMS 64A X IET 27253	0.292	-0.327	-2.395	-1.102	0.269 *	-0.101	0.252 **	-12.679 **
JMS 13A X IET 27253	-0.883	-1.152	-1.983	-2.202	0.182	0.048	0.015	0.689
CMS 23A X RNR 26085	-0.148	-0.714	-2.052	6.817 **	0.137	-0.044	0.112	5.972 *
CMS 59A X RNR 26085	-0.832	1.817	1.655	-1.389	-0.095	-0.023	0.001	-8.844 **
CMS 64A X RNR 26085	0.802	-1.114	-0.008	0.811	0.007	0.047	-0.066	7.717 **
JMS 13A X RNR 26085	0.177	0.011	0.405	-6.239 **	-0.050	0.020	-0.047	-4.845 *
CMS 23A X JAYA	0.213	3.548 **	1.911	3.130	-0.059	0.003	0.000	-4.897 *
CMS 59A X JAYA	-0.345	-0.020	0.417	-0.927	0.134	-0.085	0.163	-3.018
CMS 64A X JAYA	-0.592	-2.952 *	-2.545	-5.377 **	-0.014	0.034	-0.078	6.653 **
JMS 13A X JAYA	0.723	-0.577	0.217	3.173	-0.061	0.048	-0.085	1.261

*Significant at 5% level, **Significant at 1% level

RNR 28355 (3.26) and RNR 26085 (3.09), were the best combiners for grain yield and important yield components due to positive GCA effects. Hybrids JMS 13A x MTU 1153, CMS 59A x RNR 26015and CMS 64A x MTU 1153 were stable with favourable SCA effects, heterosis and per se performance for grain yield and its component traits. These hybrids could be tested in multi-site trials for commercial use.

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