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Understanding Gene Action and Combining Ability in Rice (*Oryza sativa* L.) A Line × Tester Analysis Approach

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

The study was carried out to understand the nature of gene action and combining ability in rice hybrids for grain yield and its component traits. For this, five lines were crossed with two testers in a Line x Tester mating design. The analysis of variance revealed a substantial difference between

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the parents and hybrids for all the characters studied. For the majority of traits *viz.,* days to 50% flowering, number of tillers per plant, number of productive tillers per plant, number of grains per panicle, 1000 grain weight, grain yield per plant, hulling (%), milling (%), and kernel length-breadth ratio, SCA variances were greater than GCA variations, indicating the predominance of non additive gene action. In contrast GCA variations were greater than SCA variances, suggesting that additive gene action predominates for characteristics such as plant height, panicle length, head rice recovery (%), kernel length and kernel breadth. The hybrids JGL 27356 x PTB 33 and KPS 3018 x IET 23993 were stable with favourable SCA effects, heterosis and per se performance for grain yield and its component traits. Among lines WGL 962 was the best combiner for grain yield and important yield components due to positive GCA effects and in testers IET 23993 for early and dwarfness. In order to provide a higher heterosis for yield, the aforementioned cross combinations might be used in further breeding programs.

Keywords: Gene action; general combing ability; specific combining ability; line x tester analysis; grain yield.

1. INTRODUCTION

"Rice (*Oryza sativa*) is one of the world's most important staple foods, feeding over half of the global population daily. Cultivated primarily in Asia, where over 90% of the world's rice is grown and consumed, this crop is a foundation for food security, economic stability and cultural heritage. Its cultivation, which dates back thousands of years, has profoundly influenced agricultural practices, rural livelihoods and even social structures in societies worldwide" (Mohidem et al*.* 2024).

"Globally, rice is being cultivated in an area of 167.2 million hectares with an annual production of 769.6 million tonnes and productivity of 4,600 kg ha^{-1}. In India, during 2022-23, the rice crop was cultivated in an area of 47.83 million ha with an annual production of 150.04 million tonnes and productivity of 2,838 kg ha^{-1}" (Indiastat, 2022-23). 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.

Economically, rice is a major contributor to the GDP of many developing countries, where it not only provides sustenance but also supports millions of smallholder farmers. In many regions, rice cultivation is more than a source of income, it is integral to cultural identity and community traditions. However, as the global population continues to grow, the demand for rice increases, placing pressure on agricultural systems to produce more with limited resources.

Climate change, water scarcity and soil degradation are emerging challenges that threaten rice production, underscoring the need for innovative solutions to ensure sustainable cultivation. Advances in agricultural technology, from high-yield rice varieties to water efficient farming practices offer potential pathways to meet these challenges. The genetic improvement of rice through breeding programs aimed at increasing yield, disease resistance and other desirable traits is essential for meeting the food demands of a growing global population (Priyanka et al*.* 2024). The selection of appropriate parental lines with high grain yield and resistance to biotic and abiotic stresses plays a pivotal role in crop improvement programs. The precise knowledge of the nature of gene action for yield and yield-attributing traits helps to choose an effective breeding strategy to accelerate the pace of genetic improvement of seed yield and quality traits in rice (Ghosh et al*.* 2013).

Gene action and combining ability are two fundamental elements that guide the selection of superior parental lines and development of high yielding varieties. Gene action refers to the underlying genetic mechanisms by which traits are inherited. These mechanisms include the types of gene interactions (additive, dominance, and epistatic effects) that govern the expression of agronomic traits. Understanding gene action allows breeders to predict how traits will behave in progeny, facilitating more efficient breeding strategies. Combining ability is a measure of a parent's genetic potential for contributing to the performance of hybrid offspring (Ananda Lekshmi et al*.* 2020). It assesses the ability of different parental lines to combine and transmit desirable traits to the next generation. By evaluating combining ability, breeders can identify the best parents for hybridization, thus optimizing the genetic progress made through breeding programs.

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. The study of gene action and combining ability plays a crucial role in designing effective breeding schemes for improving complex traits such as yield, resistance to biotic and abiotic stresses and grain quality.

2. MATERIALS AND METHODS

The current study was conducted at the Agricultural Research Station, Kampasagar, Nalgonda, from 2021 to 2022. The materials for the present study comprised a total of seven parents. Among them, five parents were considered as lines (WGL 962, KNM 1638, KPS 3018 and JGL 27356) and these are high yielding and popular for their good cooking quality and lack of resistance to brown plant hoppers, whereas the testers (IET 23993 and PTB 33) were resistant in nature, having high adaptability. To achieve synchronization between the female and male parents staggered sowing of entries was done. The selected lines and testers were crossed in (5x2) line x tester fashion to generate 10 F_1 hybrids during *Kharif* 2021.

Ten hybrids were planted in a randomized block design in three replications along with parents and checks at a spacing of 20 cm x 15 cm during *Rabi* 2021-2022. To raise and maintain a good, healthy crop, all recommended practices were followed. The biometrical observations, *viz.,* days to 50 percent flowering, plant height (cm), the number of tillers per plant, the number of productive tillers per plant, panicle length (cm), the number of grains per panicle, test weight (g), grain plant yield (g), hulling(%), milling (%) and head rice recovery (%), grain length (mm), grain breadth (mm) and length breadth ratio (mm) were noted down in five randomly tagged plants in each one of the cross combinations and parents in each replication and the mean performance was worked out and tabulated. Out of the parental genotypes and 10 crosses, good combiners and good cross combinations were deduced using gca and sca effects (Sprague and Tatum, 1942).

3. RESULTS AND DISCUSSION

An analysis of variance for combining ability revealed that treatments registered highly significant differences for all the characters (Table 1). The parents differed significantly for all the characters except for the number of tillers per plant and effective bearing tillers per plant, indicating the existence of sufficient variability in the material studied. The lines differed significantly for most of the traits except for number of tillers per plant and effective bearing tillers per plant, number of grains per panicle and head rice recovery (%). Whereas the testers differed significantly for all the characters except number of tillers per plant and effective bearing tillers per plant. The interaction between lines and testers was significant for the traits, *viz.,* days to 50% flowering, plant height, test weight, grain yield per plant, kernel length, kernel length breadth ratio, hulling (%), milling (%) and head rice recovery (%) (Garkoti et al. 2022).

Mean squares due to parents *vs.* hybrids were significantly different for all the characters except for the kernel L/B ratio, revealing good scope for manifestation of heterosis in most of the characters studied. The effect of hybrids was partitioned into lines, testers and their interactions. The mean squares due to the lines effect were nonsignificant for all traits and the mean squares due to the testers effect were significant observed in kernel length. The mean squares due to Line × Tester interaction effects were significant for all the characters studied; it revealed the significant contribution of hybrids for specific combining ability variance components (Modarresi et al*.* 2024).

Estimates of combining ability variances and gene action: Genetically, general combining ability (*gca*) variance is associated with genes which are additive in their effect, while specific combining ability (*sca*) variance is attributed to dominance and epistatic gene action (Kambal and Webster, 1965). Genetic information about the combining ability of parents and the nature of gene action involved in the inheritance of a trait would be of immense value to breeders to judge the suitability of parents, to identify potential hybrids and breeding methodology.

The variance estimates for GCA and SCA, as well as their ratios, are presented in Table 2. In the current study, it was observed that SCA variances were higher than GCA variances for most of the characters, which indicated the predominance of non additive gene action for the traits *viz*., days to 50% flowering, number of tillers per plant, number of productive tillers per plant, number of grains per panicle, 1000 grain weight, hulling, milling, kernel length-breadth

Table 1. Analysis of variance for combining ability in rice

Source of variations	Degrees of freedom	Days to 50% flowering	Plant height (cm)	Number of tillers per plant	Productive tillers per plant	Panicle length (cm)	No. of filled grains /panicle	1000 grain weight (g)
Replicates	2	4.47	23.60	2.39	1.48	1.37	133.45	0.32
Treatments	16	169.29**	849.36**	12.54**	5.75**	6.18**	7560.20**	38.36**
Parents	6	265.94**	2091.09**	3.02	1.25	7.16**	1414.16**	48.12**
Parents (Line)	4	66.43**	9.66*	3.19	1.45	6.91**	159.46	8.37**
Parents (Testers)	1	228.17**	1209.84**	4.51	1.50	10.72*	4471.74**	3.34**
Parents (L vs T)	1	1101.72**	1129.03**	0.88	0.23	4.63	79743.34	251.90**
Parents vs Crosses	1	155.47**	39.96*	48.24**	15.31**	25.43**	1077.46**	168.47**
Crosses	9	106.39**	111.48**	14.91	7.68**	3.39*	2815.10**	17.39**
Line Effect	4	150.83	170.85	12.38	6.62	4.62	2817.13	11.81
Tester Effect	1	67.50	124.30	3.47	2.95	5.89	1.20	39.93
Line * Tester Eff.	4	71.67**	48.91**	20.30**	9.92**	1.54**	3516.53**	17.34**
Error	32	4.35	7.52	3.44	1.74	1.51	4.19	0.34
Total	50	57.13	277.56	6.31	3.01	3.00	277.20	12.51

Table continues……

Table 1. Analysis of variance for combining ability in rice

Source of variations	Degrees of freedom	Grain yield per plant (g)	Kernel length (mm)	Kernel breadth (mm)	Kernel length breadth ratio (mm)	Hulling (%)	Milling (%)	Head rice recovery (%)
Replicates	2	41.78	0.01	0.002	0.01	0.13	1.24	1.43
Treatments	16	225.37**	0.53**	0.50**	0.94**	78.28**	64.09**	69.77**
Parents	6	115.87**	0.14**	0.75**	1.32**	50.13**	53.55**	56.41**
Parents (Line)	4	36.10*	0.12**	0.05**	0.27**	22.81**	9.97	8.98
Parents (Testers)	1	48.17*	0.14**	0.06**	0.09**	47.02**	72.41**	79.63**
Parents (L vs T)	1	502.65**	0.19**	4.26**	6.70**	162.53**	209.03**	222.91**
Parents vs Crosses	1	1523.21**	4.18**	0.24**	0.02	113.03**	97.76**	164.06**
Crosses	9	154.16**	0.38**	0.37**	0.80**	93.18**	67.37**	68.20**
Line Effect	4	234.28	0.14	0.39	0.97	94.39	69.86	71.01
Tester Effect	1	9.19	1.94	0.68	0.75	105.98	106.70	126.11
Line * Tester Eff.	4	110.28**	0.22**	0.27**	0.64**	88.77**	55.06**	50.92**
Error	32	11.50	0.01	0.02	0.01	5.58	5.45	4.98
Total	50	81.15	0.18	0.16	0.31	28.62	24.05	25.57

** Significant at 5 per cent level ** Significant at 1 percent level*

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	Nature of gene action
	σ^2gca	σ^2sca	σ^2gca/ σ^2sca	(σ^2sca/ σ^2gca)$^{1/2}$	
Days to 50% flowering	19.97	22.44	0.89	1.06	Non additive
Plant height (cm)	26.68	13.80	1.93	0.72	Additive
Number of tillers per plant	0.86	5.62	0.15	2.56	Non additive
Number of productive tillers per plant	0.58	2.73	0.21	2.17	Non additive
Panicle length (cm)	0.71	0.01	72.77	0.12	additive
Number of filled grains per panicle	190.85	1036.45	0.18	2.33	Non additive
1000 grain weight (g)	4.86	5.67	0.86	1.08	Non additive
Hulling per cent	18.02	27.73	0.65	1.24	Non additive
Milling per cent	15.78	16.54	0.95	1.02	Non-additive
Head Rice Recovery (%)	17.82	15.31	1.16	0.93	additive
Kernel length (mm)	0.20	0.07	2.84	0.59	Additive
Kernel breadth (mm)	0.10	0.09	1.15	0.93	Additive
Kernel length breadth ratio (mm)	0.16	0.21	0.77	1.14	Non additive
Grain yield per plant (g)	21.00	32.93	0.64	1.25	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 (cm)	Number of tillers per plant	Productive tillers per plant	Panicle length (cm)	No. of filled grains /panicle	1000 grain weight (g)
LINES							
WGL 962	-8.16**	-2.00	0.96	0.52	0.434	23.433 *	1.54 **
KNM 1638	4.66**	0.57	-2.00*	-1.48 *	-0.30	-30.06 **	-2.19 **
KPS 3018	-0.83	-4.97 **	-0.90	-0.71	-1.39*	-14.06	0.58*
RNR 21278	1.16	8.87 **	1.53	0.98	0.48	8.26	0.44
JGL 27356	3.16 **	-2.46*	0.40	0.68	0.78	12.43	-0.37
TESTERS							
IET 23993	-1.50 *	-2.03 *	-0.34	-0.31	0.44	0.20	-1.15 **
PTB-33	1.50 *	2.03 *	0.34	0.31	-0.44	-0.20	1.15 **

Table 3 continues…….

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

Parents	Grain yield per plant (g)	Kernel length (mm)	Kernel breadth (mm)	Kernel L/B ratio (mm)	Hulling (%)	Milling (%)	Head rice recovery (%)
Lines							
WGL 962	9.49 **	-0.29 **	-0.07 **	-0.03	5.58 **	4.879 **	4.80 **
KNM 1638	-4.07 **	0.36 **	0.22 **	-0.17 **	-2.83 **	-3.147 **	-3.19 **
KPS 3018	-6.84**	-0.09	0.06 **	-0.10	0.63	0.815	1.02
RNR 21278	1.62	-0.02	-0.41 **	0.66 **	-4.66 **	-3.390 **	-3.49 **
JGL 27356	-0.20	0.05	0.21 **	-0.34 **	1.27	0.843	0.86
TESTERS							
IET 23993	-0.55	0.16 **	0.11**	-0.14 **	-1.88 **	-1.88 **	-2.05 **
PTB-33	0.55	-0.16**	-0.11 **	0.14 **	1.88 **	1.88 **	2.05 **

** Significant at 5 per cent level ** Significant at 1 percent level*

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

Crosses	Days to 50% flowering	Plant height (cm)	Number of tillers per plant	Productive tillers per plant	Panicle length (cm)	No. of filled grains /panicle	1000 grain weight (g)
WGL 962 x IET 23993	-0.83	-0.69	1.21	0.81	0.11	10.47	0.75 *
KNM 1638 x IET 23993	0.83	0.69	-1.21	-0.81	-0.11	-10.47	-0.75 *
KPS 3018 x IET 23993	-0.33	-0.46	0.91	0.61	0.25	23.63	1.77 **
RNR 21278 x IET 23993	0.33	0.46	-0.91	-0.61	-0.25	-23.63	-1.77 **
JGL 27356 x IET 23993	-5.16 **	-1.92	1.74	1.31	0.43	16.97	-2.50 **
WGL 962 x PTB 33	5.16 **	1.92	-1.74	-1.31	-0.43	-16.97	2.50 **
KNM 1638 x PTB 33	2.83 *	-1.90	-2.56 *	-1.59	-0.86	-19.03	0.87 *
KPS 3018 x PTB 33	-2.83 *	1.90	2.56 *	1.59	0.86	19.03	-0.87 *
RNR 21278 x PTB 33	3.50 **	4.96 **	-1.29	-1.15	0.06	-32.03 *	-0.89 *
JGL 27356 x PTB 33	-3.50 **	-4.96 **	1.29	1.15	-0.06	32.03 *	0.89 *

Table 4 continues…….

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

	Grain yield per plant (g)	Kernel length (mm)	Kernel breadth (mm)	Kernel L/B ratio (mm)	Hulling (%)	Milling (%)	Head rice recovery (%)
WGL 962 x IET 23993	-0.94	-0.29 **	0.00	-0.19*	0.64	0.05	0.16
KNM 1638 x IET 23993	0.95	0.29 **	0.00	0.19 *	-0.64	-0.05	-0.16
KPS 3018 x IET 23993	4.55 *	-0.07	-0.29**	0.427 **	6.37 **	5.11 **	4.86 **
RNR 21278 x IET 23993	-4.55 *	0.07	0.29**	-0.42**	-6.37 **	-5.11 **	-4.86 **
JGL 27356 x IET 23993	4.05	0.08	0.29 **	-0.41 **	-2.50	-0.76	-0.69
WGL 962 x PTB 33	-4.05	-0.08	-0.29 **	0.41 **	2.50	0.76	0.69
KNM 1638 x PTB 33	-2.08	0.21 **	0.05 *	-0.02	-1.36	-1.89	-1.72
KPS 3018 x PTB 33	2.08	-0.21 **	-0.05 *	0.02	1.36	1.89	1.72
RNR 21278 x PTB 33	-5.58 *	0.07	-0.05 *	0.19*	-3.15 *	-2.52	-2.62
JGL 27356 x PTB 33	5.58 *	-0.07	0.05 *	-0.19 *	3.15*	2.52	2.62

ratio and grain yield per plant. 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; AnandaLekshmi et al*.,* 2020; and Gunasekaran et al*.,* 2023). The GCA variances were higher than SCA variances, which indicates the predominance of additive gene action for traits like plant height, panicle length, head rice recovery (%), kernel length and kernel breadth. The findings of Sharma et al*.* (2013), Pratap et al*.* (2013), Samrath and Deepak (2014), Ramesh et al*.* (2018) and Lingaiah et al*.* (2023) support the present results of the predominance of additive gene action for the majority of traits.

From the above discussion, it is clearly evident that most of the traits were controlled by non-additive gene action. To exploit the non-additive gene action of these traits, heterosis breeding or hybridization followed by selection in later generations is recommended for the improvement of these traits in rice.

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.

General and specific combining ability effects: The GCA effects of the parents revealed that the *GCA* effect was significant and positive for WGL 962 (9.49) among lines and none of the testers exhibited a significant positive GCA effect for grain yield per plant (Table 3).

For grain yield per plant, SCA effects ranged from -5.58 (RNR 21278 x PTB 33) to 5.58 (JGL 27356 x PTB 33). Out of 10, two hybrids JGL 27356 x PTB 33 (5.58) and KPS 3018 x IET 23993 (4.55), showed significant positive SCA effects and were selected as desirable hybrids for higher grain yield (Table 4). Hybrids demonstrated significant positive SCA effects, making such hybrids desirable. Similar findings have been reported by Raju et al*. (2014*), Parimala et al*.* (2018), Yadav et al*.* (2020) and Nivedha et al*.* (2024).

An overall appraisal of *gca* effects revealed that among the lines, WGL 962 was a good general combiner for the traits *viz.,* days to 50% flowering, number of grains per panicle, 1000 grain weight, grain yield per plant, hulling, milling and head rice recovery percent and in testers, IET 239933 was a good general combiner for the days to 50% flowering, plant height and kernel length. These findings were supported by Satheeshkumar et al*.* (2016), Azad et al*.* (2022) and El-Agoury et al*.* (2024).

In hybrids, JGL 27356 x PTB 33 (5.58) was discovered to be a good specific combiner for traits such as days to 50% flowering, plant height, number of grains per panicle, 1000 grain weight, grain yield per plant and hulling percent and KPS 3018 x IET 23993 (4.55) for 1000 grain weight, kernel breadth, kernel length breadth ratio, grain yield per plant, hulling, milling and head rice recovery percent. Previously, Priyanka et al*.* (2014), Mallikarjuna et al*.* (2016), Saravanan et al*.* (2018), Manivelan et al*.* (2022), Abd-El-Aty et al*.* (2024), Balakrishna and Satyanarayana (2013) reported similar findings.

4. CONCLUSION

According to the study, the line WGL 962 was the best combination for grain yield and important yield components due to positive GCA effects and the tester IET 23993 for early and dwarfness, as well as hybrids, JGL 27356 x PTB 33 and KPS 3018 x IET 23993, were stable with favourable SCA effects, heterosis and per se performance for grain yield and its component traits. Testing these hybrids in multi-environment trials could indeed pave the way for their potential commercial application, offering resilience and yield improvements across different growing conditions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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