

Combining ability analysis of rice genotypes for grain yield and related traits under direct-seeded conditions

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Manuscript received: 27 October 2025. Revision accepted: 27 January 2026.

Abstract. *Ali Z, Naeem M, Rafiq I, Ajmal M, Bahrn AH, Baharuddin AK, Fadhilah AN, Anshori MF. 2026. Combining ability analysis of rice genotypes for grain yield and related traits under direct-seeded conditions. Biodiversitas 27 (1): d270138. <https://doi.org/10.13057/biodiv/d270138>.* Development of rice toward water scarcity and high input costs encourages a shift toward Direct-Seeded Rice (DSR) systems. Hybrid rice development is one solution to this system's challenge. Therefore, systematic analysis through combining ability is needed to develop hybrid rice on direct-seeded systems. This study aimed to evaluate the combining ability of rice genotypes for grain yield and related traits under DSR conditions. Twenty-seven genotypes from nine parents and 18 F1 crosses were evaluated using Line × Tester design under a Randomized Complete Block Design (RCBD) with three replications during 2023-2024. The results showed that genotype-by-genotype variance for all traits was significant in the analysis of variance. Line 23765 and tester 37768 were good general combiners, while crosses 6723 × 32274, 6728 × 32274, 6880 × 37768, and 7968 × 37667 showed high Specific Combining Ability (SCA) effects. Line 6728 exhibited a significant positive General Combining Ability (GCA) effect for grain yield per plant, while 6723 for grain weight per panicle and number of grains per panicle, indicating yield improvement potential. Both additive and non-additive genetic effects influence trait expression, with non-additive effects being more prominent. This hybrid rice selection process could help develop high-yielding rice varieties under direct-seeded conditions.

Keywords: Combining ability, direct-seeded rice, gene action, *Oryza sativa*, randomized complete block design

Abbreviations: DF 50%: Days to 50% Flowering, DM: Days to Maturity, FLA: Flag Leaf Area, FLL: Flag Leaf Length, FLW: Flag Leaf Width, GW: Grain Weight per panicle, NG: Number of Grains per panicle, NP: Number of Panicles, NT: Number of Tillers per plant, PH: Plant Height, PL: Panicle Length, PW: Panicle Weight, SF: Spikelet Fertility, YP: Yield per Plant

INTRODUCTION

Rice (*Oryza sativa* L.) is a globally consumed staple crop (Wang et al. 2023), crucial for food security, particularly in Asia, where over 90% of the world's rice is produced (Bandumula 2018). Population growth and urbanization raise rice demand, pressuring arable land (Rahman and Zhang 2023). Annual consumption reaches 100-140 kg per capita in many Asian countries (Mohidem et al. 2022), providing up to 76% of caloric intake in Southeast Asia (Elkatry et al. 2023). Enhancing productivity is vital amid water scarcity, salinity, and climate change constraints (Singh et al. 2021). Developing high-yielding genotypes remains key for future rice supplies (El-Malky and Al-Daej 2023; Rahman and Zhang 2023), while cultivation depends on consumer and farmer preferences (Uyeh et al. 2021).

Grain yield in rice is influenced by genetic and environmental factors (Li et al. 2019; Ma et al. 2023). Understanding trait relationships is crucial for designing efficient breeding strategies (Zhao et al. 2019; Phyu et al. 2020; Won et al. 2020). Information on yield-influencing

traits is essential for developing high-yielding varieties. Traditional Puddled Transplanted Rice (PTR) has been used for weed control (Singh et al. 2001), nutrient availability (Sanchez 1973), and seedling establishment. PTR is labor and water-intensive, raising sustainability concerns (Kumar and Ladha 2011). Direct-Seeded Rice (DSR), where seeds are sown in unsaturated soil, has emerged as an alternative (Joshi et al. 2013), with potential for climate adaptation. Developing early-maturing cultivars for DSR is crucial (Sandhu et al. 2021). Several challenges, like lodging, declining grain quality, nematode infestations, and stagnant yields, persist in DSR systems. While DSR can increase farmers' income, adoption remains limited by technological and policy challenges.

Kumar and Ladha (2011) and Jat et al. (2022) reported that DSR can overcome labor and irrigation needs while maintaining productivity when managed properly. However, DSR adoption faces challenges like weed pressure, poor establishment, lodging, and variable genotype performance (Ahmed et al. 2025). Recent advances emphasize the need for DSR-adapted varieties with early vigor, strong roots,

and stress tolerance (Goyal et al. 2022). The lack of studies on combining ability under Direct-Seeded Rice (DSR) conditions has hindered the identification of appropriate parental lines.

Hybrid rice with enhanced vigor and yield potential presents a viable solution by improving productivity and climate resilience under DSR conditions. Mechanized postharvest techniques can reduce losses, enhance quality, and increase farmers' income (Sandhu et al. 2021). Rice grows across diverse environments, from the wettest regions to the driest deserts (Mohanty et al. 2013). The identification of suitable parental combinations with favorable gene interactions remains crucial for stable hybrid performance across environments.

Combining ability analysis serves as a breeding tool to partition variance into additive and non-additive components (Kempthorne 1957). Specific Combining Ability (SCA) reflects non-additive gene actions, while General Combining Ability (GCA) relates to additive effects (Karaağaç 2021). These analyses facilitate the identification of superior parents and hybrids for complex traits, including yield and stress tolerance (Fellahi et al. 2013). The Line \times Tester method is a widely used biometrical approach to determine gene action and select optimal parents for hybrid breeding programs across crop species (Kempthorne 1957). Studies have used line \times tester analysis to assess combining ability in rice (Sandhyakishore et al. 2017; Rasheed et al. 2021; Abd El-Aty et al. 2022; Maring et al. 2023). Nevertheless, studies on its application in DSR systems remain limited, despite the strong influence of environmental stresses on genotype performance. This study addresses this gap by evaluating combining ability and selecting promising parents for the direct-seeded system. Understanding combining ability under these conditions is crucial for identifying high-yielding, resilient genotypes. Combining ability analysis identifies parents with favorable traits and helps understand gene influences on trait expression. This study aimed to evaluate rice genotypes' combining ability and identify promising parents and hybrids under direct-seeded conditions.

MATERIALS AND METHODS

Research materials

The breeding material comprised 27 rice genotypes, including nine parental lines, six high-yielding lines (6723, 6728, 6880, 7860, 7968, and 23765) and three testers with inferior performance for yield and associated traits (32274, 37667, and 37768) and eighteen F1 crosses (Table 1). All materials were sourced from the Department of Plant Breeding and Genetics, Faculty of Agriculture and Environment, The Islamia University of Bahawalpur, Bahawalpur, Pakistan.

Procedures

Research design

The study was conducted at the experimental area of the Department of Plant Breeding and Genetics, The Islamia

University of Bahawalpur, Bahawalpur, Pakistan, during the 2023 and 2024 growing seasons, which were characterized by warm temperatures and seasonal rainfall typical of the region. A nested randomized complete block design was employed, with three replications per season. Each season was treated as a separate entity, but combined for joint analysis. The experimental layout followed a nested structure, with replications nested within seasons to account for seasonal variation. The season was treated as a fixed effect, while replications within the seasons were considered random effects.

The parental lines were selected based on both phenotypic performance and genetic diversity to optimize the potential expression of heterosis in the F1 crosses. The six lines comprised high-yielding rice genotypes exhibiting superior performance in yield and yield-related attributes, such as panicle weight, grain number, and spikelet fertility. In contrast, the three testers were low-yielding yet genetically diverse genotypes with suboptimal performance in these traits, employed to assess combining ability effects. To achieve parental genetic diversity, diversity assessment based on pedigree information and prior molecular characterization (utilizing departmental germplasm database-based SSR genetic diversity data) was considered during selection. The chosen parental lines represented various genetic backgrounds and ecotypes to ensure broad genetic variability. This diversity among parents provided a robust foundation for detecting both additive and non-additive gene effects and determining the likelihood of hybrid vigor (heterosis) in the resulting hybrids.

Traits observation

Breeding materials were sown under direct-seeded conditions in both seasons. The field was prepped one month before planting to improve pulverization, germination, and effective weed control. Standard agronomic practices were performed, and weeds were managed as required. The sowing was done 2 cm deep in non-puddle soil (Kaur and Singh 2017). Each entry was planted in a plot consisting of four rows, each 3 m long, with 20 cm spacing between plants and row-to-row distance (Thakur et al. 2010). Each plot represented a single experimental unit for analysis. Five plants per row were sown, and the middle three plants of each plot were chosen at maturity for yield and yield-related trait measurements to avoid border effects. Trait values were averaged to obtain a single plot mean for each replication. Each plot mean was then used as the experimental unit for statistical analysis, thereby avoiding pseudo-replication and ensuring that inference was made at the plot level rather than the individual plant level. Fertilizer applications were made 25–40 days following seeding, using nitrogen, phosphorus, and potassium fertilizers supplied as urea (46% nitrogen), diammonium phosphate (DAP, 18% N and 46% P₂O₅), and muriate of potash (MOP, 60% K₂O), respectively. All plots remained wet throughout the crop season until they reached maturity.

Table 1. List of parents and crosses used in the study

Serial no.	Genotype	Serial no.	Genotype
1	6723	15	6728 × 37768
2	6728	16	6880 × 32274
3	6880	17	6880 × 37667
4	7860	18	6880 × 37768
5	7968	19	7860 × 32274
6	23765	20	7860 × 37667
7	32274	21	7860 × 37668
8	37667	22	7968 × 32274
9	37768	23	7968 × 37667
10	6723 × 32274	24	7968 × 37668
11	6723 × 37667	25	23765 × 32274
12	6723 × 37768	26	23765 × 37667
13	6728 × 32274	27	23765 × 37668
14	6728 × 37667		

Observations were conducted to examine the phenological phases of rice by monitoring each plot. Three plants from each replication of each genotype were chosen at maturity to evaluate the general and specific ability between the lines and the tester for different yields and associated characteristics. Phenotypic data of 14 parameters included Days to 50% Flowering (DF50%) (Sujariya et al. 2023), Days to Maturity (DM), Flag Leaf Length (FLL, cm), Flag Leaf Width (FLW, cm), Flag Leaf Area (FLA, cm²) (Amin and Haque 2009), Plant Height (PH, cm), Panicle Length (PL, cm), Number of Tillers per plant (NT) (Huang et al. 2010), Number of Panicles (NP), Panicle Weight (PW, g), Grain Weight per panicle (GW, g), Number of Grains per panicle (NG), Spikelet Fertility (SF, %) (Ghosh et al. 2013) and Yield per Plant (YP, g) were observed.

Data analysis

Analysis was conducted on plot-level means, with each plot serving as one experimental unit. This approach appropriately accounts for subsampling within the plots and prevents inflation of degrees of freedom that would result from treating individual plants as independent replicates. Data collected from both seasons were combined for joint analysis to determine the significance of differences of genotypes, lines, tester, and lines × tester effects across environments. The combined data were subjected to Analysis of Variance (ANOVA) for combining analysis using a nested Randomized Complete Block Design (RCBD), as described by Steel et al. (1997) and Fellahi et al. (2013). The statistical model is used as follows:

$$Y_{ijkl} = \mu + S_i + R_{j(i)} + L_k + T_l + (L \times T)_{kl} + (L \times T \times S)_{kli} + \epsilon_{ijkl}$$

Where:

- Y_{ijkl} : Observed value of the trait
- μ : overall mean
- S_i : Fixed effect of the i th season
- $R_{j(i)}$: Random effect of replication j nested within season i
- L_k : Effect of the k th line
- T_l : Effect of the l th tester
- $(L \times T)_{kl}$: Line × tester interaction
- $(L \times T \times S)_{kli}$: Interaction of line × tester × season
- ϵ_{ijkl} : Random error term

Seasonal variation was incorporated as a fixed factor in the ANOVA model. The analysis was performed using the `aov()` function and utilities from the `Agricolae` package in R Studio. The following linear model was fitted. Trait = Season + Line + Tester + Line × Tester + Season × Line + Season × Tester + Replication (season) (de Mendiburu 2019). This model allowed portioning of total variation into main effects (season, lines, tester), first-order interactions (lines × tester), and second-order interactions (lines × tester × season), while correctly accounting for replication nested within season as the experimental error term. The model incorporates season as a fixed factor and replications as a random factor to appropriately partition variation due to seasonal differences and within-seasonal variation. The inclusion of seasons as a fixed factor provided an effective means to quantify the environmental variability between growing periods. Although the climatic variables were not incorporated as a continuous covariate in the statistical model, their influence was captured through the season factor and line × tester × season interaction term.

The study performed a combining ability analysis, as described by Kempthorne (1957) and Singh et al. (2022), to assess the effects of General Combining Ability (GCA) for lines and testers and the implications of Specific Combining Ability (SCA) for hybrids. For mean comparison, post-hoc test was conducted using Tukey's honest significant difference test at $p < 0.05$ and $p < 0.01$ levels to identify significant differences among genotype means. Tukey's HSD was preferred for the post-hoc pairwise comparison because it effectively controls the family-wise error rate when performing multiple comparisons and provides reliable separation among the treatment means. The statistical significance levels were denoted as * for $0.01 < p < 0.05$ and ** for $p < 0.01$. Significant notation was removed from the SE rows to maintain clarity. Before the analysis, data of all the traits were examined for normality and homogeneity of variance using the Shapiro-Wilk and Levene's test, respectively. Where assumptions were violated, data were appropriately transformed prior to analysis, log transformation ($\log_{10} \times$) for skewed variables, such as GW, YP, and PW, and square-root transformation (\sqrt{x}) for count-type traits such as TP and GN. These transformations were used for the ANOVA to model assumptions; however, results and means were untransformed for presentation and interpretation to maintain biological relevance. Proportional contribution of lines, testers, and their interactions was calculated by (Singh and Chaudhary 1985) as follows:

$$\text{Contribution of lines} = \frac{S.S(\text{lines})}{S.S(\text{crosses})} \times 100$$

$$\text{Contribution of tester} = \frac{S.S(\text{testers})}{S.S(\text{crosses})} \times 100$$

$$\text{Contribution of lines} \times \text{tester} = \frac{S.S(\text{lines} \times \text{testers})}{S.S(\text{crosses})} \times 100$$

RESULTS AND DISCUSSION

Analysis of variance for combining ability of yield and related traits

The combined ANOVA across two seasons demonstrated significant differences among the genotypes for most of the studied traits under direct-seeded conditions (Table 2). Total variation was partitioned into sources due to seasons, replications, genotypes, parents, crosses, and their interaction. The crosses were further partitioned into lines, testers, and line \times tester interaction. Genotypic main effects (parents and crosses) were tested against the genotypes \times season mean square, whereas lines, testers, and lines \times tester effects were tested against their respective season interaction mean squares. Each source of variation was tested against the appropriate error mean square derived from the RCBD model. Significant levels were reported to improve clarity and auditability. The genotype effect, representing variation among lines, testers, and crosses, was significant for all examined traits. ANOVA results demonstrated significant differences for DF50% in replication, genotypes, parents, crosses, and lines \times tester interaction. For DM, replication, genotypes, parents, and lines \times tester interaction were significant. FLA exhibited significant variation for all factors except lines. There was significant variation in all factors except parents and testers for PH and PL. NT and NP, but NT was non-significant for replication. The tester effect was non-significant for PW, GW, and NG, while other factors were significant. SF was non-significant for line, and YP was non-significant for replication and parents' crosses but significant for the remaining factors.

Mean performance of lines, testers, and crosses

The mean performance of studied traits in the direct-seeded condition is presented in Table 3. Among lines, minimum DF50% was exhibited by line 6723 (64.50 days), while maximum was shown by 6728 (80.00 days). Among testers, the maximum days to 50% flowering (86.00 days) was recorded for tester 32274, whereas the minimum (65.50 days) was observed for tester 37667. In crosses, maximum DF50% was exhibited by 23765 \times 32274 (83.00 days), while the minimum was in 7860 \times 37668 (65.50 days). Minimum DM (94.00 days) was found in lines 6723 and 7860, and maximum (108.00 days) in 6728, while in testers, the highest (117.00 days) DM was in 32274, and the lowest (95.50 days) in 37667. Lowest values (96.50 days) for DM in crosses were in 7860 \times 37668 and 7968 \times 32274. However, the highest and lowest values for FLA were 6723 \times 37768 (1.98 cm²) and 6880 \times 32274 (1.28 cm²).

The highest flag leaf area (63.77cm²) in lines was found in 7860, while in tester 32274 (63.49 cm²), and in cross 7860 \times 37668 (85.39 cm²). Among lines, the shortest (121.42 cm) PH was in 7968, and in tester 37667 (119.85 cm), while in crosses, 7860 \times 37667 showed (112.92 cm). Maximum (28.08 cm) PL among lines is in 6728, while in the tester, the highest (31.80 cm) is in 32274. The best panicle length in crosses was in 23765 \times 37667 (30.58 cm). Based on maximum tillers and panicles, line 7968 contained (12.80 and 12, respectively). Among testers, maximum values (10.17) were in 37667; cross 23765 \times 37667 indicated the

highest NT and NP (13.00 and 12.83). The highest (4.37 g and 4.20 g) panicle and grain weight in lines was in 7860, while the tester maximum (3.40 g and 3.07 g) was in 32274. In crosses, the highest (4.43 g and 4.12 g) panicle and grain weight was in 6728 \times 37768.

General Combining Ability (GCA) effects

The general combining ability of lines and testers is presented in Table 4. Line 7860 demonstrated a highly significant GCA effect for DF50% (-3.16**). Tester 37768 showed a highly negative GCA effect (-1.33). Negative GCA suggested a reduction in days to 50% flowering. For DM, line 7968 indicated a significant negative GCA effect (-2.58**). Tester 37768 indicated a significant negative (-1.08) GCA. The GCA results showed line 23765 exhibited a highly significant positive GCA (2.42**) of FLA. Tester 37768 had a significant positive GCA effect of (6.86**). For plant height, line 7860 demonstrated a negative (-9.22**) significant GCA effect, while tester 37768 exhibited a non-significant negative GCA effect (-0.34). Line 7860 revealed a significant positive GCA effect (1.35**) for PL. Tester 37667 had a significant positive GCA (1.94**) for PL. For the number of tillers per plant, line 23765 had a significant positive GCA effect (1.12**), while tester 37667 showed a highly positive GCA (0.56**).

Line 23765 indicated a significant positive GCA (1.38**) for the number of panicles per plant. Line 6723 exhibited a positive GCA effect (1.70**) for PW, suggesting increased PW. All testers had non-significant GCA for this trait. Line 6723 showed a significant GCA effect (1.67**) for GW. For grains per panicle, line 6723 demonstrated a significant positive (102.90**) general combining ability effect. Among testers, 32274 indicated a positive GCA effect (5.57**). Line 6723 exhibited significant positive GCA (6.51**) for SF; tester 37768 had significant positive GCA (4.54**) for SF. Line 6728 showed a significant positive GCA effect (1.85**) for grain yield per plant. No tester demonstrated significant GCA.

Specific Combining Ability (SCA) effects

The specific combining ability effects of the studied traits under direct-seeded conditions are presented in Table 5. The difference between parental lines' general combining ability and crossing performance is known as Specific Combining Ability (SCA) (Fasahat et al. 2016). Among crosses, SCA for DF50% was significantly negative for 6723 \times 32274, 6728 \times 37667, 6880 \times 32274, 7860 \times 37667, 7860 \times 37668, 7968 \times 32274, and 23765 \times 37667. Adverse SCA effects for DM were observed in crosses 6723 \times 32274, 6728 \times 37667, 6880 \times 32274, 7860 \times 37667, 7860 \times 37668, 7968 \times 32274, and 23765 \times 37667. Combinations 6723 \times 32274, 6728 \times 32274, 6880 \times 37667, 6880 \times 37768, 7860 \times 37668, 7968 \times 37668, 23765 \times 32274, and 23765 \times 37667 exhibited positive SCA effects for FLA traits. Short plant stature is preferred in rice due to lodging. Adverse SCA for combinations 6723 \times 32274, 6728 \times 37667, 6728 \times 37768, 6880 \times 32274, 6880 \times 37768, 7860 \times 37667, 7968 \times 32274, 7968 \times 37668, and 23765 \times 32274 suggest short PH. A significant positive SCA effect (1.43**) for panicle length was found in cross 23765 \times 37667, followed by

6723 × 32274 (1.41**) and 7860 × 32274 (1.29**). Other crosses were non-significant for PL.

Significant and positive SCA values for number of tillers and panicle were included 6723 × 32274 (0.57** and 0.38**), 6723 × 37667 (0.38** and 0.30**), 6728 × 37768 (1.15** and 1.02**), 6880 × 32274 (0.74** and 1.00**), 6880 × 37768 (0.54** and 0.25**), 7860 × 32274 (1.40** and 1.27**), 7968 × 37667 (2.15** and 2.69**) and 23765 × 37667 (1.06** and 0.86**) respectively. Cross 23765 × 37667 had a significant positive SCA effect for NT but was non-significant for NP. Furthermore, the panicle weight and grain weight per panicle traits showed positive and significant SCA in 6728 × 37768 (0.51** and 0.58**) and 7968 × 32274 (0.58** and 0.54**).

In this study, crosses such as 6723 × 32274 (32.92**), 6728 × 32274 (13.14**), 6728 × 37768 (9.12**), 6880 × 37768 (19.89**), 7860 × 37667 (4.62**), 7860 × 37668 (5.00**), 7968 × 32274 (30.70**), and 23765 × 37667 (59.00**) exhibited significant positive SCA for NG. SF crosses 6728 × 37768, 6880 × 37667, 6880 × 37768, 7860 × 32274, 7968 × 32274, 7968 × 37667, and 23765 × 37667 exhibited a significant positive SCA effect. Several crosses exhibited significant and positive SCA effect for yield per plant, indicating favourable non-additive gene action. Notably, crosses such as 6723 × 32274 (1.31**), 6728 × 32274 (1.85**), 6880 × 37768 (2.66**), 7968 × 37667 (4.08**) demonstrated significant and positive SCA effect for YP. This showed that these crosses could improve the rice grain yield. Among these, 7968 × 37667 (4.80**) had the highest positive SCA effect for YP (4.80**) and also had a moderately high mean yield (32.00 g). Similarly, 6880 × 37768 also indicated a significant and positive SCA effect (2.66**) along with a mean yield of 27.78 g, reflecting non-additive gene action for yield improvement. Moreover, crosses 6723 × 32274 (1.31**), 6728 × 32274 (1.85**) had a positive SCA effect for yield, together with mean yield of 42.38 g and 37.93 g, respectively. These crosses could be used for rice productivity enhancement due to consistent performance across GCA and mean yield data. Joint analysis across two seasons clearly indicated that environmental variation had a significant influence on the expression of yield and linked traits under direct-seeding conditions.

Relative contribution of lines, testers, and crosses

Results of the relative contribution of lines, testers, and their interaction under direct-seeded conditions for yield and associated traits are presented in Table 6 and Figure 1. Significant differences were observed among traits regarding the relative influence of additive (lines, testers), non-additive (tester × testers). For most of the traits, lines × tester interaction contributed to the greatest proportion, indicating the presence of non-additive gene action. Traits such as DF50% (76.10%), DM (75.89%), FLL (69.80), FLW (52.58%), FLA (75.18%), NT (52.00%), NP (46.86%), SF (81.23%), and YP (55.97%) revealed the highest lines × tester contribution. This suggests the strong SCA effect, reflecting the importance of hybrid-specific allele interaction. These traits revealed high L × T contribution are highly influenced by non-additive gene action, implying that heterosis breeding and strict parent selection are essential

for improving these parameters. In contrast, lines contributed the highest proportion of variation for PH (58.46%), PW (80.38%), GW (78.04%), and NG (79.74%). These traits are controlled by additive gene effects, reflecting the stable inheritance and importance of parental performance. This indicates that these parameters can be effectively improved through direct selection and line breeding. The PL tester contributed the highest proportion (57.14%), suggesting that tester choice had a comparatively greater influence on the expression of PL than lines' interaction. Overall, results indicated that additive effects were more dominant for yield components such as DF50%, DM, FLL, FLW, FLA, NT, NP, SF, and YP, while non-additive effects were prominent for PH, PW, GW, and NG. Thus, this pattern needs a combined strategy of selecting superior parents for additive traits and exploiting heterosis through hybrid development.

Discussion

The analysis of variance confirms the presence of genetic variability among the parental lines and their hybrids. The mean sum of squares for parental characteristics was substantial, which was anticipated given that these genotypes were selected based on multiple criteria. High variation among progeny resulting from crosses is desirable, as it enhances breeders' capacity to select superior plants (Begna 2021). Significant differences between parents and crosses for all parameters observed, except DF50%, DM, PL, and YP, confirming both additive and non-additive gene action in the inheritance of these traits and also indicating the presence of heterosis and variation in mean traits between parents and offspring (Labroo et al. 2021). The variance in hybrids was attributed to the effects of lines, testers, and their interactions. This result correlated with Modarresi et al. (2024), who found that the genotypes exhibited broad genetic diversity, as evidenced by significant variances across lines, testers, and line × tester interactions (Table 2). Additive variance was prevalent, as indicated by the significance of the mean sum of squares from lines and testers. Notable variations from line × tester interactions for each trait underscore the importance of both additive and non-additive variance (Modarresi et al. 2024).

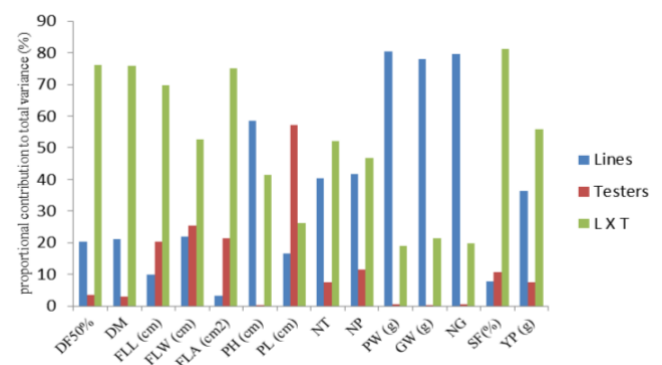


Figure 1. Proportional contribution of lines, testers, and their interaction to total variance for yield and related traits under direct-seeded conditions

Table 2. Analysis of Variance (ANOVA) for combining ability of yield and related traits under direct-seeded conditions

SOV	Df	DF50%	DM	FLL (cm)	FLW (cm)	FLA (cm ²)	PH (cm)	PL (cm)	NT	NP	PW (g)	GW (g)	NG	SF (%)	YP (g)
Replication (season)	2	54*	73.55**	820.30**	0.01ns	1454.70**	283.15**	1.56ns	1.5ns	2.66*	0.34*	0.13*	414.81*	8.16*	1.72ns
Genotypes	26	70.77*	60.92*	86.37*	0.05**	266.37**	190.91**	7.82**	1.75**	6.37**	1.77**	1.64**	5560.71**	319.01**	11.13**
Parents	8	114.30**	109**	48.25ns	0.03**	155.34*	101.12ns	9.75**	5.37**	7.63**	1.17**	1.11**	2680.09**	263.56**	10.96**
Parents*crosses (contrast)	1	10.70 ^{ns}	0.75ns	291.86**	0.05**	989.32**	829.44**	1.98ns	4.61**	7.60**	0.81**	0.30**	3355.59**	224.53**	0.72ns
Crosses	17	53.82*	41.83ns	92.26**	0.06**	276.09**	195.61**	7.26**	4.46**	5.70**	2.10**	1.98**	7046.01**	350.66**	11.82**
Lines	5	37.20 ^{ns}	30.05ns	31.11ns	0.04*	31.41ns	388.85**	4.12**	6.13**	8.07**	5.76**	5.25**	19104.89**	94.35ns	14.62**
Testers	2	16.33 ^{ns}	10.58ns	159.00**	0.13**	503.93**	1.53ns	35.29**	2.87*	5.58**	0.10ns	0.06ns	282.00ns	323.46*	7.67*
Lines*tester	10	69.63*	53.98*	109.49**	0.05**	352.87**	137.80*	3.23ns	3.94**	4.54**	0.68**	0.72**	2369.37**	484.25**	11.24**
Genotype x season (interaction)	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Error	104	71.53 ^{ns}	65.23	91.25	0.02	204.93	173.30	5.17	3.82	3.29	0.35	0.26	632.98	47.85	9.90
Total	161	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Note: df: Degree of freedom, ns: Non-significant, *: Significant at $p \leq 0.05$, **: Significant at $p \leq 0.01$, DF50%: Days to 50% Flowering, DM: Days to Maturity, FLL: Flag Leaf Length, FLW: Flag Leaf Width, FLA: Flag Leaf Area, PH: Plant Height, PL: Panicle Length, NT: Number of Tillers per plant, NP: Number of Panicles, PW: Panicle Weight, GW: Grain Weight per panicle, NG: Number of Grains per panicle, SF: Spikelet Fertility, and YP: Yield per Plant. The experiment followed a line \times tester mating design evaluated under a randomized complete block design with three replications. Each F-test was performed using the appropriate mean square error term derived from the RCBD model

Table 3. Mean performance of lines, testers, and their F₁ crosses for yield and related traits under direct-seeded conditions

Line	DF 50%	DM	FLL (cm)	FLW (cm)	FLA (cm ²)	PH (cm)	PL (cm)	NT	NP	PW (g)	GW (g)	NG	SF (%)	YP (g)
6723	64.50	94.00	45.83	1.60	55.11	135.50	27.75	9.83	8.55	3.40	3.28	190.33	72.56	33.93
6728	80.00	108.00	36.62	1.67	45.90	135.92	28.08	11.67	10.83	3.22	2.90	163.83	76.30	31.39
6880	78.00	106.50	44.00	1.62	51.07	129.33	25.83	8.50	7.33	2.13	2.02	141.33	63.13	14.79
7860	65.50	94.00	51.08	1.67	63.77	132.42	24.38	12.50	10.50	4.37	4.20	249.83	67.72	45.02
7968	68.00	98.00	39.37	1.40	40.84	121.42	26.37	12.83	12.00	1.73	1.58	122.17	45.09	22.13
23765	71.00	100.50	43.33	1.37	44.83	124.83	25.33	13.00	13.00	2.72	2.57	156.50	80.95	34.30
32274	86.00	117.00	50.77	1.67	63.49	140.83	31.80	10.00	10.00	3.40	3.07	145.17	82.16	31.20
37667	65.50	95.50	40.12	1.42	42.56	119.50	25.37	10.17	10.17	2.93	2.67	164.83	73.04	29.41
37768	74.50	104.50	45.50	1.70	58.22	132.33	27.47	9.50	9.17	2.90	2.83	173.83	62.00	26.22
6723 × 32274	67.50	97.00	47.67	1.77	64.70	132.42	26.75	9.00	8.50	5.32	5.00	325.67	71.83	42.38
6723 × 37667	78.00	106.50	43.85	1.57	52.01	135.33	28.42	9.67	9.33	4.47	4.20	252.50	66.01	38.73
6723 × 37768	72.50	100.50	46.42	1.98	69.94	134.08	24.68	7.50	7.00	5.05	4.68	283.33	76.37	32.78
6728 × 32274	76.50	105.50	49.75	1.80	69.43	153.83	26.00	10.83	10.83	4.02	3.52	232.00	60.11	37.93
6728 × 37667	71.00	101.00	49.87	1.57	59.18	143.17	29.67	10.83	10.50	3.22	2.80	188.67	53.53	29.73
6728 × 37768	75.00	102.00	43.12	1.57	50.96	142.83	28.22	12.17	11.33	4.43	4.12	219.17	90.81	45.89
6880 × 32274	72.00	101.00	37.05	1.28	35.18	142.25	24.75	10.67	10.83	2.15	1.73	150.50	47.76	18.74
6880 × 37667	76.50	105.00	61.43	1.58	72.77	158.08	29.58	9.50	9.50	3.13	2.95	148.50	62.05	27.82
6880 × 37768	80.50	109.00	47.72	1.85	66.45	145.42	26.52	10.50	9.67	3.03	2.83	174.50	76.35	27.78
7860 × 32274	79.00	107.50	42.77	1.53	49.17	138.30	28.70	11.50	11.00	3.08	2.93	138.83	84.09	32.37
7860 × 37667	66.50	96.50	44.60	1.63	54.49	112.92	28.58	9.67	9.17	2.38	2.17	145.17	59.43	19.74
7860 × 37668	65.50	95.50	58.57	1.93	85.39	136.75	28.78	10.00	9.50	2.75	2.38	144.67	44.10	22.07
7968 × 32274	68.00	95.50	41.67	1.43	45.94	129.25	25.13	7.50	6.50	3.35	3.02	191.83	70.56	19.60
7968 × 37667	74.00	101.00	50.07	1.53	57.45	135.83	28.88	12.33	12.17	2.88	2.63	151.17	67.99	32.00
7968 × 37668	72.00	102.00	59.92	1.62	72.16	130.25	25.80	9.00	7.50	1.82	1.67	123.67	51.89	12.85
23765 × 32274	83.00	109.00	49.93	1.73	64.48	137.42	25.00	10.33	10.33	1.97	1.70	100.17	61.70	17.74
23765 × 37667	78.00	106.00	58.47	1.47	64.05	145.83	30.58	13.00	12.83	2.72	2.43	205.50	46.38	31.21
23765 × 37668	67.50	97.00	49.07	1.60	61.25	139.85	26.03	10.83	10.50	2.53	2.35	140.83	77.09	24.58

Note: DF50%: Days to 50% Flowering, DM: Days to Maturity, FLL: Flag Leaf Length, FLW: Flag Leaf Width, FLA: Flag Leaf Area, PH: Plant Height, PL: Panicle Length, NT: Number of Tillers per plant, NP: Number of Panicles, PW: Panicle Weight, GW: Grain Weight per panicle, NG: Number of Grains per panicle, SF: Spikelet Fertility, and YP: Yield per Plant. Values represent plot-level means averaged over replications

Table 4. Estimates of General Combining Ability (GCA) effect for yield and related traits under direct-seeded conditions

Category	Genome name	DF 50%	DM	FLL (cm)	FLW (cm)	FLA (cm ²)	PH (cm)	PL (cm)	NT	NP	PW (g)	GW (g)	NG	SF (%)	YP (g)
Lines	6723	-0.83	-0.75	-3.01**	0.13**	1.38**	-4.60**	-0.72	-1.54**	-1.55**	1.70**	1.67**	102.90**	6.51**	-1.51**
	6728	0.66	0.75	-1.41**	0.008	-0.97	8.06**	0.62	1.00**	1.05**	0.65**	0.52**	29.01**	3.25**	1.85**
	6880	2.83**	2.91**	-0.26	-0.06	-2.70**	10.03**	-0.38	-0.04	0.16	-0.46	-0.44	-26.42**	-2.83	-0.61
	7860	-3.16**	-2.25**	-0.35	0.06	2.18**	-9.22**	1.35**	0.12	0.05	-0.50**	-0.45	-41.37**	-2.35	0.86
	7968	-2.16**	-2.58**	1.55**	-0.10**	-2.31**	-6.76**	-0.73	-0.65**	-1.11**	-0.55**	-0.51**	-28.70**	-1.41	-1.89**
	23765	2.66**	1.91**	3.49**	-0.03	2.42**	2.48**	-0.13	1.12**	1.38**	-0.83**	-0.79**	-35.42**	-3.16**	1.31**
Tester	32274	0.83	0.50	-4.19**	-0.04	-6.01**	0.36	-1.28**	-0.29**	-0.16	0.07	0.03	5.57**	1.11	-0.85
	37667	0.50	0.58	2.35**	-0.07	-0.84	-0.01	1.94**	0.56**	0.75**	-0.10	-0.08	-2.34**	-5.66**	0.13
	37768	-1.33**	-1.08**	1.80**	0.12**	6.86**	-0.34	-0.66	-0.26**	-0.58**	0.03	0.05	-3.23**	4.54**	0.72

Note: *, Significant at $p \leq 0.05$, **, Significant at $p \leq 0.01$, DF50%: Days to 50% Flowering, DM: Days to Maturity, FLL: Flag Leaf Length, FLW: Flag Leaf Width, FLA: Flag Leaf Area, PH: Plant Height, PL: Panicle Length, NT: Number of Tillers per plant, NP: Number of Panicles, PW: Panicle Weight, GW: Grain Weight per panicle, NG: Number of Grains per panicle, SF: Spikelet Fertility, and YP: Yield per Plant

Table 5. Estimates Specific Combining Ability (SCA) effects for yield and related traits under direct-seeded conditions

Category	Geno. name	DF50%	DM	FLL (cm)	FLW (cm)	FLA (cm ²)	PH (cm)	PL (cm)	NT	NP	PW (g)	GW (g)	NG	SF (%)	YP (g)
Crosses	6723 × 32274	-6.00**	-4.83**	5.87**	0.03	8.50**	-1.89**	1.41**	0.57**	0.389**	0.29	0.34	32.92**	-0.68	1.31**
	6723 × 37667	4.83**	4.58**	-4.51**	-0.12**	-9.36**	1.40**	-0.14	0.38**	0.30**	0.37	-0.34	-32.32**	0.26	-0.29
	6723 × 37768	1.16**	0.25	-1.36**	0.08	0.86	0.48	-1.26**	-0.95**	-0.69**	0.07	-0.001	-0.60	0.42	-1.02
	6728 × 32274	1.50**	2.16**	6.36**	0.20**	15.58**	6.85**	-0.67	-0.14	0.11	0.05	0.006	13.14**	-9.15**	1.85**
	6728 × 37667	-3.66**	-2.41**	-0.09	0.00	0.16	-3.42**	-0.24	-1.00**	-1.13**	-0.56**	-0.59**	-22.26**	-8.95**	-1.65**
	6728 × 37768	2.16**	0.25	-6.26**	-0.20**	-15.75**	-3.43**	0.92	1.15**	1.02**	0.51**	0.58**	9.12**	18.11**	-0.20
	6880 × 32274	-5.16**	-4.50**	-7.49**	-0.24**	-16.93**	-6.69**	-0.91	0.74**	1.00**	-0.69**	-0.80**	-12.90**	-15.41**	-1.51**
	6880 × 37667	-0.33	-0.58	10.31**	0.08	15.48**	9.51**	0.68	-1.28**	-1.25**	0.46	0.53**	-6.99**	5.65**	-1.14**
	6880 × 37768	5.50**	5.08**	-2.82**	0.15**	1.45**	-2.81**	0.23	0.54**	0.25**	0.23	0.27	19.89**	9.75**	2.66**
	7860 × 32274	7.83**	7.16**	-1.68**	-0.12**	-7.82**	8.61**	1.29**	1.40**	1.27**	0.26	0.40	-9.63**	20.43**	0.94
	7860 × 37667	-4.33**	-3.91**	-6.43**	0.01	-7.68**	-16.38**	-2.05**	-1.28**	-1.47**	-0.25	-0.24	4.62**	2.54	-1.92**
	7860 × 37668	-3.50**	-3.25**	8.11**	0.11**	15.51**	7.77**	0.76	-0.12	0.19	-0.01	-0.16	5.00**	-22.98**	0.97
	7968 × 32274	-4.16**	-4.50**	-4.69**	-0.05	-6.56**	-2.89**	-0.19	-1.81**	-2.05**	0.59**	0.54**	30.70**	5.96**	-3.15**
	7968 × 37667	2.16**	0.91	-2.86**	0.08	-0.22	4.07**	0.33	2.15**	2.69**	0.30	-0.28	-2.04**	10.17**	4.08**
	7968 × 37668	2.00**	3.58**	7.56**	-0.03	6.78**	-1.18**	-0.14	-0.34**	-0.63**	-0.89**	-0.82**	-28.65**	-16.13**	-0.92
	23765 × 32274	6.00**	4.50**	1.63**	0.17**	7.23**	-3.98**	-0.92	-0.75**	-0.72**	-0.51**	-0.49	-54.24**	-1.13	0.55
	23765 × 37667	1.33**	1.41**	3.59**	-0.05	1.63**	4.81**	1.43**	1.06**	0.86**	0.41	0.35	59.00**	-9.68**	0.94
	23765 × 37668	-7.33**	-5.91**	-5.22**	-0.12**	-8.86**	-0.83	-0.50	-0.28**	-0.13	0.09	0.13	-4.76**	10.82**	-1.49**

Note: **: significant at $p \leq 0.01$, DF50%: Days to 50% Flowering, DM: Days to Maturity, FLL: Flag Leaf Length, FLW: Flag Leaf Width, FLA: Flag Leaf Area, PH: Plant Height, PL: Panicle Length, NT: Number of Tillers per plant, NP: Number of Panicles, PW: Panicle Weight, GW: Grain Weight per panicle, NG: Number of Grains per panicle, SF: Spikelet Fertility, and YP: Yield per Plant

Table 6. Proportional contribution of lines, testers, and their interaction to total variance for yield and related traits under direct seeded conditions

Contributor	DF50%	DM	FLL (cm)	FLW (cm)	FLA (cm²)	PH (cm)	PL (cm)	NT	NP	PW (g)	GW (g)	NG	SF(%)	YP (g)
Lines	20.32	21.12	9.91	22.01	3.34	58.46	16.69	40.42	41.61	80.38	78.04	79.74	7.91	36.45
Testers	3.57	2.97	20.27	25.40	21.47	0.09	57.14	7.57	11.51	0.59	0.41	0.47	10.85	7.63
L X T	76.10	75.89	69.80	52.58	75.18	41.44	26.15	52.00	46.86	19.01	21.53	19.78	81.23	55.97

Note: Values indicate the percentage contribution of lines (additive genetic effects), tester (main effects of tester), and their interaction (non-additive effects) to the total sum of squares for each trait derived from the line \times tester analysis. DF50%: Days to 50% Flowering, DM: Days to Maturity, FLL: Flag Leaf Length, FLW: Flag Leaf Width, FLA: Flag Leaf Area, PH: Plant Height, PL: Panicle Length, NT: Number of Tillers per plant, NP: Number of Panicles, PW: Panicle Weight, GW: Grain Weight per panicle, NG: Number of Grains per panicle, SF: Spikelet Fertility, and YP: Yield per Plant

Estimating GCA effects serves as an effective indicator of a parent line's potential to produce superior progeny through favorable alleles' transmission. The GCA effect is adaptable, as it represents the genetic value of parents for a trait through additive gene effects (Gaballah et al. 2022). A small or negative combining ability effect suggests that the organism transmits genetic advantages to offspring poorly, whereas larger positive values indicate more significant effects. Although parents in crosses may possess desired traits, this does not ensure the transfer of these traits to offspring. The ability of parents to integrate along with heritability and trait transmission is crucial for the success of breeding programs (Suvi et al. 2020). Evaluations of GCA impact demonstrate the mean performance of parents in rice crossings concerning yield qualities. The study exhibited a significant GCA effect for all traits (Table 4) and no parent exhibited a significant positive GCA effect for all traits, aligning with the findings of Gaballah et al. (2022). We identified negative GCA for DF50% in lines 7860 and 7968, and tester 37768, which is desirable in rice because earliness shortens the life cycle and improves adaptability in diverse climates, as Azad et al. (2022) indicated that negative combining ability is preferable for the days-to-flowering characteristic. Positive GCA is not advantageous for this parameter, as noted by Modarresi et al. (2024). Based on significant positive and negative GCA effects, early and late flowering lines may be utilized to develop rice hybrids and cultivars (Ali et al. 2025). We observed both positive and negative GCA effects for DM, with a negative GCA effect being preferred in rice for early maturation. Similarly, Ali et al. (2025) identified both positive and negative GCA effects for DM.

The results obtained from the GCA effects were consistent with those reported by Nivedha et al. (2024) and several other studies in rice. Similar trends for FLL and FLW were also observed by Nivedha et al. (2024), while comparable results for FLA were reported by Gaballah et al. (2022). We identified that parents, such as 6880, 7860, 32274, and 37768, exhibited negative and significant GCA for PH, which was desirable in rice, as these parents were selected due to the preference for semi-dwarf plants. Semi-dwarf plants may exhibit greater resilience to lodging issues at the end of the growing season (Aamer and Ibrahim 2020). Positive GCA effect for yield-related components, such as panicle length, number of tillers, number of panicles, panicle weight, grain weight, number of grains, and spikelet fertility, are all positively associated with improvements in rice production. For example, the present results are consistent with those of Dianga et al. (2020) for PW, PL and SF, Al-Khayri and El-Malky (2023) for NT, Modarresi et al. (2024) for Yield Potential (YP), NG, NP, and PL, Nivedha et al. (2024) for PL and NT, and Singh et al. (2025) for SF and YP. The consistency of our GCA results with different scientists collectively supports the additive gene action prominent for key yield traits, and the selection of superior general combiners can be effectively used to enhance rice hybrid performance. Positive GCA effect of these lines, testers for yield and related traits suggested that they have a potential for improving these yield-related characters, which directly affect rice production,

so these lines and testers could be useful for improving yield indirectly through improvement of these traits. Significant and positive, and negative GCA effects in the present study indicated that these lines or testers were good general combiners for a particular trait and could be useful for this trait improvement in hybrid development.

To optimize hybrid selection, it is advisable to consider SCA in conjunction with the GCA of the parents. Previous studies indicate that hybrid combinations involving at least one parent with high GCA, superior mean performance, and favorable SCA effects are more likely to produce beneficial allele combinations (Demisse 2023). In self-pollinated plants, SCA is typically not prioritized unless the goal is to exploit heterosis for superior hybrid production. A hybrid exhibiting high SCA values suggests that non-additive gene effects predominantly influence the trait (Suvi et al. 2020). Due to transgressive segregation, optimal hybrids should produce suitable homozygous lines (Mackay et al. 2021). The study identified significant positive and negative SCA values for the traits examined. These findings are in agreement with previous reports by Bano et al. (2017), Yuga et al. (2018), Dubey et al. (2020), Sharma and Jaiswal (2020), and Sharma and Pandey (2021). Conversely, positive SCA is favored for PL, as validated by Dubey et al. (2020). The findings for NT align with those of Bano et al. (2017) and Yuga et al. (2018). The present findings on grain yield per plant are in agreement with earlier studies by Sharma and Jaiswal (2020), Singh et al. (2020), El-Mowafi et al. (2021), and Sharma and Pandey (2021). Our results are consistent with earlier studies in rice, indicating the importance of both additive (via the selection of superior general combiners) and non-additive (through hybridization) genetic effects for improving hybrid performance (Griffing 1956; Nivedha et al. 2024). These studies highlight that additive effects, as reflected by GCA, play a key role in the inheritance of yield-related traits. Likewise, non-additive effects, captured through SCA, play an important role in heterosis expression, which is important for rice hybrid breeding (Suvi et al. 2020).

In our study, the crosses demonstrated significant and positive SCA, indicating strong hybrid potential and suitability as promising candidates for high-yield rice hybrids under direct-seeded conditions. A positive SCA effect implies the presence of dominance and epistatic interactions, which are key contributors to heterosis. These interactions enhance the expression of favorable alleles that are complementary between lines and testers, resulting in superior hybrid performance. The presence of both high GCA and SCA effects in parents and crosses, indicates that while additive effects contribute to the stable inheritance of yield components, non-additive effects drive immediate hybrid superiority. We observed a higher contribution of line and tester interactions on traits, such as DF50%, DM, FLL, FLW, FLA, NT, NP, SF%, and YP. Kargbo et al. (2019) and Tiwari et al (2024) also reported comparable findings for DM, NT, NP, SF%, and YP. Lines exhibited the highest contribution for PH, PW, GW, and NG, which is similar to Singh et al. (2022) for PH. A higher contribution of the tester was noted for PL, as reported by Kulsum et al. (2017).

The present study was conducted over two consecutive growth seasons (2023-2024) at a single location under direct-seeded rice conditions, enabling uniform crop management and precise estimation of combining ability effects. Although this design limited the evaluation of Genotype \times Environment ($G \times E$) interactions (Abdel-Aty et al. 2023), the consistent performance across the seasons and highly significant effects of lines, testers, and their interactions indicate that the genetic differences are stable and biologically significant. These findings provide a robust basis for future multi-location validation of the most promising crosses. Significant GCA and SCA effects for most of the studied traits demonstrate the contribution of additive and non-additive gene action under direct-seeded rice conditions. The stability of combining ability across seasons supports the reliability of the identified superior parents and cross combinations. These outcomes suggest that selection based on GCA can effectively improve parental lines while SCA can be exploited to identify high-performance hybrids. Although this study employed three replications per season to ensure adequate statistical precision, it was conducted at a single experimental location. This allowed for strict control of agronomic treatments, uniform irrigation, and soil management, thereby minimizing confounding environmental heterogeneity that could obscure true genetic contrasts.

The Line \times Tester model proved suitable for this preliminary genetic evaluation, as it efficiently partitioned genetic variance into additive and non-additive genetic components and facilitated the identification of a promising parental combination (Mohanty et al. 2025). While more advanced approaches, including epistatic or mixed model analysis, can provide more comprehensive insights into genetic architecture, they require multi-environment datasets or molecular information beyond the scope of the present study (Verhoeven et al. 2006). Despite single location nature of the experiment, the pronounced genetic differences and consistent combining ability pattern observed across seasons provide a reliable foundation for future multi-location and multi-environment trials aimed at validating the yield stability and adaptability of the selected crosses under diverse agro-ecological conditions.

Future research should integrate additional agronomic and physiological traits, such as water-use efficiency, resistance to pests and diseases, and nutrient uptake efficiency, which are essential for adaptability and sustainability of rice genotypes in DSR systems (Joshi et al. 2013). Incorporating physiological, morphological, and molecular characteristics associated with stress tolerance and resource-use efficiency will enable a more comprehensive evaluation of hybrid performance. Furthermore, future studies should investigate the functional relationship among yield and related components, such as flag leaf area, panicle weight, and grain number using correlation, path analysis, and multivariate modeling approaches (Fatima 2019). Integrating these analyses with combining ability estimates will enhance the precision of the selection process for developing high-yielding genotypes suited to the direct-seeded rice system.

In conclusion, this study revealed significant genetic variability among rice genotypes evaluated under direct-seeded conditions. Both parents, line 23765 and tester 37768, exhibited superior GCA for yield-related traits, indicating their potential as a valuable source of favorable alleles. The hybrid 6880 X 32274 showed the highest SCA, suggesting strong non-additive genetic effects contributing to yield performance. These findings highlight the importance of selecting parental combinations with complementary gene action to enhance hybrid performance. The identified parents and crosses provide a strong genetic foundation for developing high-yielding, water-efficient, and climate-resilient rice varieties. Combining GCA and SCA results with heterosis and stability of traits analysis provides valuable suggestions to improve inbred line as well as hybrid rice development, thereby bridging the gap between applied breeding and quantitative genetics. However, these experimental results didn't fully reveal genotype-environment interactions.

ACKNOWLEDGEMENTS

We are grateful to the Faculty of Agriculture and Environment, the Islamia University of Bahawalpur, Pakistan, for supporting the continuation of this research. We are also deeply grateful to Universitas Hasanuddin, Indonesia, for covering the Journal APC of this article.

REFERENCES

- Aamer S, Ibrahim H. 2020. Assessment of combining ability for some grain yield and quality traits in rice (*Oryza sativa* L.) by using the Griffing method and biplot analysis. *J Plant Prod* 11 (12): 1615-1623. <https://doi.org/10.21608/jpp.2020.149834>.
- Abd El-Aty MS, Katta YS, El-Abd AEMB, Mahmoud SM, Ibrahim OM, Eweda MA, El-Saadony MT, AbuQamar SF, El-Tarabily KA, El-Tahan AM. 2022. The combining ability for grain yield and some related characteristics in rice (*Oryza sativa* L.) under normal and water stress conditions. *Front Plant Sci* 13: 866742. <https://doi.org/10.3389/fpls.2022.866742>.
- Abdel-Aty MS, Sorour FA, Yehia WMB, Kotb HMK, Abdelghany AM, Lamlof SF, Shah AN, Abdelsalam NR. 2023. Estimating the combining ability and genetic parameters for growth habit, yield, and fiber quality traits in some Egyptian cotton crosses. *BMC Plant Biol* 23: 121. <https://doi.org/10.1186/s12870-023-04131-z>.
- Ahmed S, Kumar V, Uz Zaman A, Dewan MR, Khatun A, Hossain K, Singh S, Timsina J, Krupnik TJ. 2025. Dry direct-seeded and broadcast rice: A profitable and climate-smart alternative to puddled transplanted aus rice in Bangladesh. *Field Crops Res* 322: 109739. <https://doi.org/10.1016/j.fcr.2025.109739>.
- Ali Z, Naeem M, Rafiq I, Ikram RM, Akram MI, Taha EI, Bekhit MM, Simsek O, Izgu T, Ahmed T, Iqbal J, Iqbal R. 2025. Study of variability, combining ability, genetics and association of different yield related traits in rice (*Oryza sativa* L.) genotypes. *Genet Resour Crop Evol* 72: 2925-2938. <https://doi.org/10.1007/s10722-024-02131-y>.
- Al-Khayri JM, El-Malky MM. 2023. Genetic parameters and principal component analysis for quantitative traits in rice (*Oryza sativa* L.). *Sabrao J Breed Genet* 55 (5): 1547-1560. <http://doi.org/10.54910/sabrao2023.55.5.9>.
- Amin AKMK, Haque MA. 2009. Seedling age influences rice (*Oryza sativa* L.) performance. *Philipp J Sci* 138: 219-226.
- Azad AK, Sarker U, Ercisli S, Assouguem A, Ullah R, Almeer R, Sayed AA, Peluso I. 2022. Evaluation of combining ability and heterosis of popular restorer and male sterile lines for the development of superior

- rice hybrids. *Agronomy* 12 (4): 965. <https://doi.org/10.3390/agronomy12040965>.
- Bandumula N. 2018. Rice production in Asia: Key to global food security. *Proc Natl Acad Sci India Sect B Biol Sci* 88: 1323-1328. <https://doi.org/10.1007/s40011-017-0867-7>.
- Bano DA, Singh SP, Waza SA. 2017. Generation mean analysis for yield and quality traits in aromatic genotypes of rice (*Oryza sativa* L.). *Intl J Pure Appl Biosci* 5 (6): 870-878. <https://doi.org/10.18782/2320-7051.6055>.
- Begna T. 2021. Combining ability and heterosis in plant improvement. *Open J Plant Sci* 6 (1): 108-117. <https://doi.org/10.17352/ojps.000043>.
- de Mendiburu F. 2019. *Agricolae: Statistical Procedures for Agricultural Research*. R Package version 1.3-1. <https://CRAN.R-project.org/package=agricolae>
- Demisse FA. 2023. Combining ability and heterosis of Ethiopian sorghum [*Sorghum bicolor* (L.) Moench] landraces in Eastern Oromia, Ethiopia. [Dissertation]. Haramaya University, Dire Dawa, Ethiopia.
- Dianga A-I, Joseph KW, Musila RN. 2020. Analysis of combining ability for early maturity and yield in rice (genus: *Oryza*) at the Kenyan coast. *Intl J Agron* 2020 (1): 6230784. <https://doi.org/10.1155/2020/6230784>.
- Dubey R, Kar S, Pramanik A. 2020. Combining ability analysis and gene action for blast resistance in rice (*Oryza sativa* L.). *J Pharmacogn Phytochem* 9 (6): 131-135.
- Elkatry HO, El-Beltagi HS, Ahmed AR, Mohamed HI, Al-Otaibi HH, Ramadan KMA, Mahmoud MAA. 2023. The potential use of Indian rice flour or husk in fortification of pan bread: Assessing bread's quality using sensory, physicochemical, and chemometric methods. *Front Nutr* 10: 1240527. <https://doi.org/10.3389/fnut.2023.1240527>.
- El-Malky M, Al-Daej M. 2023. Assessment of inbreeding depression, genetic variability, and genetic diversity in rice (*Oryza sativa* L.) based on agro-morphological traits. *Fresenius Environ Bull* 32 (4): 2067-2077.
- El-Mowafi HF, AlKahtani MDF, Abdallah RM, Reda AM, Attia KA, El-Hity MA, El-Dabaawy HE, Al Husnain L, Al-Ateeq TK, El-Esawi MA. 2021. Combining ability and gene action for yield characteristics in novel aromatic cytoplasmic male sterile hybrid rice under water-stress conditions. *Agriculture* 11 (3): 226. <https://doi.org/10.3390/agriculture11030226>.
- Fasahat P, Rajabi A, Rad JM, Derera J. 2016. Principles and utilization of combining ability in plant breeding. *Biom Biostat Intl J* 4 (1): 00085. <https://doi.org/10.15406/bbij.2016.04.00085>.
- Fatima S. 2019. Effect of flag leaf clipping on growth, yield and yield attributes of hybrid rice in Boro season. [Dissertation]. Department of Agricultural Botany, Sher-E-Bangla Agricultural University, Dhaka.
- Fellahi ZEA, Hannachi A, Bouzourou H, Boutekrabi A. 2013. Line x tester mating design analysis for grain yield and yield related traits in bread wheat (*Triticum aestivum* L.). *Intl J Agron* 2013 (1): 201851. <https://doi.org/10.1155/2013/201851>.
- Gaballah MM, Attia KA, Ghoneim AM, Khan N, El-Ezz AF, Yang B, Xiao L, Ibrahim EI, Al-Doss AA. 2022. Assessment of genetic parameters and gene action associated with heterosis for enhancing yield characters in novel hybrid rice parental lines. *Plants* 11 (3): 266. <https://doi.org/10.3390/plants11030266>.
- Ghosh M, Swain DK, Jha MK, Tewari VK. 2013. Precision nitrogen management using a chlorophyll meter for improving growth, productivity, and N use efficiency of rice in a subtropical climate. *J Agric Sci* 5 (2): 253-266. <https://doi.org/10.5539/jas.v5n2p253>.
- Goyal A, Sharma PC, Munjal R, Krishnamurthy SL, Jat HS, Lokeshkumar BM, Kumar V. 2022. Identifying rice genotypes suitable for aerobic direct-seeded conditions. *Environ Sci Proc* 16 (1): 68. <https://doi.org/10.3390/environsciproc2022016068>.
- Griffing B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust J Biol Sci* 9 (4): 463-493.
- Huang X, Wei X, Sang T, Zhao Q, Feng Q, Zhao Y, Li C, Zhu C, Lu T, Zhang Z, Li M, Fan D, Guo Y, et al. 2010. Genome-wide association studies of 14 agronomic traits in rice landraces. *Nat Genet* 42: 961-967. <https://doi.org/10.1038/ng.695>.
- Jat RK, Meena VS, Kumar M, Jakkula VS, Reddy IR, Pandey AC. 2022. Direct seeded rice: Strategies to improve crop resilience and food security under adverse climatic conditions. *Land* 11 (3): 382. <https://doi.org/10.3390/land11030382>.
- Joshi E, Kumar D, Lal B, Nepalia V, Gautam P, Vyas AK. 2013. Management of direct-seeded rice for enhanced resource-use efficiency. *Plant Knowl J* 2 (3): 119-134.
- Karaağaç O. 2021. Combining ability and heterosis for root structure and graft-related traits of interspecific *Cucurbita* rootstocks. *Euphytica* 217: 166. <https://doi.org/10.1007/s10681-021-02884-y>.
- Kargbo SS, Showemimo FA, Akintokun PO, Porbeni JBO. 2019. Combining ability analysis and gene action for yield and yield-related traits in rice (*Oryza sativa* L.) under saline conditions. *J Plant Breed Crop Sci* 7 (2): 63-74. <https://doi.org/10.33687/pbg.007.02.2831>.
- Kaur J, Singh A. 2017. Direct seeded rice: Prospects, problems/constraints and researchable issues in India. *Curr Agric Res J* 5 (1): 13-32. <https://doi.org/10.12944/carj.5.1.03>.
- Kempthorne O. 1957. *An Introduction to Genetic Statistics*. John Wiley and Sons, New York.
- Kulsum MU, Iftekharuddaula KM, Saikat MMH, Karim MA, Mian MAK, Rasul MG. 2017. Combining ability for yield and yield associated traits in rice. *Ann Bangladesh Agric* 21 (2): 21-31.
- Kumar V, Ladha JK. 2011. Direct seeding of rice: Recent developments and future research needs. *Adv Agron* 111: 297-413. <https://doi.org/10.1016/b978-0-12-387689-8.00001-1>.
- Labroo MR, Studer AJ, Rutkoski JE. 2021. Heterosis and hybrid crop breeding: A multidisciplinary review. *Front Genet* 12: 643761. <https://doi.org/10.3389/fgene.2021.643761>.
- Li R, Li M, Ashraf U, Liu S, Zhang J. 2019. Exploring the relationships between yield and yield-related traits for rice varieties released in China from 1978 to 2017. *Front Plant Sci* 10: 543. <https://doi.org/10.3389/fpls.2019.00543>.
- Ma B, Zhang L, He Z. 2023. Understanding the regulation of cereal grain filling: The way forward. *J Integr Plant Biol* 65 (2): 526-547. <https://doi.org/10.1111/jipb.13456>.
- Mackay IJ, Cockram J, Howell P, Powell W. 2021. Understanding the classics: The unifying concepts of transgressive segregation, inbreeding depression and heterosis and their central relevance for crop breeding. *Plant Biotechnol J* 19 (1): 26-34. <https://doi.org/10.1111/pbi.13481>.
- Maring KM, Madhubala, Patel PB. 2023. Combining ability analysis for grain yield and its attributes in Rice (*Oryza sativa* L.). *Pharma Innov* 12 (5): 2959-2964.
- Modarresi M, AllahGholipour M, Ebadi AA. 2024. Estimation of gene effect and combining ability for yield and yield components using line x tester analysis in rice (*Oryza sativa*). *Plant Breed Biotechnol* 12: 17-29. <https://doi.org/10.9787/pbb.2024.12.17>.
- Mohanty S, Wassmann R, Nelson A, Moya P, Jagadish KSV. 2013. Rice and climate change: Significance for food security and vulnerability. *Intl Rice Res Inst* 14 (1): 1-14.
- Mohanty TA, Kumaresan D, Manonmani S, Ramalingam S, Boopathi NM, Natarajan S. 2025. Enhancing rice breeding through two-line hybrids: Integrative analysis of combining ability, heterosis, MGIDI, and grain quality traits. *Euphytica* 221: 29. <https://doi.org/10.1007/s10681-025-03474-y>.
- Mohidem NA, Hashim N, Shamsudin R, Man HC. 2022. Rice for food security: Revisiting its production, diversity, rice milling process and nutrient content. *Agriculture* 12 (6): 741. <https://doi.org/10.3390/agriculture12060741>.
- Nivedha R, Manonmani S, Kalaimagal T, Raveendran M, Kavitha S. 2024. Comprehensive assessment of combining ability and heterosis for the development of superior three-line hybrids in rice (*Oryza sativa* L.). *Electron J Plant Breed* 15 (1): 1-11. <https://doi.org/10.37992/2024.1501.005>.
- Phyu P, Islam MR, Sta Cruz PC, Collard BCY, Kato Y. 2020. Use of NDVI for indirect selection of high yield in tropical rice breeding. *Euphytica* 216: 74. <https://doi.org/10.1007/s10681-020-02598-7>.
- Rahman ANMRB, Zhang J. 2023. Trends in rice research: 2030 and beyond. *Food Energy Secur* 12 (2): e390. <https://doi.org/10.1002/fes3.390>.
- Rasheed A, Ashfaq M, Sajjad M. 2021. Combining ability and heterosis analysis for grain yield traits in fine long grain rice (*Oryza sativa* L.). *J Anim Plant Sci* 31 (3): 764-772. <https://doi.org/10.36899/japs.2021.3.0266>.
- Sanchez PA. 1973. Puddling tropical rice soils: 2. Effects of water losses. *Soil Sci* 115 (4): 303-308.
- Sandhu N, Yadav S, Singh VK, Kumar A. 2021. Effective crop management and modern breeding strategies to ensure higher crop productivity under direct-seeded rice cultivation system: A review. *Agronomy* 11 (7): 1264. <https://doi.org/10.3390/agronomy11071264>.
- Sandhyakishore N, Praveenkumar G, Pallavi M, Kamalakar J, Shahana F, Tagore KR. 2017. Combining ability analysis for yield and related traits in rice (*Oryza sativa* L.). *Agric Update* 12: 1573-1577. [https://doi.org/10.15740/has/au/12.techsear\(6\)2017/1573-1577](https://doi.org/10.15740/has/au/12.techsear(6)2017/1573-1577).

- Sharma A, Jaiswal HK. 2020. Combining ability analysis for grain yield and quality traits in basmati rice (*Oryza sativa* L.). *Plant Arch* 20 (Suppl 1): 2367-2373.
- Sharma A, Pandey DP. 2021. Gene action and combining ability for yield and its component traits of rice in the upland condition of Himachal Pradesh. *Himachal J Agric Res* 47 (1): 33-35.
- Singh MK, Banshidhar, Kumar A, Tigga A, Singh SK. 2020. Exploration of possibilities to identify heterotic cross combinations in aromatic rice (*Oryza sativa* L.) for grain yield and quality parameters. *Curr J Appl Sci Technol* 39 (11): 92-98. <https://doi.org/10.9734/cjast/2020/v39i1130651>.
- Singh RK, Chaudhary BD. 1985. *Biometrical Methods in Quantitative Genetic Analysis*. Kalyani Publishers, New Delhi.
- Singh S, Sharma A, Verma OP. 2022. Line x tester analysis for yield and yield attributing traits of rice (*Oryza sativa* L.) genotypes under sodic soil conditions. *Oryza* 59 (3): 301-308. <https://doi.org/10.35709/ory.2022.59.3.5>.
- Singh S, Sharma SN, Prasad R. 2001. The effect of seeding and tillage methods on the productivity of the rice-wheat cropping system. *Soil Tillage Res* 61 (3-4): 125-131. [https://doi.org/10.1016/S0167-1987\(00\)00188-4](https://doi.org/10.1016/S0167-1987(00)00188-4).
- Singh U, Sao A, Verma SK. 2025. Unlocking hybrid potential: A detailed analysis of heterosis, GCA, and SCA for enhancing agronomic performance and yield in rice (*Oryza sativa* L.). *Plant Arch* 25 (1): 971-978. <https://doi.org/10.51470/plantarchives.2025.v25.supplement-1.132>.
- Singh VJ, Vinod KK, Krishnan SG, Singh AK. 2021. Rice adaptation to climate change: Opportunities, and priorities in molecular breeding. In: Hossain MA, Hassan L, Ifterkharuddaula KM, Kumar A, Henry R (eds). *Molecular Breeding for Rice Abiotic Stress Tolerance and Nutritional Quality*. John Wiley and Sons, New York. <https://doi.org/10.1002/9781119633174.ch1>.
- Steel RG, Torrie JH, Dickey DA. 1997. *Principles and Procedures of Statistics: A Biometrical Approach*. 3rd Edition, McGraw Hill, Inc. Book Co., New York.
- Sujariya S, Jongdee B, Fukai S. 2023. Estimation of flowering time and its effect on grain yield of photoperiod sensitive varieties in rainfed lowland rice in Northeast Thailand. *Field Crops Res* 302: 109075. <https://doi.org/10.1016/j.fcr.2023.109075>.
- Suvi WT, Shimelis H, Laing M, Mathew I, Shayanowako AIT. 2020. Determining the combining ability and gene action for rice yellow mottle virus disease resistance and agronomic traits in rice (*Oryza sativa* L.). *Agronomy* 11 (1): 12. <https://doi.org/10.3390/agronomy11010012>.
- Thakur AK, Rath S, Roychowdhury S, Uphoff N. 2010. Comparative performance of rice with System of Rice Intensification (SRI) and conventional management using different plant spacings. *J Agron Crop Sci* 196 (2): 146-159. <https://doi.org/10.1111/j.1439-037x.2009.00406.x>.
- Tiwari AK, Tiwari J, Upadhyayi S, Sharma D. 2024. Combining ability analysis for yield and yield contributing traits using cytoplasmic male sterile lines in aromatic hybrids of rice. *Plant Arch* 24 (1): 649-657. <https://doi.org/10.51470/plantarchives.2024.v24.no.1.088>.
- Uyeh DD, Asem-Hiablie S, Park T, Kim K, Mikhaylov A, Woo S, Ha Y. 2021. Could Japonica rice be an alternative variety for increased global food security and climate change mitigation? *Foods* 10 (8): 1869. <https://doi.org/10.3390/foods10081869>.
- Verhoeven KJF, Jannink J-L, McIntyre LM. 2006. Using mating designs to uncover QTL and the genetic architecture of complex traits. *Heredity* 96: 139-149. <https://doi.org/10.1038/sj.hdy.6800763>.
- Wang J, Xu J, Wang L, Zhou M, Nian J, Chen M, Lu X, Liu X, Wang Z, Cen J, Liu Y, Zhang Z, et al. 2023. Semi-rolled leaf 10 stabilizes catalase isozyme B to regulate leaf morphology and thermotolerance in rice (*Oryza sativa* L.). *Plant Biotechnol J* 21 (4): 819-838. <https://doi.org/10.1111/pbi.13999>.
- Won PLP, Liu H, Banayo NPM, Nie L, Peng S, Islam MR, Cruz PS, Collard BCY, Kato Y. 2020. Identification and characterization of high-yielding, short-duration rice genotypes for tropical Asia. *Crop Sci* 60 (5): 2241-2250. <https://doi.org/10.1002/csc2.20183>.
- Yuga ME, Kimani JM, Kimani PM, Olubayo MF, Muthomi JW, Nzuve FM. 2018. Combining ability and heterosis for agronomic and yield traits in Indica and Japonica rice crosses. *J Agric Sci* 10 (12): 92-103. <https://doi.org/10.5539/jas.v10n12p92>.
- Zhao Y-F, Peng T, Sun H-Z, Teotia S, Wen H-L, Du Y-X, Zhang J, Li J-Z, Tang G-L, Xue H-W, Zhao Q-Z. 2019. miR1432-OsACOT (Acyl-CoA thioesterase) module determines grain yield via enhancing grain filling rate in rice. *Plant Biotechnol J* 17 (4): 712-723. <https://doi.org/10.1111/pbi.13009>.