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Nature of gene action and combining ability effects for grain yield and quality traits in rice (*Oryza sativa* L.)

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Abstract
Combining ability, along with heterosis was elucidated for nine yield attributing and 10 grain quality traits in a set of 40 rice hybrid combinations derived from 13 parents using Line × Tester mating approach. The analysis of combining ability unveiled significant GCA and SCA variances, highlighting the importance of both additive and non-additive genetic components. The ratio of dominant genetic variance to additive genetic variance exceeded unity, indicating the prevalence of non-additive gene action in governing the inheritance of all examined traits. The parental line CO 55 and the testers IC 457996 and IC 208262 were recognized as good combiners for the majority of yield-related and grain-quality traits. Regarding *per se* performance, heterosis, and *sca* effects, the crosses CO 55 × IC 457996 and ADT 54 × IC 115439 were found promising. Consequently, these combinations could be exploited for recombination breeding aimed at developing early maturing, high-yielding fine-grain rice varieties with market acceptance.

Keywords: Combing ability, Line x Tester, Gene action, Heterosis, Rice

INTRODUCTION

Rice stands as the foremost important food crop in the world, especially in Asian countries. Despite being the primary dietary source for more than one-third of the world's population, its demand is increasing day by day. Projections indicate that by 2050, the global demand for rice will surge to 943.6 million tonnes, necessitating an annual production increase of 5.8 million tonnes from current levels (FAO, 2017). However, earlier records revealed that the annual growth in yield has been limited to ≤ 1% over the past decade, failing to keep pace with the escalating demand due to various constraints (Khush, 2013). In the present era, the significance of quality parameters is on the rise globally, especially in regions with self-sustaining rice production alongside improvements in people's per capita income and living standards. This prioritizes the need for the development of rice varieties that are both high-yielding and of superior quality. In light of the presently recognized constraints in resources and diverse environmental challenges, enhancing rice production through sustainable methods poses a significant challenge. Examining combining ability is one among many genetic approaches aimed at surpassing the yield barrier in rice and enhancing productivity. Selection of parental lines is crucial for the success of crop variety development, as the performance of the progeny relies primarily on the genetic potential of the parents (Sprague and Tatum, 1942). Combining ability studies helps to pinpoint optimal combiners that can be incorporated into crosses to exploit heterosis, accumulate fixable genes and acquire desirable segregants. This, in turn, enables breeders to effectively outline the breeding plan for the future enhancement of existing materials

(Abd-El-Aty *et al.*, 2023). The line × tester mating designs are frequently employed to screen parents for different sorts of gene activities and provide accurate information of GCA and SCA even when working with small sample sizes (Dimaano *et al.*, 2020; Kempthorne, 1957). Hence, this study was conducted with the objectives of 1) assessing the nature and extent of gene action related to yield, yield-contributing factors and grain quality traits, 2) estimating the General Combining Ability (GCA) of chosen parents and the Specific Combining Ability (SCA) of the resulting hybrid crosses and 3) quantifying the degree of heterosis exhibited by the generated hybrids.

MATERIALS AND METHODS

Five popular rice varieties *viz.,* CO 52, CO 54, CO 55, ADT 53 and ADT 54 (lines) and eight landraces *viz.,* IC 457996, IC 206282, IC 378202, IC 464685, IC 115439, IC 67496 and IC 458210 (testers) were chosen as parents based on their yield and quality characters. Hybridization was effected during *Rabi,* 2022 at the experimental plot in the Department of Rice, TNAU, Coimbatore. The resulting 40 hybrids from line × tester mating fashion along with thirteen parents were evaluated in a randomized complete block design with two replications during *Summer*, 2023 at the experimental farm of the Department of Rice, TNAU, which is located at 11° N latitude and 77° E longitude. Twenty-one-day-old seedlings were transplanted with one seedling per hill, with a spacing of 30 × 30 cm between rows and plants. The crop was grown by adopting recommended agronomic practices. Nine yield attributing traits *viz.*, days to fifty per cent flowering (DFF), plant height (cm; PH), number of productive tillers (NPT), flag leaf length (cm; FLL), flag leaf width (cm; FLB), panicle length (cm; PL), spikelet fertility (%; SF), thousand grain weight (g; TSW), single plant yield (g; SPY) and ten grain quality traits *viz.*, kernel length (mm; KL), kernel breadth (mm; KB), length breadth ratio (LB ratio), kernel length after cooking (mm; KLAC), kernel breadth after cooking (mm; KBAC), linear elongation ratio (LER), breadth-wise expansion ratio (BER), alkali spreading value (ASV), volume expansion ratio (VER) and water uptake ratio (WUR) were recorded on true F_1's from each replication. Combining ability analysis was performed through the line × tester method as suggested by Kempthorne (1957). Estimates of GCA and SCA effects and their variances were computed according to the method of Singh and Chaudhary (1977) as implemented through the '*Agricolae*' package (Gramaje *et al.*, 2020) of R software v4.3.1. The relative weight of additive versus non-additive type of gene actions was assessed according to Verma and Srivastava (2004). Heterotic effects were computed relative to standard parent CO 55 (best-performing check) as described by Liang *et al.* (1972) and their significance was evaluated using the t-test as outlined by Turner (1953).

RESULTS AND DISCUSSION

The rapid rise in population growth acts as the most influential driver for enhancing rice productivity. To meet the anticipated surge in food demand by 2050, there is a continual need for the enhanced creation of high-yielding rice varieties with improved grain qualities. Consequently, assessing the hybrid combining ability of parental lines proves to be an effective strategy for enhancing rice production.

Combining ability analysis: The combining ability was investigated to identify genotypes exhibiting high genetic potential for creating cross-combinations with desired traits and to examine the nature of gene action of targeted traits. The mean square estimates of combining ability analysis for yield, yield attributing and grain quality traits are summarized in **Table 1**. According to the analysis of variance, the highly significant mean squares due to the crosses and their partitions, lines, tester and line × tester interaction for the studied traits indicate a high degree of genetic diversity among the studied genotypes. The variance due to lines was significant for all the traits except flag leaf width and thousand grain weight whereas, the tester showed significant mean squares for all the examined traits. These significant mean squares for lines and tester indicate the prevalence of additive variances for these traits. The significant mean squares between lines x testers interaction except for thousand grain weight, kernel length, linear elongation ratio and volume expansion ratio emphasize the relevance of dominance or non-additive genetic factors in determining the expression of these traits. Consistent with our findings, the occurrence of both additive and non-additive genetic factors for yield, yield attributing and grain quality traits were previously reported by Manivelan *et al.* (2022), Gramaje *et al.* (2020) and Singh *et al.* (2012).

Estimates of genetic parameters: Understanding the gene action of traits is essential for implementing an appropriate breeding program. The findings demonstrated that the dominant genetic variance (σ^2H) was greater than the additive genetic variance (σ^2D) in controlling the inheritance of all examined traits (**Table 2**). This emphasized the significant contribution of non-additive gene effects in determining the genetic expression of these traits, as evidenced by the elevated values of $\sigma^2H/\ \sigma^2D$. Hence, the selection of desired genotypes based on phenotype performance may be ineffective for these traits, thus offering scope for hybridization and the strategic selection of families or progenies in subsequent generations to enhance the desired traits. Notably, for all traits except kernel length, the degree of dominance surpassed unity, indicating the prevalence of over-dominance in the manifestation of these traits during crosses. Consistent with our findings, previous research by Abd-El-Aty *et al.* (2023), Manivelan *et al.* (2022) and Gramaje *et al.* (2020) also highlighted the substantial role of non-additive gene action in influencing yield components, emphasizing their relevance in hybrid rice development. Proportional contribution to the total

Table 1. Mean square estimates of combining ability analysis for yield, yield attributing and grain quality traits

S.No	Traits	Mean sum of squares					
		Replications	Crosses	Lines	Testers	Lines × Testers	Error
	df	1	39	4	7	28	52
1	Days to fifty per cent flowering	2.07	10.40**	55.33**	7.02**	4.83**	6.21
2	Plant height	2.47	4.22**	18.34**	3.56**	2.36**	59.64
3	Number of productive tillers	1.87	3.77**	4.21**	8.03**	1.77*	16.02
4	Flag leaf length	3.94	6.45**	35.58**	4.66**	2.74**	11.49
5	Flag leaf breadth	2.56	2.20**	2.33	3.73**	1.80*	0.01
6	Panicle length	0.20	12.03**	9.87**	32.06**	7.33**	11.92
7	Thousand grain weight	0.04	3.05**	1.47	10.60**	1.39	0.84
8	Spikelet fertility	0.20	12.03**	9.87**	32.06**	7.33**	11.92
9	Single plant yield	2.06	5.80**	4.40**	13.16**	4.16**	13.65
10	Kernel length	0.03	4.83**	8.91**	16.45**	1.34	0.02
11	Kernel breadth	1.47	22.18**	38.38**	51.37**	12.57**	0.00
12	Length Breadth ratio	1.33	19.99**	40.18**	52.25**	9.04**	0.01
13	Kernel length after cooking	1.16	9.32**	31.19**	17.48**	4.16**	0.13
14	Kernel breadth after cooking	0.02	2.87**	4.17**	3.36**	2.57**	0.06
15	Linear Elongation Ratio	0.73	3.08**	8.09**	5.74**	1.70	0.01
16	Breadthwise Expansion Ratio	0.61	2.34**	3.51*	2.63*	2.11*	0.02
17	Alkali Spreading value	0.45	13.14**	7.32**	36.48**	8.14**	0.11
18	Volume Expansion Ratio	1.03	2.25**	6.71**	3.00*	1.42	0.27
19	Water Uptake Ratio	3.63	3.66**	8.17**	5.85**	2.46**	0.12

** 1% level of significance; *5% level of significance

Table 2. Estimate of genetic variance and proportional contribution of lines, tester and line × tester interaction

S.No	Traits	σ^2D	σ^2H	σ^2H/σ^2D	Degree of dominance	Proportional contribution		
						Lines	Testers	Line × Tester
1	Days to fifty per cent flowering	1.831	11.881	6.490	2.547	54.560	12.120	33.320
2	Plant height	5.849	40.629	6.947	2.636	44.610	15.150	40.230
3	Number of productive tillers	0.956	13.132	13.736	3.706	11.460	38.240	50.300
4	Flag leaf length	2.258	9.991	4.425	2.104	56.570	12.960	30.480
5	Flag leaf breadth	0.000	0.003	16.000	4.000	10.860	30.420	58.720
6	Panicle length	0.204	1.834	8.990	2.998	38.750	20.100	41.150
7	Thousand grain weight	0.074	0.164	2.232	1.494	4.930	62.330	32.740
8	Spikelet fertility	2.964	37.744	12.733	3.568	8.410	47.830	43.750
9	Single plant yield	1.184	21.571	18.225	4.269	7.780	40.710	51.510
10	Kernel length	0.003	0.003	0.941	0.970	18.920	61.170	19.900
11	Kernel breadth	0.002	0.017	10.750	3.279	17.750	41.570	40.680
12	Length Breadth ratio	0.004	0.027	6.850	2.617	20.610	46.920	32.460
13	Kernel length after cooking	0.035	0.203	5.800	2.408	34.310	33.640	32.050
14	Kernel breadth after cooking	0.001	0.050	50.300	7.092	14.890	21.000	64.110
15	Linear Elongation Ratio	0.001	0.003	5.000	2.236	26.930	33.450	39.610
16	Breadthwise Expansion Ratio	0.000	0.012	60.000	7.746	15.090	18.370	66.530
17	Alkali Spreading value	0.029	0.392	13.500	3.674	5.710	49.820	44.470
18	Volume Expansion Ratio	0.012	0.057	4.822	2.196	30.590	23.970	45.430
19	Water Uptake Ratio	0.008	0.091	11.628	3.410	22.920	28.700	48.380

σ^2D – Additive genetic variance; σ^2H – Dominance genetic variance

variance by lines, testers and interactions revealed that the magnitude of the contribution of the line × tester interaction was high for most of the examined traits *viz*., number of productive tillers, flag leaf breadth, panicle length, kernel breadth after cooking, linear elongation ratio, breadth-wise expansion ratio, volume expansion ratio and water uptake ratio (**Table 2**). This emphasizes the significance of the specific combining ability of crosses, providing additional confirmation of the non-additive gene action in manifesting these traits. Likewise, testers had contributed a maximum for thousand grain weight, spikelet fertility, kernel length, kernel breadth, length breadth ratio and alkali spreading value indicating their more diverse nature.

General Combining Ability: The success of any plant breeding effort revolves around the selection of superior parents that can transmit the intended traits to the progenies. From a genetic standpoint, the GCA assesses both additive and additive × additive gene activity. Hence, the success of any breeding program relies on selecting parents with favorable GCA effects. The selection of parents based on their *per se* performance and the general combining ability (*gca*) effect facilitates the identification of lines harboring favorable alleles for the desired trait, in view of the preponderant additive gene action. This has also been advocated by Abd El-Aty *et al.* (2022) and Sunny *et al.* (2022) in rice and Rajan *et al.* (2022) in brinjal. In the present study, the line CO 55 exhibited significant mean performance and *gca* effects in the desirable direction for days to fifty per cent flowering and most of the grain quality traits *viz.,* kernel length, kernel breadth, length breadth ratio, kernel length after cooking and kernel breadth after cooking, a major factor in determining the market value and consumer preferences. Also, it showed high positive *gca* effects for single plant yield, linear elongation ratio, volume expansion ratio and water uptake ratio. Similarly, the line ADT 53 showed low mean and negative *gca* effects for days to fifty per cent flowering and plant height making it well-suited for developing short-duration semi-dwarf rice varieties. The line CO 52 had high positive *gca* effects for number of productive tillers, kernel length, length breadth ratio, kernel length after cooking, volume expansion ratio and water uptake ratio. Moreover, the line ADT 54 showed high positive *gca* effects for panicle length, spikelet fertility and alkali spreading value whereas, negative *gca* effects for breadth-wise expansion ratio.

The tester IC 457996 exhibited high inherent performance with favorable *gca* in the desirable direction for numerous yield-attributing traits *viz.,* days to fifty per cent flowering, panicle length, thousand grain weight, spikelet fertility and single plant yield. Also, they were found to be good combiners for grain quality traits *viz*., kernel length, kernel breadth, length breadth ratio, kernel length after cooking and alkali spreading value. Similarly, the tester IC 206282 was found to be a good combiner for yield-attributing traits (flag leaf breadth and panicle length) and grain quality traits (kernel breadth, length breadth ratio, kernel length after cooking, linear elongation ratio, volume expansion ratio and water uptake ratio). Highly significant positive *gca* effects for thousand grain weight and single plant yield were noticed in the tester IC 115439. Likewise, the tester IC 115406 recorded negative *gca* effects for days to fifty per cent flowering, kernel breadth and kernel breadth after cooking while positive *gca* effects were found for spikelet fertility and length breadth ratio. The results revealed that none of the parents exhibited significant *gca* effects in preferred directions for all the examined traits. Consequently, to enhance the precision of selection, parents were scored based on their *gca* effects. A score of '+1' was assigned for the significant positive *gca* effect, '-1' for the negative significant *gca* effects and '0' for non-significance in the traits (**Fig. 1**). The results indicated that among the lines CO 55 and testers IC 457996 followed by IC 206282 registered a high score for most of the yield attributing and grain quality traits indicating a sizable quotient of additive variance in operation for these traits and hence could be utilized in breeding programs to facilitate the development of fine-grain rice varieties characterized by high yield in a short duration and with market acceptance.

Specific combining ability: The Specific Combining Ability (SCA) of the crosses determines the genetic potential of the crosses in harnessing heterosis for use in breeding material as they comprehend the non-additive impact on a trait. These have been attributed to the existence of linkage during the repulsion phase or the combination of desirable genes with favourable effects from parents (Sunny *et al*., 2022). Similar to the outcomes observed in GCA, none of the hybrid combinations simultaneously demonstrated desirable *sca* effects for all of the examined traits. Similar scenario was reported earlier by Gramaje *et al.* (2020), Rahman *et al.* (2022) and Kahani *et al.* (2018). Kernel breadth and length breadth ratio (27.50%) exhibited the highest percentage of crosses with desirable *sca* effects, followed by alkali spreading value (20.00%) and number of productive tillers and spikelet fertility (12.50%). The *sca* effects along with mean performance could be a precise measure of identifying desirable hybrids for different traits. The best-performing F_1 hybrids in terms of *per se* performance and *sca* effect for yield attributing and grain quality traits are summarized in **Table 3**. Yield improvement is the prime objective of any breeding program. Although rice often displays superior *sca* effects for grain yield (Sari *et al*., 2020), only 17.50% of the crosses showed statistically significant positive *sca* effects, suggesting a careful selection of parents for generating L × T population. Notably, only two crosses *viz*., ADT 53 × IC 115439 and ADT 54 × IC 115439 demonstrated a combination of high mean and desirable *sca* effects for single plant yield. In addition, higher *per se* performance with significant positive *sca* effects were exhibited by ADT 54 × IC 115439 for spikelet fertility, which

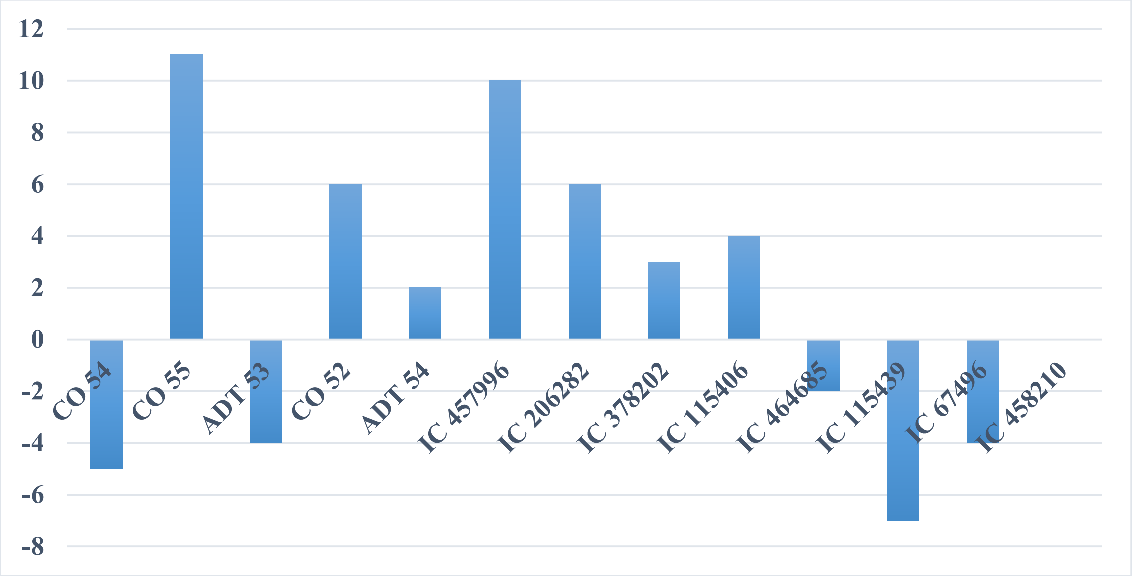

Fig. 1. Ranking parents as per *gca* effects for yield, yield attributing and grain quality traits

plays a major role in enhancing the yield while integrating desirable traits from landraces. The crosses CO 55 × IC 378202 and ADT 54 × IC 457996 exhibited higher *per se* performance and significant *sca* in the desirable direction for grain quality traits *viz.,* kernel breadth, length breadth ratio and kernel breadth after cooking. Similarly, higher *per se* performance and significant *sca* in the desirable direction for kernel breadth, kernel breadth after cooking and alkali spreading value were noticed in CO 55 × IC 458210 along with significant positive *sca* for single plant yield and spikelet fertility. Significant *sca* alone was observed in the crosses CO 52 × IC 378202 and ADT 54 × IC 206282 kernel breadth, length breadth ratio and kernel breadth after cooking followed by ADT 53 × IC 115439 and CO 54 × IC 458210 for length breadth ratio and alkali spreading value. Moreover, CO 52 × IC 378202 exhibited high *sca* for the number of productive tillers, while ADT 54 × IC 206282 revealed high *sca* for plant height, flag leaf length and alkali spreading value. Furthermore, ADT 53 × IC 115439 displayed high *sca* effects for single plant yield and kernel breadth, while CO 54 × IC 458210 exhibited high *sca* effects for kernel breadth after cooking and breadthwise expansion ratio. Therefore, these crosses can be employed for harnessing heterosis and transgressive segregants identified for both grain yield and quality from the best-performing crosses can be stabilized in subsequent generations through pedigree selection.

Heterosis**:** Among the three types of heterosis, standard heterosis could be a better measure for breeding purposes as it reflects the actual superiority of F_1 hybrids over the existing best cultivar for replacement, making it more relevant and advantageous (Virmani *et al.*, 1982). Therefore, in the current study, heterosis over the elite cultivars CO 55 was considered as the criterion to assess the best hybrid for both grain yield and quality. The best-performing F_1 hybrids in terms of *per se* performance and standard heterosis for yield attributing and grain quality traits are summarized in **Table 4**. Heterosis for grain yield results from the simultaneous enhancement in the expression of its components (Grafius, 1959). Almost all the hybrids i.*e.* 52.5% of them with significant positive heterosis for grain yield also demonstrated significant positive heterosis for thousand grain weight. Similarly, in the case of the number of productive tillers among the nine hybrid combinations, four specific combinations CO 55 × IC 457996, ADT 53 × IC 378202, CO 55 × IC 464685, and ADT 54 × IC 67496 manifested noteworthy positive heterosis for both the number of productive tillers and grain yield. Furthermore, CO 55 × IC 457996 and ADT 54 × IC 67496 also exhibited superior heterosis for panicle length. Early-maturing rice hybrids are desirable for their suitability in multiple cropping systems. Out of the six hybrid combinations displaying noteworthy negative heterosis for days to fifty per cent flowering, three combinations *viz.,* CO 55 × IC 457996, ADT 53 × IC 378202, and CO 52 × IC 457996 proved to be superior over the check, in terms of both grain yield and thousand grain weight. Cultivars characterized by longer grain length are predominantly favored, as they contribute significantly to determining market value. Significantly, CO 52 × IC 457996 exhibited positive heterosis for kernel length, while CO 55 × IC 457996 demonstrated superior heterosis for kernel length after cooking. Therefore, these hybrid combinations can be employed in the development of short-duration, high-yielding rice cultivars with better market acceptability. These results are in close

Table 3. Comparison of crosses with significant *sca* effects and *per se* performance with the *gca* status of parents for yield attributing and grain quality traits

Traits	Hybrids	*Per se* performance	*sca* effects	*gca* status
Number of productive tillers	CO 52 × IC 378202	39.00**	6.03 *	H x H
	ADT 54 × IC 67496	31.00*	5.84 *	L x L
Flag leaf length	CO 52 × IC 458210	38.45*	5.09 *	L x H
	ADT 54 × IC 457996	47.02**	7.30 **	H x L
	ADT 54 × IC 206282	45.25**	5.95 *	H x L
	ADT 54 × IC 458210	47.35**	6.34 *	H x H
Flag leaf breadth	CO 52 × IC 67496	1.43*	0.14 *	L x L
Panicle length	ADT 54 × IC 458210	32.02**	3.58 **	H x L
Spikelet fertility	ADT 53 × IC 378202	88.08**	13.89 **	L x L
	ADT 54 × IC 115439	84.97**	9.62 **	H x L
Single plant yield	CO 54 × IC 378202	44.08*	5.64 *	L x H
	ADT 53 × IC 115439	45.36*	6.52 *	L x H
	ADT 54 × IC 115439	47.23**	6.16 *	L x H
Kernel breadth	CO 55 × IC 378202	1.88**	-0.11 **	L x L
	CO 55 × IC 458210	1.85**	-0.08 *	L x L
	CO 52 × IC 378202	1.93**	-0.12 **	L x L
	ADT 54 × IC 457996	1.98*	-0.21 **	H x L
Length breadth ratio	CO 55 × IC 378202	3.23**	0.22 **	H x H
	CO 55 × IC 458210	3.11**	0.14 *	H x L
	ADT 53 × IC 115406	3.08**	0.17 **	L x H
	CO 52 × IC 378202	3.12**	0.21 **	H x H
	ADT 54 × IC 457996	3.09**	0.29 **	L x H
Kernel breadth after cooking	CO 55 × IC 378202	2.00**	-0.46 *	L x L
	CO 55 × IC 464685	2.3*	-0.36 *	L x L
Alkali Spreading value	CO 54 × IC 457996	4.75**	0.58 *	L x H
	CO 54 × IC 67496	4.34*	1.08 **	L x L
	CO 55 × IC 458210	4.59**	0.87 **	L x L
	ADT 53 × IC 378202	4.84**	0.71 **	L x H

** 1% level of significance; *5% level of significance; L - Parents with low GCA; H - Parents with high GCA

agreement with Yadav *et al.*(2021), Sunny *et al.* (2022) and Manivelan *et al.* (2022).

Heterosis and Combining ability: The parents were categorized into high GCA (with a significant *gca* effect in the desired direction) and low GCA parents (with non-significant and significant *gca* effects in an undesirable direction). The F_1 hybrids exhibiting significant *sca* effects and heterosis were grouped with the three distinct groups based on the GCA effects of the parents associated (**Fig. 2 and Fig. 3**). Our findings align with the outcome of Mallikarjuna *et al.* (2016) where crosses involving various combinations, including High × High, High × Low, Low × High, and Low × Low general combiners, yield superior *sca* effects. The combination of a desirable *sca* effect along with parents exhibiting desirable *gca* effect indicates an additive x additive effect and thus, simple selection can be employed for improvements. Our findings indicate that the highest proportion of hybrids exhibiting significant *sca* effects was linked to parents with Low × Low GCA (60.56%), followed by those with High × Low GCA (32.39%), and High × High GCA parents (7.04%). The superior performance of most hybrids expressed by low × low crosses can be primarily attributed to epistatic interaction (dominance × dominance), leading to over-dominance. Likewise, the highest proportion of hybrids exhibiting significant heterosis was linked to parents with Low × Low GCA (43.62%), followed by those with High × Low GCA (42.55%), and High × High GCA parents (13.83%). A similar grouping pattern was also observed by Sunny *et al.* (2022) and Rahman *et al.* (2022). This emphasizes the importance of parental diversity *i.e.* in

Table 4. Comparison of crosses with significant standard heterosis with the *gca* status of parents for yield attributing and grain quality traits

Traits	Hybrids	Standard heterosis	*gca* status
Days to fifty per cent flowering	CO 55 × IC 457996	-6.06 *	L x L
	ADT 53 × IC 457996	-5.77 *	L x L
	ADT 53 × IC 378202	-5.23 *	L x L
	ADT 53 × IC 115406	-6.40 *	L x L
	ADT 53 × IC 464685	-6.13 *	L x L
	CO 52 × IC 457996	-5.69 *	L x L
Number of productive tillers	CO 52 × IC 378202	103.12 **	H x H
	ADT 54 × IC 67496	61.46 **	L x L
	CO 52 × IC 67496	63.65 **	H x L
	CO 52 × IC 458210	61.46 **	H x L
Flag leaf length	CO 52 × IC 458210	20.93 *	L x L
	ADT 54 × IC 457996	47.86 **	H x L
	ADT 54 × IC 206282	42.30 **	H x L
	ADT 54 × IC 458210	48.90 **	H x H
Panicle length	CO 55 × IC 457996	11.38 *	L x H
	CO 55 × IC 206282	11.46 *	L x H
	ADT 54 × IC 457996	12.78 **	H x H
	ADT 54 × IC 206282	16.50 **	H x H
	ADT 54 × IC 115406	13.59 **	H x L
	ADT 54 × IC 458210	24.35 **	H x L
Thousand grain weight	ADT 53 × IC 115439	56.23 **	L x H
	CO 52 × IC 115439	54.66 **	L x H
	ADT 54 × IC 115439	56.72 **	L x H
Single plant yield	CO 54 × IC 457996	43.16 **	L x H
	CO 54 × IC 378202	42.65 **	L x H
	CO 55 × IC 457996	48.71 **	H x H
	ADT 54 × IC 457996	47.18 **	L x H
	ADT 53 × IC 115439	46.80 **	L x H
	ADT 54 × IC 115439	52.83 **	H x L
Kernel length	CO 52 × IC 457996	4.60 *	H x H
Kernel length after cooking	CO 55 × IC 457996	12.79 *	H x H
Alkali Spreading value	CO 55 × IC 457996	17.65 *	L x H
	CO 52 × IC 206282	46.15 **	H x L
Volume Expansion Ratio	ADT 54 × IC 206282	38.46 *	H x H
Water Uptake Ratio	CO 52 × IC 206282	28.28 *	H x H
	CO 52 × IC 458210	28.10 *	H x L

** 1% level of significance; *5% level of significance; L - Parents with low GCA; H - Parents with high GCA

terms of the *gca* effect, in determining the expression of observed SCA and heterosis. The high-yielding potential of crosses *viz*., CO 54 × IC 378202, ADT 53 × IC 115439 and ADT 54 × IC 115439 with high *sca* effect and standard heterosis can be attributed to the presence of high × low combiners as a result of interaction between positive alleles from good combiners and negative alleles from poor combiners (**Table 3 and Table 4**). The high *sca* effect observed in these crosses could be attributed to the complementary type of gene action. Crosses involving good general combiners, specifically High × High GCA as seen in CO 55 × IC 457996, led to the discovery of a cross that is early maturing, high yielding with significant mean and standard heterosis which might be the

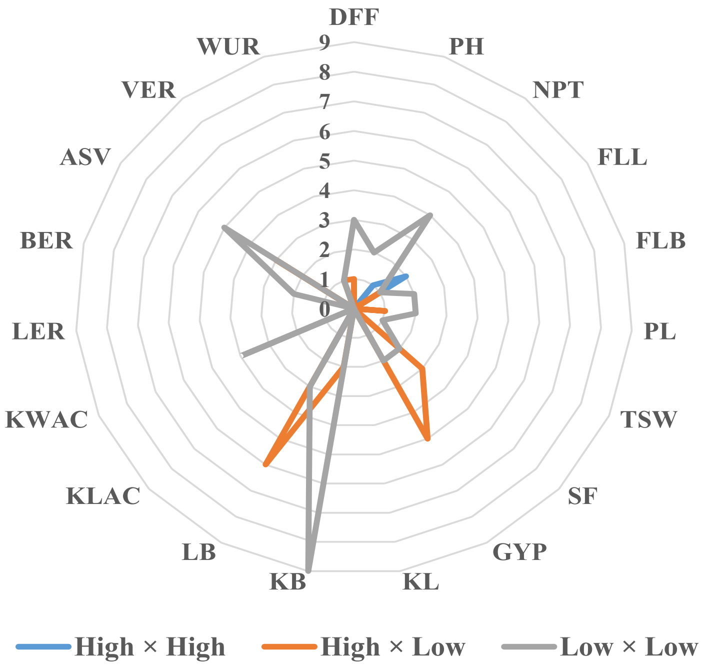

Fig. 2. Frequency of crosses as per gca effects of parents for yield, yield attributing and grain quality traits

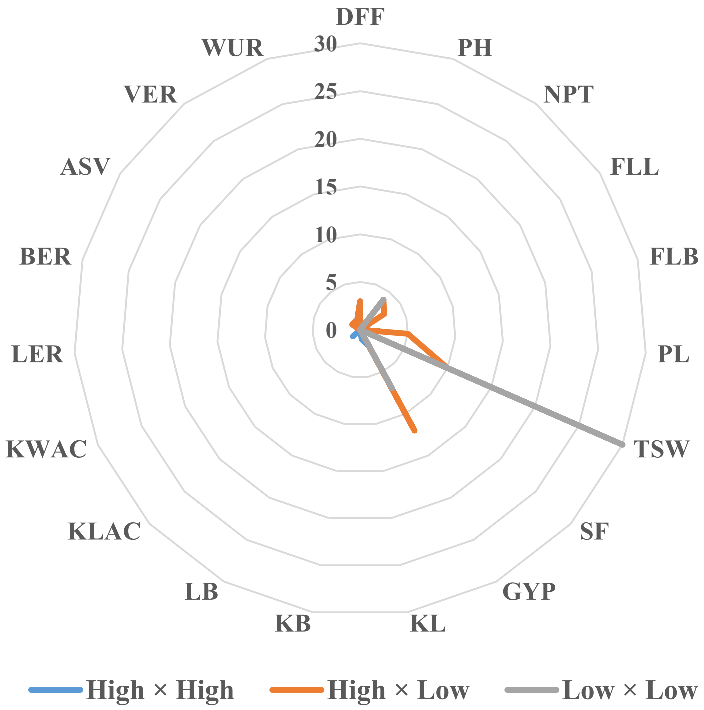

Fig. 3. Frequency of crosses exhibiting heterosis as per gca effects of parents for yield, yield attributing and grain quality traits

result of interaction between positive × positive alleles (**Table 4**). Additionally, CO 55 × IC 457996 exhibited superior performance compared to a standard check in terms of number of productive tillers, panicle length, thousand grain weight, kernel length after cooking and alkali spreading value. Therefore, the likelihood of obtaining superior segregants from CO 55 × IC 457996 is high, especially when the additive genetic system in the good combiner and the epistatic effect in the crosses complement each other to maximize desirable plant traits. These anticipated transgressive segregants could be utilized in identifying early maturing, high-yielding fine-grain rice varieties with market acceptance through the pedigree method of selection. Similar findings were reported by Sing *et al*. (1971), ElShamey *et al.* (2022) and Sunny *et al.* (2022).

In the present study, the parental line CO 55 and the testers IC 457996 and IC 208262 were recognized as good combiners for the majority of yield-related and grain-quality traits. Consequently, these parent lines can be strategically utilized in pedigree breeding to produce superior recombinants through selection in subsequent generations. Moreover, the cross combinations CO 55 × IC 457996, ADT 54 × IC 115439 and ADT 54 × IC 115439 emerged as particularly promising based on *per se* performance, specific combining ability effects and heterosis, suggesting that they could be considered for use in future breeding programs.

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