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RESEARCH ARTICLE

Exploring gene action and combining ability for yield improvement in rice (*Oryza sativa* L.) landraces

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Abstract

Estimating combining ability is essential for evaluating genotypes and understanding the nature and magnitude of gene actions involved in plant breeding. In a study involving four lines and seven testers, a Line × Tester mating design was employed to analyze combining ability, heterosis, and gene action across 16 yield-related traits. The results indicated significant variances for general combining ability (GCA) and specific combining ability (SCA), underscoring the relevance of additive and non-additive genetic components in trait inheritance. The analysis revealed that the ratio of dominant genetic variance to additive genetic variance was greater than one for most traits, with the exceptions being test weight and the grain length:breadth ratio. This suggests that non-additive gene action predominantly influences the inheritance of the examined traits. Among the parental lines studied, CO 54, CO 55, RL 8601, RL 6298, and RL 27 emerged as the best general combiners for single-plant yield and other traits. Based on the outcomes of standard heterosis, the following hybrid combinations were identified as optimal for augmenting single-plant yield: ADT 58 × RL 2348 (105.33%), CO 55 × RL 6298 (104.5%), CO 54 × RL 6298 (103.87%), CO 54 × RL 8601 (100.76%), ADT 58 × RL 2196 (99.8%), and ADT 56 × RL 6298 (97.65%). These results indicate that the identified cross combinations could be effectively employed in recombination breeding programs focused on producing early-maturing, high-yielding fine-grain rice varieties that align with market requirements.

Keywords

combining ability; gene action; heterosis; Line × Tester; rice

Introduction

Rice (*Oryza sativa* L.) is a cornerstone of Indian agriculture and occupies a distinctive role among domesticated crops serving as the primary food source for approximately two-thirds of the country's population. It contributes significantly to the country's nutritional needs, supplying 43% of the required calorie intake and accounting for 20–25% of agricultural income (1, 2). Globally, over 90% of rice production and consumption occurs in Asia, often referred to as the "rice bowl of the world", this region is home to 60% of the global population and two-thirds of the world's impoverished communities (1). With the increasing global population, the global demand for rice consumption is projected to increase significantly, from 450 million tons in 2011 to approximately 510 million tons in 2024, potentially reaching around 650 million tons by 2050.

Global rice production is anticipated to reach an unprecedented 520.9 million tonnes in the 2023-2024 period, with projections indicating further expansion to 527.6 million tonnes in 2024-2025. India's 2023-2024 fiscal year rice production reached an all-time high of 1378.25 lakh tonnes, exhibiting a 20.70 lakh tonnes surge from the preceding year and a 173.95 lakh tonnes increase from the five-year average. Notably, the harvested area for 2023-2024 spanned 47.8 million hectares, marking a 2% increase from the previous year. In Tamil Nadu, rice is cultivated over an area of 2.10 million hectares, producing 6.80 million tons with an average productivity of 2.965 tons per hectare. To meet these growing food demands, it is estimated that rice production will need to increase by 40% by 2050 to support the ever-growing population (3). Projections indicate that India will need to produce 138 million tons of rice on 37 million hectares of land by 2050 to sustain its food security. Achieving this target will require a 50% increase in yield over the next three decades (4). However, the escalating occurrence of both biotic and abiotic stresses, exacerbated by climate change, presents significant challenges to achieving these production targets (3). Both developed and developing nations strive to meet their consumption needs.

Enhancing grain yield and improving quality traits are crucial factors for boosting national income and ensuring food security. Investing in rice research is essential for enhancing productivity, which directly benefits both farmers and consumers in developing countries (5). Recent technological advancements have made it increasingly feasible to combine high-yield potential with improved grain and nutritional quality (6). The careful selection of appropriate genotypes as parents for hybridization is crucial for establishing an effective breeding program, ultimately leading to the development of high-yielding cultivars (7). Combining ability analysis plays a significant role in this process, as it provides insights into the nature and magnitude of gene effects that influence yield and yield-contributing traits. This analysis not only identifies superior parent lines but also helps determine optimal cross combinations. By understanding the genetic potential of different genotypes, breeders can formulate systematic breeding plans aimed at enhancing rice yield. Such strategic approaches are essential for developing cultivars that can meet the increasing demands for rice production while addressing challenges posed by environmental stresses and changing agricultural conditions (2).

The Line × Tester technique (8) is widely utilized for screening germplasm based on general combining ability (GCA) and specific combining ability (SCA) variances and effects. This method opens the door for evaluating the relative ability of female and male lines to produce desirable hybrid combinations. Non-additive gene effects were found to be important for most traits across the studies. Several researchers reported a predominance of non-additive gene action, as SCA variances exceeded GCA variances for most traits (7, 9, 10). Combining ability studies in rice have been instrumental in identifying superior combiners for yield traits, enabling the development of high-performing hybrids. However, a significant research gap exists in understanding the specific combining ability of diverse rice genotypes, which can be leveraged to enhance yield potential. Previous studies have primarily focused on evaluating the combining ability of a limited set of parental lines, neglecting the vast genetic diversity available in rice germplasm. This study seeks to overcome existing limitations by assessing an extensive and diverse array of rice genotypes, thereby providing a more nuanced understanding of combining ability for yield traits. The research aims to identify optimal cross-combinations, novel combiners, and the underlying gene action, as well as the degree of heterosis that can be leveraged in hybrid breeding programs to develop high-yielding rice varieties, ultimately enhancing rice productivity.

Materials and Methods

The present study was conducted during the *Kharif* season of 2024 at the Department of Rice, Paddy Breeding Station, Centre for Plant Breeding and Genetics, TNAU, Coimbatore. Current research utilized four high-yielding superior varieties as lines, namely (CO 54, CO 55, ADT 56, and ADT 58) along with seven traditional Landraces as testers: (RL 27, RL 292, RL 2196, RL 2348, RL 4452, RL 6298, RL 8601). The seven diverse rice (*Oryza sativa* L.) landraces were meticulously selected as research samples due to their distinct characteristics and agronomic significance. These landraces were chosen for their unique origins, which are expected to contribute to a broader genetic diversity, as well as their high-yielding ability, making them ideal candidates for improving yield resilience in rice. The selected parental testers consisted of high-yielding germplasm, serving as a benchmark for yield potential, and adopted local cultivars as lines that exhibit desirable traits such as early maturation, compact stature, and fine grain type. By incorporating these diverse genotypes into the study, we aimed to capture a wide range of genetic variation and identify valuable traits that can be harnessed to develop high-performing rice varieties, ultimately enhancing rice productivity and sustainability. To ensure synchronization between female and male parents, staggered sowing of the entries was performed. Hybridization was carried out during the *Rabi* season of 2023 using the Line × Tester mating design (8) to generate hybrids. In this mating system, a random selection of 'l' lines is paired with each of the 't' testers. The seeds were planted in raised nursery beds at intervals of ten days to ensure synchronized flowering (11). In the crossing block, 25-day-old seedlings were transplanted, with two seedlings per hill, maintaining a spacing of 30 cm between rows and 20 cm within rows. Crosses were conducted following a Line × Tester design (Fig. 1 & 2), involving four female and seven male parents, resulting in a total of 28 cross combinations.

The process utilized hand emasculation and artifi-

	TESTERS (MALE)						
LINES (FEMALE)	RL 27	RL 292	RL 2196	RL 2348	RL 4452	RL 6298	RL 8601
CO 54	*	*	*	*	*	*	*
CO 55	*	*	*	*	*	*	*
ADT 56	*	*	*	*	*	*	*
ADT 58	*	*	*	*	*	*	*

Fig. 1. Crossing plan of Line × Tester cross.

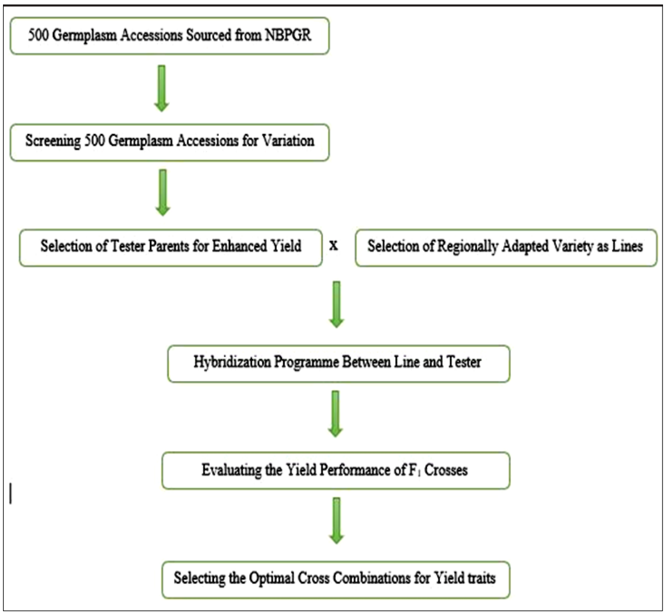

Fig. 2. Workflow chart of heterosis and combining ability analysis.

cial pollination, with the inflorescence covered by a butter paper bag before anthesis and left undisturbed until the flowers had fully opened. The experimental setup included 28 hybrids along with eleven parental lines, which were initially raised in nursery beds before being transplanted into the main field. The planting formation consisted of rows spaced 20 cm apart, with 20 cm between individual plants. Each hill was maintained with one seedling that was 25 days old at the time of transplantation. A uniform row length of 2 m was established for each genotype. The experiment was organized using a Randomized Block Design with three replications to ensure statistical validity. Additionally, standard cultural practices and targeted plant protection measures were implemented to support the establishment and growth of the crop throughout the experimental period.

At the appropriate growth stages, biometric observations were recorded on five randomly selected and tagged plants for each cross combination and parent in each replication. The traits measured included days to 50% flowering (DFF), days to maturity (DM), plant height (PH) (cm), total tillers per plant (TTP), effective tillers per plant (ETP), flag leaf length (FL) (cm), flag leaf breadth (FB) (cm), panicle length (PL) (cm), panicle weight (PW) (g), grains per panicle (GPP), spikelet fertility (SF) (%), test weight (TW) (g), grain yield per plant (GYP) (g), grain length (GL) (mm), grain breadth (GB) (mm), and grain length-to-breadth ratio (GL/GB) (mm). The mean performance of these traits was calculated and compiled into tables. Using the parental genotypes and the 28 crosses, GCA and SCA effects were determined (12), to identify superior combiners and promising cross combinations. Heterotic effects were calculated about the standard parent CO 55, recognized as the best-performing check (13). The significance of these effects was assessed using the t-test (14).

Statistical analysis

The presuppositions underlying the application of analysis of variance (ANOVA) and other statistical methodologies are as follows: the data points should exhibit observational independence, meaning they should be uninfluenced by one another, while the data within each group should demonstrate normality of distribution, approximating a normal distribution. Additionally, the groups should exhibit homoscedasticity, where the variance of the groups is equivalent, and the data should be collected through random sampling. Furthermore, the scale of measurement is also crucial, as the dependent variable should be quantified on an interval or ratio scale, ensuring that the data is measured in a way that allows for meaningful comparisons and analyses.

Results and Discussion

ANOVA for combining ability analysis

The analysis of variance for parents and hybrids concerning 16 traits was conducted and is summarized in (Table 1). The variance attributed to lines and testers was statistically significant for all traits, except for FB, GB, and GL/GB. The significant mean squares observed for lines and testers indicate the predominance of additive genetic variances for these traits. Similarly, the variance for line × tester interactions and hybrids was significant for most traits, excluding FB, PW, GL, GB, and the GL/GB. The significant mean squares for line × tester interactions highlight the importance of dominance or non-additive genetic factors in governing the expression of these traits. Non-additive genetic interactions refer to the synergistic effects of distinct alleles, encompassing genetic dominance and epistasis. In contrast to additive genetic influence, where multiple genes exhibit a linear or cumulative effect, non-additive genetic effects involve allelic interactions where one allele predominates over the other. In breeding initiatives, when dominant effects are pronounced, selection may target either homozygous dominant or heterozygous individuals, depending on the desired phenotypic outcomes. This, in turn, influences the trajectory and efficacy of selection. To enhance these traits, breeders may defer selection to advanced segregating generations, allowing dominance and epistasis to dissipate, thereby optimizing the selection process. For instance, A cross between inbred lines like IR64 and KMR3 often results in hybrids with superior yields due to non-additive interactions between complementary alleles, enhancing traits such as panicle length, grain number, and biomass. In line with our results, the presence of both additive and non-additive genetic factors influencing yield, yield-related traits, and grain traits has been previously reported (12, 15). These findings highlight the presence of significant differences among lines, testers, and hybrids involved in the study.

Table 1. Mean square estimates of combining ability analysis for yield and yield-attributing traits

Traits	**Mean sum of squares**					
Source of Variation	**Replication**	**Crosses**	**Lines**	**Testers**	**Lines × Testers**	**Error**
DF	2	27	3	6	18	54
Days to 50% flowering	0.14	438.99**	2138.42**	710.63**	65.20**	1.39
Days to maturity	0.44	502.43**	1773.24**	939.02**	145.10**	3.60
Plant height (cm)	1.85	1033.27**	694.51**	3520.69**	260.59**	15.61
Total tillers per plant	1.32	62.72**	22.95**	172.00**	32.92**	3.63
Effective tillers per plant	0.11	55.27**	27.47**	136.32**	32.89**	2.44
Flag leaf length (cm)	4.84**	277.20**	537.57**	301.21**	225.80**	8.19
Flag leaf breadth (cm)	0.00	0.25	0.16	0.86	0.06	0.01
Panicle length (cm)	0.65	27.75**	34.17**	75.40**	10.80**	1.29
Panicle weight (g)	0.02	3.53**	12.52**	4.59**	1.68	0.01
Grain per panicle	0.94	11109.10**	38309.28**	15989.73**	4948.86**	60.62
Grain yield per plant (g)	0.20	149.87**	35.11**	256.76**	133.36**	1.29
Spikelet’s fertility	2.98	105.30**	139.27**	253.99**	50.08**	4.65
Test weight (g)	0.23	21.05**	35.57**	7.81**	23.04**	0.38
Grain length (mm)	0.01	2.52**	4.90**	3.81**	1.70	0.01
Grain breadth (mm)	0.01	0.25	0.07	0.39	0.24	0.02
Grain length/breadth ratio	0.07	0.70	1.03	0.39	0.74	0.07

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

Estimates of genetic parameters

Understanding gene action for various traits is crucial for implementing effective breeding programs. An examination of the results revealed that the ratio of GCA variance to SCA variance was less than one for all the traits studied (16, 17). This indicates the predominance of non-additive gene action, suggesting that dominance and epistatic interactions play a significant role in the expression of these traits (Table 2). Consequently, there is potential for heterosis breeding by leveraging hybrid vigor. These findings align with the earlier reports (10, 18). The mean degree of dominance exceeded unity (> 1) for all the traits except TW, GL/GB, indicating the presence of overdominance. The findings revealed that the dominant genetic variance (σ^2H) exceeded the additive genetic variance (σ^2D) for all traits analyze (Table 2).

This observation underscores the significant role of non-additive gene effects in shaping the genetic expression of these traits, as reflected by the high values of the ratio (σ^2H/σ^2D). Consequently, relying solely on phenotypic performance for selecting desired genotypes may prove

Table 2. Estimates of genetic variance

Traits	**σ^2 GCA**	**σ^2 SCA**	**σ^2 GCA/ σ^2 SCA**	**σ^2 D**	**σ^2 H**	**σ^2 H/ σ^2 D**	**Degree of dominance**
Days to 50% flowering	7.142	21.271	0.336	14.285	21.271	1.489	1.726
Days to maturity	6.828	47.166	0.145	13.656	47.166	3.454	2.628
Plant height (cm)	14.765	81.660	0.181	29.529	81.660	2.765	2.352
Total tillers per plant	0.569	9.762	0.058	1.139	9.762	8.571	4.141
Effective tillers per plant	0.428	10.150	0.042	0.855	10.150	11.865	4.871
Flag leaf length (cm)	0.982	72.536	0.014	1.964	72.536	36.927	8.594
Flag leaf breadth (cm)	0.004	0.015	0.237	0.007	0.015	2.111	2.055
Panicle length (cm)	0.324	3.171	0.102	0.648	3.171	4.895	3.129
Panicle weight (g)	0.035	0.555	0.064	0.071	0.555	7.845	3.961
Grain per panicle	117.712	1629.412	0.072	235.423	1629.412	6.921	3.721
Grain yield per plant (g)	0.315	44.024	0.007	0.631	44.024	69.790	11.814
Spikelet’s fertility	1.055	15.143	0.070	2.110	15.143	7.175	3.788
Test weight (g)	-0.038	7.552	-0.005	-0.076	7.552	-99.240	14.098
Grain length (mm)	0.016	0.563	0.028	0.032	0.563	17.867	5.968
Grain breadth (mm)	0.000	0.074	0.004	0.001	0.074	122.500	15.652
Grain length/breadth ratio	-0.001	0.225	-0.004	-0.002	0.225	-125.000	15.811

** 1% level of significance; *5% level of significance, **σ^2 GCA** = variance due to General Combining Ability, **σ^2 SCA** = variance due to Specific Combining Ability, **σ^2H**

ineffective for these traits. Therefore, it is advisable to postpone the selection of superior individual plants until later generations, specifically F_4 or F_5. This situation highlights the potential for hybridization and the strategic selection of families or progenies in subsequent generations to enhance the desired characteristics. Aligning with our findings, prior studies (12, 15, 19) also underscored the significant role of non-additive gene action in shaping yield components, highlighting its importance in the development of hybrid rice varieties.

Mean performance of parents for grain yield and yield attributing trait

The mean performance of genotypes and hybrids across various biometric traits is presented in (Supplementary Tables 1 & 2). Among the lines, CO 54 exhibited highly significant performance for DFF, DM, GPP, and GYP. Similarly, CO 55 demonstrated highly significant performance for DFF, DM, TTP, ETP, GPP, GL, and GL/GB. The line ADT 56 showed superior performance for traits such as DFF, DM, PH, TW, GL, and GL/GB. Among the testers, RL 27 demonstrated highly significant performance for traits such as DFF, DM, TTP, ETP, PH, TW, GL, and GB. Similarly, RL 292 was highly substantial for DFF, DM, and PH, while RL 2196 excelled in the GL/GB. Tester RL 4452 showed highly significant performance for FB, PL, PW, GPP, TW, and GB. Additionally, RL 6298 performed notably well for traits including TTP, ETP, FL, PL, GPP, GYP, TW, SF, and PW, and RL 8601 performed notably well for GPP, GYP, SF, GL, GL/GB.

The analysis of the proportional contribution to the total variance by lines, testers, and their interactions showed that testers and the line × tester interaction contributed more to the variance than the lines for all traits, except for DFF, DM, PW, and GPP (Supplementary Table 3). The cross combinations, specifically CO 54 × RL 27, CO 54 × RL 2196, CO 54 × RL 6298, CO 54 × RL 8601, CO 55 × RL 27, CO 55 × RL 6298, ADT 56 × RL 4452, and ADT 56 × RL 6298 exhibited highly significant performance for GYP and GPP (9, 20).

General combining ability

The effectiveness of any plant breeding initiative hinges on the selection of superior parents capable of transmitting desired traits to their offspring. From a genetic perspective, GCA evaluates additive gene effects and additive × additive interactions. GCA is critical for identifying superior parental lines, while SCA aids in detecting optimal hybrid combinations. An evaluation of the mean performance of the parents (Supplementary Table 2) and their GCA effects revealed that GCA is a reliable indicator of the mean values for nearly all traits studied (Supplementary Table 4). Thus, the effectiveness of a breeding program depends on selecting parents with favorable GCA effects. Negative GCA effects are considered advantageous for traits such as DFF, DM, and PH, while positive GCA effects are essential for other characteristics.

Among the parental lines, CO 54 exhibited significant positive and negative GCA effects in the desired direction for traits such as DFF, DM, FB, PL, PW, GPP, SF, and GL. Likewise, CO 55 demonstrated significant positive and negative GCA effects in the desirable direction for DFF, DM, FL, FB, PL, PW, GPP, SF, TW, and GL. ADT 56 showed significant positive and negative GCA effects in the desired direction for DFF, DM, PH, PW, GYP, TW, GL, and GL/GB. Furthermore, ADT 58 exhibited significant positive and negative GCA effects in the desired direction for PH, TTP, and ETP. In this context, the lines CO 54, CO 55, ADT 56, and the testers RL 292 and RL 2348 demonstrated highly significant negative GCA effects for both DFF and DM. These parental lines are valuable contributors to efforts aimed at reducing the duration of the vegetative growth phase and developing early maturing varieties. The elite lines CO 54, CO 55, ADT 56, and the tester lines RL 292 and RL 2348, which demonstrated highly significant negative GCA effects for both DFF and DM, can be strategically utilized in practical breeding initiatives. These parental lines are instrumental in curtailing the vegetative growth phase and expediting the development of early-maturing rice cultivars. By integrating these lines into hybridization and selection schemes, breeders can accelerate the development of high-yielding, short-duration rice varieties that are tailored to specific agro-climatic conditions, ultimately enhancing rice productivity and sustainability.

For plant height, the genotypes ADT 56, ADT 58, RL 292, RL 2196, and RL 2348 recorded significantly negative GCA effects, indicating their potential utility in breeding semi-dwarf varieties. This selection strategy emphasizes the importance of identifying genotypes with desirable GCA effects to enhance breeding outcomes. Line CO 55 exhibited highly significant positive GCA effects as well as desirable negative GCA effects for several traits, including DFF, DM, FL, FB, PL, PW, GPP, SF, TW, and GL.

This indicates that CO 55 is a strong combiner among the evaluated lines. In addition, three testers demonstrated significantly positive GCA values along with desirable negative GCA effects for various traits. Specifically, RL 8601 showed positive GCA effects for FB, PW, GPP, GYP, SF, TW, GL, and GL/GB. RL 6298 exhibited positive GCA effects for FL, FB, PL, PW, GPP, GYP, and SF. Lastly, RL 27 recorded positive GCA effects for TTP, ETP, FL, PL, PW, GPP, and GYP. These lines have the potential to be effectively utilized in developing promising hybrids.

Specific combining ability

Although SCA effects typically have limited impact on the improvement of self-pollinated crops, except in cases where heterosis can be exploited, superior hybrids are anticipated to produce transgressive segregants that can be selected as promising homozygous lines. Cross-combinations characterized by high mean performance, favorable SCA values, and the involvement of at least one parent with high GCA are likely to enhance the accumulation of favorable alleles, thereby improving the desired traits. An analysis of SCA effects (Supplementary Table 5) and per se performance (Supplementary Table 1) revealed that the cross combinations CO 55 × RL 2348, ADT 56 × RL 2348, and ADT 58 × RL 292 exhibited favorable and significant SCA effects. Additionally, these combinations demonstrated promising performance for the trait of DFF. ADT 56

× RL 2196 and ADT 58 × RL 292 displayed significant and favorable SCA effects. This suggests their potential for promising performance regarding DM. The cross combinations CO 55 × RL 292, ADT 58 × RL 8601, and ADT 58 × RL 2196 exhibited significant and desirable SCA effects, with promising per se performance for PH. Similarly, CO 54 × RL 6298, CO 55 × RL 27, ADT 56 × RL 8601, and ADT 58 × RL 2196 showed significant and favorable SCA effects, demonstrating the potential for TTP.

Additionally, the same combinations (CO 54 × RL 6298, CO 55 × RL 27, ADT 56 × RL 8601, and ADT 58 × RL 2196) displayed significant and desirable SCA effects, with promising per se performance for ETP. The cross combinations CO 54 × RL 8601, CO 55 × RL 27, CO 55 × RL 6298, ADT 56 × RL 8601, and ADT 56 × RL 4452 demonstrated significant and favorable SCA effects, with promising per se performance with (FL). Similarly, the combinations CO 55 × RL 4452 and CO 54 × RL 8601 exhibited notable SCA effects and favorable performance concerning FB. For PL, the crosses CO 55 × RL 4452, CO 55 × RL 6298, CO 54 × RL 8601, and ADT 56 × RL 4452 showed significant and desirable SCA effects. Furthermore, ADT 56 × RL 6298, ADT 56 × RL 4452, CO 54 × RL 8601, CO 55 × RL 27, and CO 54 × RL 2196 demonstrated positive SCA effects and promising performance regarding PW.

The analysis of SCA effects and the per se performance of various cross combinations indicated promising results for grains per panicle GPP. The combinations CO 54 × RL 2196, CO 54 × RL 6298, CO 54 × RL 8601, CO 55 × RL 2348, CO 55 × RL 6298, and ADT 56 × RL 4452 exhibited significant and favorable SCA effects with promising per se performance for GPP trait. For GYP, the combinations CO 54 × RL 6298, CO 54 × RL 8601, CO 55 × RL 6298, ADT 56 × RL 6298, ADT 56 × RL 4452, ADT 58 × RL 2196, and ADT 58 × RL 2348 also showed significant and desirable SCA effects with promising per se performance, indicating their potential for improved performance. In terms of SF, the combinations CO 54 × RL 2196, CO 55 × RL 27, and ADT 56 × RL 8601 demonstrated significant and favorable SCA effects, with promising per se performance suggesting their usefulness in breeding programs. Additionally, the combinations CO 54 × RL 4452, CO 55 × RL 27, CO 55 × RL 292, ADT 56 × RL 6298, and ADT 56 × RL 8601 exhibited significant and desirable SCA effects with promising per se performance for TW, highlighting their potential for enhancing this trait in future breeding efforts.

The analysis of SCA effects and per se performance revealed that the cross combinations CO 54 × RL 6298, CO 54 × RL 8601, CO 55 × RL 6298, ADT 56 × RL 6298, ADT 58 × RL 2196, and ADT 58 × RL 2348 were promising for GYP. These combinations represented three types of parental GCA effects: low × low, low × high, and high × low. A favorable cross combination is characterized by a high SCA effect, with both parents exhibiting high GCA. Notably, the crosses CO 55 × RL 6298 and ADT 58 × RL 2196, which exhibited significant SCA effects, involved parents with low × high GCA effects, suggesting the presence of dominance × additive gene interaction in these combinations. The cross -combination ADT 58 × RL 2348 where both parents exhibited low GCA, was influenced by dominance epistatic effects. Among the six cross combinations with SCA effects, CO 54 × RL 6298, CO 54 × RL 8601, and ADT 56 × RL 6298 involved parents with high GCA, indicating the predominance of additive gene action (Supplementary Table 6). These observations align with the previous findings (10, 20, 21).

Heterosis

Jones first characterized heterosis in rice in 1926, highlighting the need to identify promising hybrid combinations with significant heterosis for commercial use. The performance of hybrids is typically assessed as a percentage increase compared to a standard parent. The evaluation of F_1 hybrids was conducted based on standard heterosis relative to the best high-yielding variety (22). Consequently, plant breeders tend to favor standard heterosis over other forms when assessing hybrid performance. In this study, the hybrid combinations CO 54 × RL 6298 and CO 54 × RL 8601 exhibited notable positive standard heterosis for key traits, including PW, GPP, SF, and GYP (Supplementary Table 7). For the traits of GYP and PW, as well as PL, significant positive heterosis was observed in the hybrid's CO 55 × RL 6298 and ADT 56 × RL 6298 (Table 3). These findings are consistent with the earlier reports (10) regarding traits that contribute to yield. The hybrids ADT 56 × RL 8601 and ADT 58 × RL 2348 have been recognized as promising candidates for improving GYP. Significant positive heterosis in the favorable direction was noted for days to 50% flowering DFF and DM in the hybrid's CO 54 × RL 292, CO 55 × RL 292, and ADT 58 × RL 292. For the trait of PL, significant positive heterosis was observed in the hybrid's CO 54 × RL 8601, CO 55 × RL 4452, ADT 56 × RL 4452, and ADT 58 × RL 4452. In terms of TW, significant positive heterosis was achieved in the hybrid's CO 54 × RL 292, CO 55 × RL 27, CO 55 × RL 292, ADT 56 × RL 6298, and ADT 56 × RL 8601.

Conclusion

Single plant selection in segregating generations proves to be an effective strategy for enhancing yield in crosses that exhibit high SCA effects. This selection method is particularly beneficial when both parents in the cross possess high GCA, characterized as high × high combinations. In cases where crosses with high SCA effects involve a combination of high and low GCA parents, such as low x high, mass selection combined with random mating during early segregating generations is an effective population improvement strategy. In contrast, heterosis breeding emerges as a viable strategy for crosses with high SCA effects involving low x low general combiners. Based on the preceding discussion, it was noted that the gene action influencing the traits examined in this study was non-additive and non-fixable. Therefore, efforts to select for the enhancement of these traits may be deferred to subsequent generations. From the results and discussions presented, it can be concluded that non-additive gene action plays a crucial role in the expression of various traits in this study. To optimize breeding efficacy, it is crucial to elucidate the molecular underpinnings of the observed gene actions, thereby illuminating the genetic interactions that underlie these superior performances. This insight could enable the implementation of marker-assisted selection and precision breeding strategies, streamlining the development of high-yielding rice varieties and revolutionizing the field of rice breeding. By deciphering the genetic code, breeders can harness the power of molecular genetics to inform and accelerate the breeding process, ultimately enhancing rice productivity and sustainability. The best combiners identified CO 54, CO 55, RL 8601, RL 6298, and RL 27 should be considered as parental lines in breeding programs aimed at developing high-yielding varieties. As a result, these parent lines can be effectively employed in pedigree breeding to generate superior recombinants by selecting in later generations. The hybrids CO 54 × RL 6298, CO 54 × RL 8601, CO 55 × RL 6298, ADT 56 × RL 6298, ADT 58 × RL 2196, and ADT 58 × RL 2348 are particularly promising for harnessing heterosis to enhance yield.

Table 3. Comparison of crosses with significant standard heterosis with the GCA status of parents for yield attributing traits

DF	CO 54 × RL 292	-18.25**	H × H
	CO 55 × RL 292	-17.06**	H × H
	ADT 56 × RL 292	-17.86**	H × H
	ADT 58 × RL 292	-15.08**	L × H
DM	CO 54 × RL 292	-11.18**	H × H
	CO 55 × RL 292	-12.08**	H × H
	ADT 56 × RL 292	-13.29**	H × H
	ADT 56 × RL 2196	-11.78**	H × L
	ADT 58 × RL 292	-11.18**	L × H
FL	CO 54 × RL 8601	59.87**	H × H
	CO 55 × RL 27	76.65**	H × H
	CO 55 × RL 6298	116.77**	H × H
	ADT 56 × RL 4452	64.54**	H × H
	ADT 56 × RL 6298	59.24**	H × H
	ADT 56 × RL 8601	54.46**	H × H
FB	CO 54 × RL 4452	85.71**	H × H
	CO 54 × RL 8601	97.14**	H × H
	CO 55 × RL 4452	108.57**	H × H
	ADT 56 × RL 4452	85.71**	L × H
PL	CO 54 × RL 8601	25.14**	H × L
	CO 55 × RL 4452	44.31**	H × H
	CO 55 × RL 6298	35.14**	H × H
	ADT 56 × RL 4452	32.92**	L × H
	ADT 56 × RL 6298	23.89**	L × H
PW	CO 54 × RL 4452	80.12**	H × H
	CO 54 × RL 6298	103.01**	H × H
	CO 54 × RL 8601	95.18**	H × H
	CO 55 × RL 27	98.07**	H × H
	CO 55 × RL 6298	113.25**	H × H
	ADT 56 × RL 6298	108.67**	H × H
GPP	CO 54 × RL 2196	44.18**	H × H
	CO 54 × RL 6298	61.24**	H × H
	CO 54 × RL 8601	59.17**	H × H
GYP	CO 54 × RL 6298	103.87**	H × H
	CO 54 × RL 8601	100.76**	H × H
	CO 55 × RL 6298	104.5**	L × H
	ADT 58 × RL 2348	105.33**	L × L
SF	CO 54 × RL 2196	11.59**	H × H
	CO 54 × RL 4452	8.1**	H × H
	ADT 56 × RL 8601	9**	L × H
TW	CO 54 × RL 4452	60.11**	L × H
	CO 55 × RL 27	62.73**	H × L
	CO 55 × RL 292	64.88**	H × H
	ADT 56 × RL 6298	70.95**	H × L
	ADT 56 × RL 8601	99.41**	H × H
GB	CO 54 × RL 4452	65.84**	H × H
	CO 55 × RL 4452	63.54**	H × H
	ADT 56 × RL 4452	61.06**	L × H
	ADT 58 × RL 27	72.74**	H × H

H – Positive values in desired direction, **L** – Negative values in desired direction.

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Authors' contributions

PM performed the field experiments, measurements, and data analysis and drafted the manuscript. PR supervised and worked on the manuscript. All authors were involved in planning and provided critical feedback on the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Supplementary data

Supplementary Table 1. Per se performance of hybrids

Supplementary Table 2. Per se performance of parents

Supplementary Table 3. The proportional contribution of lines, tester, and line × tester interaction

Supplementary Table 4. General combining ability effects of parents for different quantitative characters in rice

Supplementary Table 5. Specific combining ability effects of hybrids for different quantitative characters in rice

Supplementary Table 6. Estimates of standard heterosis for quantitative characters in rice (per cent)

Supplementary Table 7. Comparison of crosses with significant SCA effects and per se performance with the GCA status of parents for yield attributing traits

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