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Estimation of Heterosis for Grain Yield and Yield Components in Upland Rice

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Abstract

The present study estimated heterosis for grain yield and related traits in rice (*Oryza sativa* L.) using a line × tester mating design, generating 22 F1 hybrids evaluated for 13 traits against the standard check HPR 2656. Analysis of variance revealed highly significant genotypic differences for all traits, indicating sufficient genetic variability for heterosis breeding. Significant negative standard heterosis was observed for days to 50% flowering (up to -5.56% in HPR 2887 × HPR 1156) and plant height (up to -13.48% in HPR 2847 × HPR 2656), desirable for earliness and lodging resistance. Significant positive standard heterosis was recorded for effective tillers per plant (13 crosses), spikelet fertility (15 crosses), grain yield per plant (14 crosses, maximum 59.13% in HPR 2877 × HPR 2656), grain length (14 crosses) and grain length-breadth ratio (11 crosses, maximum 15.76% in HPR 2877 × HPR 1156). Crosses HPR 2887 × HPR 2656, HPR 2877 × HPR 2656 and HPR 2877 × HPR 1156 showed consistently high heterosis across various grain yield and quality traits simultaneously. Four crosses with high SCA effects for grain yield per plant and favourable parental GCA were identified as promising for further pedigree selection.

Keywords: Hybrid Vigour, Line × Tester, *Oryza sativa* L., Pedigree, Standard Heterosis

Rice is a major staple food crop in India, providing about 43% of the calorie requirement for more than 70% of the population. Global rice demand is expected to rise by approximately 25% by 2050 due to rapid population growth, urbanisation and changing dietary patterns, posing an unprecedented challenge to the rice production system already affected by shrinking arable land, climate change and rising input costs[1]. Bridging this demand-supply gap requires the development of rice varieties with substantially improved yield potential, resilience and grain quality.

The productivity of a crop can be improved in the shortest duration of time by raising hybrids, which in general, are uniform for different traits along with resistance to several biotic and abiotic stresses[2]. In plant breeding, the selection of hybrids needs a good magnitude of heterosis and combining ability[3]. Heterosis in rice is one of the most scientifically robust and commercially proven strategies for achieving gains in rice productivity and has led to a significant contribution to food security in the last half of the century[4]. Commercial cultivation of hybrid rice, first pioneered in China and later extended to South and Southeast Asia, has consistently shown yield advantages of 15–20% over elite inbred check varieties across environments[5]. However, adoption of hybrid

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rice remains limited in many rice-growing countries, including India, largely because of the unavailability of hybrids with superior grain quality and adequate adaptation to local agroclimatic conditions, highlighting the need for systematic evaluation of new hybrid combinations.

The exploitation of heterosis in rice breeding is governed by both general combining ability (GCA) and specific combining ability (SCA) effects of parental lines used in hybrid development. GCA reflects the average performance of a parent across different crosses and is primarily associated with additive gene action, whereas SCA refers to the performance of a specific cross based on the GCA of its parents and is largely influenced by non-additive (dominance and epistatic) gene effects[6]. A high SCA effect, particularly when combined with at least one parent having high GCA for the target trait, is considered a reliable indicator of exploitable heterosis in hybrid breeding programmes[7]. Therefore, estimates of GCA and SCA effects are essential for identifying promising parental combinations, predicting the direction of heterosis and designing efficient breeding strategies.

Among the mating designs used for heterosis and combining ability analysis, the line × tester design proposed by Kempthorne[8] is widely used in self-pollinated crops such as rice. In this design, a set of female lines is crossed with a smaller number of male testers to produce F_1 hybrids, enabling the estimation of GCA effects for lines and testers and SCA effects for individual crosses. The line × tester approach is particularly useful in hybrid rice breeding because it allows the evaluation of a large number of parental combinations in a manageable number of field plots. Therefore, this design was selected in the present study to identify promising parents and crosses for hybrid development and to assess the extent of heterosis for economically important traits. Standard heterosis is of special economic importance in plant breeding because it directly measures the performance advantage of a hybrid over the currently cultivated benchmark varieties under farmers' conditions. The present study was undertaken to assess standard heterosis for yield, yield-contributing traits and grain quality traits in 22 F_1 hybrids developed through a line × tester mating design by using 11 female lines and two male testers. The findings of this study are expected to provide useful insights into the genetics of heterosis in rice and a basis for developing high-yielding, quality-oriented hybrid varieties suited to the target environment.

MATERIALS AND METHODS

The experimental material comprised 11 diverse rice breeding lines, namely HPR 2830, HPR 2840, HPR 2841, HPR 2847, HPR 2866, HPR 2877, HPR 2887, HPR 2888, HPR 2901, HPR 2902 and HPR 2903, which were used as female parents and crossed with two testers, HPR 1156 and HPR 2656, serving as male parents to generate 22 crosses in line × tester mating design. All female parents were emasculated by the vacuum emasculation method and subsequently pollinated by male testers during *Kharif* 2023 and 2024 under controlled net house conditions to prevent outcrossing. The resulting 35 genotypes (22 F_1's, 11 lines and 2 testers) were evaluated in a Randomised Block Design (RBD) with three replications during *Kharif* 2025 at the experimental farm of Rice and Wheat Research Centre (RWRC), Malan, with a spacing of 20 cm between rows and 15 cm between plants. Observations were recorded on five randomly selected plants for days to 50% flowering, days to 75% maturity, plant height (cm), effective tillers per plant, panicle length (cm), spikelets per panicle, grains per panicle, spikelet fertility (%), 1000-grain weight (g), grain yield per plant (g), grain length (mm), grain breadth (mm) and grain length-breadth ratio. The data recorded were subjected to line × tester analysis as outlined by Kempthorne[8] using R software. The standard heterosis (SH) was estimated as the percentage deviation of the F_1 hybrid mean from the mean of the standard check, i.e., HPR 2656 (a widely recommended high-yielding variety for the

upland conditions of Himachal Pradesh), following the procedure of Fonseca and Patterson[9].

RESULTS AND DISCUSSION

The analysis of variance for combining ability revealed that the variation due to lines and lines × testers interactions was highly significant for all the traits studied, whereas testers differed significantly for most of the traits except days to 75% maturity, panicle length and 1000-grain weight (Table 1). This indicated the presence of sufficient genetic variability among the experimental material, which is a prerequisite for an effective hybrid breeding programme and provides the basis for commercial exploitation of heterosis. All the 22 generated crosses were evaluated for standard heterosis across 13 different traits and are presented in Table 2. The magnitude and direction of heterosis varied considerably across traits and cross combinations, which is consistent with the polygenic nature of yield and its component traits in rice (Figure 1).

Days to 50% flowering is one of the most important traits studied in hybrid breeding because it governs the duration of the vegetative phase and determines

Table 1. Analysis of variance for combining ability analysis for various traits in rice(*Significant at P ≤ 0.05, df = degree of freedom)

Mean Sum of Squares							
Traits		**Replications**	**Crosses**	**Lines**	**Testers**	**Lines × testers**	**Error**
	df	2	21	10	1	10	42
Days to 50% flowering		5.288	24.171*	23.309*	36.379*	23.812*	1.812
Days to 75% maturity		0.864	14.450*	19.279*	1.515	10.915*	1.626
Plant height at maturity		2.493	222.856*	300.443*	1010.892*	66.466*	2.071
Effective tillers per plant		0.104	1.900*	2.215*	0.701*	1.705*	0.034
Panicle length		0.379	4.447*	6.668*	0.336	2.636*	0.174
Spikelets per panicle		2.932	329.716*	528.367*	133.310*	150.705*	3.326
Grains per panicle		2.537	477.565*	745.836*	242.458*	232.805*	3.504
Spikelet fertility		4.459	28.626*	40.573*	20.564*	17.486*	2.035
1000-grain weight		0.671	3.543*	4.468*	0.207	2.952*	0.756
Grain yield per plant		0.268	31.860*	59.686*	1.339*	7.085*	0.235
Grain length		0.055	0.423*	0.487*	0.444*	0.356*	0.015
Grain breadth		0.003	0.012*	0.008*	0.070*	0.010*	0.003
L: B ratio		0.004	0.207*	0.191*	0.977*	0.146*	0.020

Table 2. Estimation of standard heterosis (%) for different grain yield and its component traits in rice

Cross combinations	DTF	DTM	PH	ET/P	PL	S/P	G/P	SF	TGW	GY/P	GL	GB	L/B
HPR 2830 × HPR 1156	-0.79	-0.93	24.15*	1.61*	7.05*	3.43*	0.11	3.59*	1.37	-9.16*	0.30*	-3.14*	2.86*
HPR 2830 × HPR 2656	-0.40	0.31	8.59*	1.61*	1.02	-10.26*	-19.82*	-4.40*	9.56*	-15.64*	2.34*	4.12*	-2.36*
HPR 2840 × HPR 1156	3.97*	1.85	4.44*	-24.00*	0.88	-10.55*	-16.18*	0.28	3.69*	46.63*	-2.42*	2.16*	-5.11*
HPR 2840 × HPR 2656	3.57*	1.54	8.74*	1.20*	1.75*	-18.51*	-25.53*	-2.19*	1.64*	43.49*	0.52*	-0.39*	0.24
HPR 2841 × HPR 1156	3.97*	3.09*	14.52*	1.20*	-9.91*	-11.10*	-19.44*	-2.96*	-1.64*	22.92*	-11.80*	-8.04*	-4.73*
HPR 2841 × HPR 2656	0.00	5.25*	4.30*	-10.37*	-10.75*	-11.37*	-15.10*	2.52*	-1.37	21.57*	-11.57*	1.37*	-13.35*
HPR 2847 × HPR 1156	3.17*	1.85	6.00*	-0.45*	0.61	4.34*	2.94	5.59*	-3.28*	2.21*	5.14*	1.18*	3.22*
HPR 2847 × HPR 2656	0.00	-2.16*	-13.48*	5.33*	-8.59*	4.10*	1.39	4.24*	-6.01*	-14.14*	0.78*	-2.00*	2.15*
HPR 2866 × HPR 1156	4.76*	2.16*	20.00*	-17.39*	-5.67*	2.44	1.85	6.45*	0.55	-10.48*	-8.64*	-3.73*	-5.73*
HPR 2866 × HPR 2656	5.16*	2.78*	1.33	2.44*	-4.48*	3.67*	0.49	3.75*	0.82	17.09*	2.24*	-0.98*	2.56*
HPR 2877 × HPR 1156	-5.16*	0.62	5.11*	-7.48*	0.63	6.20*	7.17*	8.00*	0.96	50.79*	3.65*	-11.06*	15.76*
HPR 2877 × HPR 2656	5.56*	2.16*	-2.81*	1.61*	0.53	-7.07*	-13.47	-0.34	4.23*	59.13*	2.58*	1.45*	0.44*
HPR 2887 × HPR 1156	-5.56*	1.23	-1.85	2.44*	-6.17*	3.69*	1.31	4.56*	8.61*	29.74*	2.40*	-0.78*	2.52*
HPR 2887 × HPR 2656	0.79	-2.16*	-5.04*	-9.13*	0.70	4.18*	2.18	4.97*	2.19*	66.44*	-2.21*	2.31*	-5.06*
HPR 2888 × HPR 1156	1.59	0.62	18.22*	6.57*	0.64	-7.22*	-14.66*	-1.57*	4.51*	5.48*	3.18*	1.45*	1.02*
HPR 2888 × HPR 2656	-0.40	-2.47*	11.48*	-5.82*	-6.93*	-11.42*	-19.77*	-3.07*	-4.92*	-20.68*	-11.35*	2.12*	-13.77*
HPR 2901 × HPR 1156	-5.16*	-1.54	5.93*	6.57*	-9.03*	-6.54*	-10.43*	2.57*	-7.79*	-17.55*	3.09*	-0.59*	3.01*
HPR 2901 × HPR 2656	3.17*	-0.31	-2.48*	5.33*	-6.70*	4.15*	1.80	4.61*	0.82	-12.82*	-12.90*	0.98*	-14.32*
HPR 2902 × HPR 1156	0.40	-1.54	19.04*	-20.69*	6.14*	2.90	1.03	5.09*	-0.96	0.76	3.28*	-0.63*	3.24*
HPR 2902 × HPR 2656	1.19	0.62	19.11*	-16.56*	2.19*	4.18*	2.01	4.80*	-7.10*	4.03*	2.96*	3.14*	-0.84*
HPR 2903 × HPR 1156	3.57*	1.85	7.78*	6.15*	-8.83*	1.88	1.03	6.14*	0.41	2.86*	0.52*	-3.14*	3.08*
HPR 2903 × HPR 2656	5.56*	2.78*	-2.07	6.15*	0.73	5.19*	6.20*	8.05*	1.50	1.34*	-2.95*	3.61*	-6.95*
SE ±	1.26	1.11	1.32	0.18	0.55	1.65	1.57	0.50	0.81	0.44	0.14	0.08	0.19
Number of significant/ desirable crosses	3	3	4	13	4	10	2	15	7	14	14	11	11

(*Significant at P≤0.05, DTF-Days to 50% flowering, DTM-Days to 75% maturity, PH-Plant height, ET/P-Effective tillers per plant, PL-Panicle length, S/P-Spikelets per panicle, G/P-Grains per panicle, SF-Spikelet fertility (%), TGW-1000-grain weight, GY/P-Grain yield per plant, GL-Grain length, GB-Grain breadth, L/B-Grain length-breadth ratio

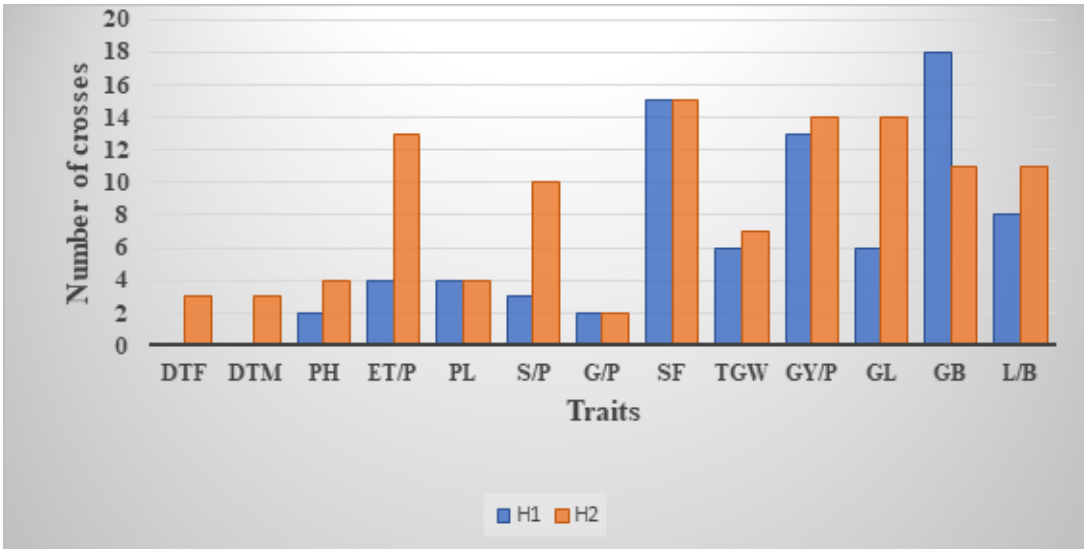


Figure 1. Distribution of crosses exhibiting heterosis (%) by different traits.

the adaptability of a variety to a given photoperiod and agro-climatic zone. Negative heterosis for days to flowering, indicating hybrids that flower earlier than the commercial standard variety, is therefore a desirable breeding objective. In the present study, three crosses showed significant negative standard heterosis for this trait, with the highest value of -5.56 % recorded in HPR 2887 × HPR 1156, followed by -5.16 % in both HPR 2877 × HPR 1156 and HPR 2901 × HPR 1156. Similar significant negative heterosis for days to 50% flowering in *indica* rice crosses has been reported by Singh and Kumar[10]. An ideal hybrid rice genotype should combine high yield with early maturity to suit intensive cropping systems, reduce the risk of lodging in late-maturing crops and minimise water and other input requirements per crop cycle. Negative significant heterosis for days to 75% maturity indicates earlier crop maturity relative to the standard check and is therefore preferred in hybrid breeding. Three crosses exhibited significant negative standard heterosis for this trait, namely HPR 2888 × HPR 2656 (-2.47%), HPR 2887 × HPR 2656 (-2.16%) and HPR 2847 × HPR 2656 (-2.16%), while positive standard heterosis was as high as 5.25% in HPR 2841 × HPR 2656. Islam *et al.*,[11] reported significant heterosis in days to 50% flowering and days to maturity in boro rice hybrids; similar findings have been corroborated by Parimala *et al*[12].

Plant height is an important morpho-agronomic trait because it is closely associated with lodging susceptibility, canopy architecture and harvest index. Standard heterosis for plant height ranged from -13.48% in HPR 2847 × HPR 2656 to 24.15% in HPR 2830 × HPR 1156. Four cross combinations showed significant standard heterosis, with HPR 2847 × HPR 2656 recording the highest negative heterosis of -13.48% over the standard check. Similar significant negative heterosis for plant height in rice crosses was reported by Gaballah *et al*[13]. Effective tillers per plant is a major yield-contributing trait and therefore an important target in heterosis studies. Thirteen crosses exhibited significant positive standard heterosis for this trait, with HPR 2888 × HPR 1156 and HPR 2901 × HPR 1156 recording the highest value of 6.57% over the check HPR 2656. Similar positive heterosis for effective tillers per plant has also been reported by Patil *et al*[14]. For panicle length, four crosses exhibited significant positive heterosis over the standard check, with the maximum value of 7.05% observed in HPR 2830 × HPR 1156. High heterosis for this trait has been reported by Khoyumthem *et al*[15].

Spikelets per panicle are a key determinant of source-sink dynamics in rice because it directly reflects the potential number of grain sites available per panicle. A higher spikelet count per panicle, when paired with adequate spikelet fertility, contributes to a greater number of filled grains and consequently higher grain yield per panicle. Ten cross combinations exhibited significant positive standard heterosis for spikelets per panicle, with the highest value of 6.20% recorded in HPR 2877 × HPR 1156. For grains per panicle, only two crosses showed significant positive standard heterosis, namely HPR 2877 × HPR 1156 (7.17%) and HPR 2903 × HPR 2656 (6.20%). Similar positive heterosis for grains per panicle has been reported by Singh and Kumar[10]. Spikelet fertility, expressed as the percentage of filled spikelets to total spikelets per panicle, is an important quality trait in rice breeding because it reflects grain-setting efficiency and directly influences the conversion of potential yield into actual yield. Fifteen crosses exhibited significant positive standard heterosis for spikelet fertility, with the highest value of 8.05% recorded in HPR 2903 × HPR 2656. These results are in agreement with the findings of Ramalingam *et al.*[16] and Kumar and Adilakshmi[17].

Thousand-grain weight is an important trait as it reflects the grain-filling capacity of a genotype. Heavier grains indicate efficient translocation of photosynthates from source to sink during the grain-filling period[18]. In the present study, seven crosses showed significant positive standard heterosis for this trait, with the highest value of 9.56% recorded in HPR 2830 × HPR 2656. Similar significant positive heterosis for 1000-grain weight was reported by Ramalingam *et al*[16]. Grain yield per plant is the ultimate target and the most economically important trait in a plant breeding programme. It is routinely assessed in heterosis studies because it represents the final integrated expression of yield components such as effective tillers, panicle length, spikelets per panicle, spikelet fertility and 1000-grain weight. Grain yield per plant exhibited a significant positive standard heterosis up to 59.13% in HPR 2877 × HPR 2656. Fourteen crosses exhibited significant positive standard heterosis for this trait. Similar findings for this trait were reported by Ganapati *et al.*[19] and Sharma and Pandey[20].

Grain length and grain breadth are important quality traits in rice. Positive heterosis for grain length coupled with negative heterosis for grain breadth is desirable in quality-oriented hybrid rice breeding because it results in a higher length-breadth ratio associated with long-slender grain type[21]. Fourteen hybrids exhibited significant positive standard heterosis for grain length, with the highest value of 5.14% recorded in HPR 2847 × HPR 1156. For grain breadth, eleven crosses showed significant negative standard heterosis, which is the preferred direction for quality improvement. Similar findings have been reported by Meena *et al*[22]. For the grain length-breadth ratio, eleven crosses exhibited significant positive standard heterosis, with the highest value of 15.76% recorded in HPR 2877 × HPR 1156. This result is in agreement with the findings of Kushal *et al*[23].

Among all the traits studied, spikelet fertility was identified as the most heterotic trait, with 15 crosses exhibiting significant desirable standard heterosis, followed by grain yield per plant and grain length, with 14 crosses each and effective tillers per plant, with 13 crosses. However, not all hybrids contributed equally to yield improvement, indicating that the genetic background of parental lines plays a decisive role in determining the magnitude and direction of heterosis.

A cross-trait analysis revealed that the most heterotic crosses for grain yield per plant were consistently associated with significant heterosis for several yield-contributing traits (Table 3). HPR 2887 × HPR 2656 recorded the highest mean grain yield per plant along with desirable standard heterosis for five associated traits, namely days to 75% maturity, plant height, spikelets per panicle, spikelet fertility and 1000-grain weight. HPR 2877 × HPR 2656 also exhibited high grain yield in combination with standard heterosis

Table 3. Comparative study of nine most heterotic crosses for grain yield per plant for mean, heterosis over standard check HPR 2656 and desirable heterosis for other traits

Crosses	Mean (Grain yield per plant)	Standard heterosis (%)	Desirable heterosis for other traits
HPR 2887 × HPR 2656	20.36	66.44*	DTM, PH, S/P, SF, TGW
HPR 2877 × HPR 2656	19.46	59.13*	PH, ET/P, TGW, GL, L/B
HPR 2877 × HPR 1156	18.44	50.79*	DTF, S/P, G/P, SF, GL, GB, L/B
HPR 2840 × HPR 1156	17.93	46.63*	TGW
HPR 2840 × HPR 2656	17.55	43.49*	ET/P, PL, TGW, GL, GB
HPR 2887 × HPR 1156	15.87	29.74*	DTF, ET/P, S/P, SF, TGW, GL, GB, L/B
HPR 2841 × HPR 1156	15.03	22.92*	ET/P, GB
HPR 2841 × HPR 2656	14.87	21.57*	SF
HPR 2866 × HPR 2656	14.32	17.09*	ET/P, S/P, SF, GL, GB, L/B

for plant height, effective tillers per plant, 1000-grain weight, grain length and grain length-breadth ratio. Similarly, HPR 2877 × HPR 1156 showed significant heterosis for days to 50% flowering, spikelets per panicle, grains per panicle, spikelet fertility, grain length, grain breadth and grain length-breadth ratio. These findings indicate that heterosis for grain yield per plant was strongly associated with the simultaneous expression of heterosis in its component traits, suggesting a cumulative and interactive contribution of several yield-related components to overall hybrid vigour. This may be attributed to the fact that the yield components collectively influence the total metabolic production of the plant, and improvement in one component may sometimes adversely affect another[24]. The close correspondence between high heterosis and superior mean performance of hybrids further corroborates the use of mean performance as a practical criterion for identifying superior crosses in rice hybrid breeding programmes.

A comparative evaluation of four promising crosses based on high SCA effects for grain yield per plant, GCA effects of the parents and significant desirable standard heterosis (Table 4) revealed that all four heterotic crosses, namely HPR 2887 × HPR 2656, HPR 2888 × HPR 1156, HPR 2866 × HPR 2656 and HPR 2847 × HPR 1156, showed high SCA effects for grain yield per plant along with significant desirable SCA effects for several component traits, including days to 75% maturity, plant height, effective tillers per plant, panicle length, spikelets per panicle, grains per panicle, spikelet fertility, 1000-grain weight, grain length and grain length-breadth ratio. High SCA effects coupled with at least one parent having high GCA are indicative of dominance and/or epistatic gene action governing the expression of these traits. Similar promising cross combinations with high SCA for grain yield per plant have also been reported by Garkoti and Pandey[25] and Kumar and Pandey[26]. Therefore, these cross combinations may be effectively exploited through pedigree selection in subsequent generations to isolate

Table 4. The best cross combinations based on standard heterosis, SCA and GCA effects for grain yield, along with other traits

Crosses	Standard heterosis	SCA effects	GCA effects of parents	Desirable heterosis for other traits	Desirable SCA effects for other traits
HPR 2887 × HPR 2656	66.44*	2.10*	Good × Average	DTM, PH, S/P, SF, TGW	DTM, PL, S/P, G/P
HPR 2888 × HPR 1156	5.48*	1.74*	Poor × Average	ET/P, TGW, GL, L/B	ET/P, PL, TGW, GL
HPR 2866 × HPR 2656	17.09*	1.54*	Poor × Average	ET/P, S/P, SF, GL, GB, L/B	PH, ET/P, S/P, GL, L/B
HPR 2847 × HPR 1156	2.21*	1.14*	Poor × Average	S/P, SF, GL, L/B	PL

early-generation transgressive segregants with superior grain yield, thereby accelerating the development of improved rice varieties.

CONCLUSION

Heterosis breeding supports increasing productivity, and accordingly, there is a vast scope of improvement in yield and other economic traits through hybrid breeding exploiting genetically diverse inbred lines[27]. In the present study, crosses HPR 2887 × HPR 2656, HPR 2877 × HPR 2656 and HPR 2877 × HPR 1156 showed reliably high heterosis across various grain yield and quality traits simultaneously and can be utilised in future breeding programs.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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AUTHORS CONTRIBUTION

UB: conducted the experiment, analyzed the data and wrote the original manuscript. DPP: Conceptualized and planned the research programme. PS: edited the manuscript.