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Research Article

Exploitation of Gene Action and Heterosis for Improvement of Agronomic and Grain Quality Traits in Basmati and Red Rice under Mid-Hill Himalayas

Om Prakash Raigar[1,2], Daisy Basandrai[1,3]*, Hausila Prasad Singh[1], Archana Kumari[2] and Ashwani Kumar Basandrai[4]

[1] *Department of Genetics and Plant Breeding, CSK HPKV, Palampur -176062, India*
[2] *Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana-141004, India*
[3] *ICAR-National Institute of Biotic Stress Management, Baronda, Raipur - 493225, India*
[4] *Department of Plant Pathology, CSK HPKV, Palampur-176062, India*

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****Corresponding author:***
E-mail: daisybasandrai@gmail.com

Abstract

Gene action, combining ability and heterosis estimates were worked out through Line × Tester analysis of 20 hybrids developed by crossing 10 basmati / aromatic lines with two red rice genotypes to determine the genetic architecture of various agronomic and grain quality traits for development of superior hybrids for Himalayan hill conditions. Analysis of variance revealed significant differences among genotypes, F1 crosses, lines and testers for all the traits in the present studies. Preponderance of non-additive gene effect for all the traits, realized by ratio of σ2GCA / σ2SCA, was less than unity and magnitude of dominance variance was higher than additive variance. It was also supported by boxplot and PCA analysis. The association analysis revealed that grain yield improvement was primarily driven by enhanced tillering ability and panicle architectural traits, and also association with head rice recovery traits. It suggested the feasibility of simultaneous improvement of grain yield and quality. The estimates of GCA effects indicated that male parent "HPR 2795" and female parents "RYT 3178", "HPR 2590", "HPR 2800-2" and "Pusa Basmati 1121" were good general combiners for agronomic traits. Three heterotic cross combinations, HPR 2590 × HPR 2795, RYT 3178 × HPR 2720, and HPR 2800-2 × HPR 2795 were identified based on *per se* performance, SCA effects and standard heterosis that can be further utilized for commercial hybrid rice breeding.

Keywords: Combining ability, Gene action, Heterosis, Red rice, Basmati, Association analysis

1. Introduction

Rice (*Oryza sativa* L.) is the world's primary stable food for more than half of the global population. It is cultivated on ~ 172 million hectares area with an annual production of ~820 million tons (FAOSTAT, 2024). India is the largest rice producer and consumer in the world. In India, rice was grown in an area of 51.42 million hectares, producing about 225 million tons of paddy during 2024 (https://ipad.fas.usda.gov/). Basmati rice plays a significant role in export due to its elongated grain and its quality and aroma traits. India exported 6065483.45 MT of basmati rice worth 5944.42 million US$ to various countries of world during 2024-25 (https://apeda.gov.in/BasmatiRice). Nowadays, unpredictable and changing climatic conditions pose a major threat in sustainable rice production. It was estimated that to meet out the food demand of ever-increasing human population which require ~ 950 million tons ofrice in 2050 (FAO, 2017; Ambikabathy *et al.,* 2019) and to achieve world's targeted production, it is essential to develop superior varieties with high yield potential.

Basmati rice has become popular due to its long slender grains with post-cooking soft and fluffy texture, special delicious organoleptic taste, superior aroma and distinct astringency. It has emerged as an important foreign exchange earner commodity. Among various rice strains, red rice is a unique treasure of Himachal Pradesh and has been classified as functional food because of its pharma-nutraceutical properties and richness in zinc and iron content. Among various disease, leaf and neck blast reduce tremendous grain yield and quality (Day *et al.,* 2020), and majority basmati type cultivars are susceptible to blast pathogen in mid hill Himalayas. Red rice confined resistant source for leaf and neck blast, hence the transfer of disease resistance trait from red to basmati, and grain quality traits from basmati to red rice, to concurrently improve two populations.

Breeding strategies for developing hybrids with improved yield potential require the expected level of heterosis and higher combining ability. Combining ability provides information on the nature and magnitude of gene effects that regulate agronomic and grain quality traits. Moreover, GCA measures additive gene effects and SCA elucidates non-additive gene action resulting from dominance, over-dominance and epistatic effects (Gramaje *et al.,* 2020; Saleem *et al.*, 2010; Sprague and Tatum, 1942). Combining ability test is also important for estimation of general combining ability (GCA) and specific combining ability (SCA) effects. The GCA effects was utilized for the identification of superior parents whereas SCA effect is a useful index to specify better performing cross combinations for exploitation of heterosis breeding or for isolation of transgressive segregants in development of pure lines (Gnanasekaran *et al.,* 2006).

The phenomenon of heterosis has been applied to rice breeding for improving grain yield since the early 1970s in China (Shull, 1914; Virmani, 1996; Cheng *et al.,* 2007 and Li *et al.* 2007). The cultivation of F_1 hybrids results in 15-20% yield advantage over conventional high yielding inbred varieties (Virmani, 1996; Gramaje *et al.,* 2020). A good hybrid manifests high amount of heterosis for commercial exploitation. The hybrid performance is measured normally in terms of per cent increase over standard check, to estimates hybrid vigour for exploiting commercial heterosis (Chaudhary, 1984; Swaminathan *et al.,* 1972; Ambikabathy *et al.* ,2019), and over better parent for measures of heterobeltiosis (Liang *et al.,* 1972; Gramaje *et al.* 2020).There is limited information on heterosis and combining ability in basmati / aromatic with red rice. Keeping in this view, the present investigation was under taken to determine the combining ability, gene action and heterosis for agronomic and grain quality traits in basmati / aromatic and red rice using line × tester mating design.

2. Materials and methods

2.1. Plant materials

The experimental materials comprised of a set of twenty hybrids derived from the crossing of ten basmati/aromatic lines (females) viz., HPR 2800-2, HPR 2373, Lakha Mandal, Super Basmati, Kasturi, HPR 3003, RYT 3178, HPR 2590, Pusa Basmati 1509 and Pusa Basmati 1121 with two red rice testers (males) HPR 2795 and HPR 2720 in line × tester fashion. The female parent Kasturi was also used as a standard check.

2.2. Field experiments and experimental design

The crossing block was raised during *Kharif* (rainy) season by using lines and the testers. The crossing was effected between the lines and testers in Line × Tester mating design of Kempthorne (1957) to develop hybrids. All the hybrids along with parental genotypes was evaluated in Randomized Complete Block Design (RCBD) with two replications at Rice and Wheat Research Center (RWRC), Malan (Kangra), Himachal Pradesh, during *Kharif* 2018. It is located at an elevation of 950 m a.m.s.l. 32˚1'N latitude and 76˚1'E longitude and the area represented sub-humid conditions in Mid-Hill Himalayas. The 30 days old seedlings were transplanted in plots of 2.25 m × 0.6 m (2 rows of 10 plants each) with plant to plant and row to row spacing 15 and 20 cm, respectively. All recommended package of practices of transplanted irrigated rice cultivation were followed.

2.3. Phenotypic evaluation for agronomic and grain quality traits

The F_1 hybrids along with 12 parental genotypes were characterized for 16 yield and yield related traits on randomly selected and tagged five plants per replication except for days to 50 % flowering (DFF), which were recorded on plot basis. The data were recorded for DFF, plant height (cm) (PH), ear bearing tillers per plant (EBT), panicle length (cm) (PL), grains per panicle (GP), spikelet fertility % (SF), 1000 seed weight (g) (TSW), grain yield per plant (g) (GY), grain length (mm) (GL), grain breadth (mm) (GB), L:B ratio (L:B), hulling % (HP), milling % (MP), head rice recovery % (HRR), protein % (PP) and amylose % (AP). The total nitrogen percentage was estimated from each genotypes using Kjeldahl method followed by its protein content % which was calculated by multiplying nitrogen percentage with protein conversion factor (6.25). Amylose content was estimated as per the procedure suggested by Juliano (1971).

2.4. Statistical Analysis

The good combiners among the parental genotypes and good cross combinations from the crosses were identified using GCA and SCA effects (Sprague and Tatum, 1942). For each cross combination, the heterobeltiosis and standard heterosis were estimated according to Liang *et al.* (1972) and Nadarajan and Gunasekaram (2005). The standard heterosis was determined using variety Kasturi as standard check. Analysis of variance for line x tester and combining ability, GCA and SCA effects and heterosis was estimated using "agricolae" package in R software version 4.5.2 (https://cran.rstudio.com/). The mean performance of all genotypes as well as heterosis was represented in the heatmap by using "pheatmap" package in R. Correlation analysis was represented on the form of Correlogram by using "GGally" packages in R. Principal component analysis was performed using "FactoMineR", "factoextra" and "ggplot2" packages of R.

3. Results and discussion

3.1. Analysis of variance for combining ability

The ANOVA of the line × tester set revealed that variation due to lines as well as testers were significant for all traits, indicating significant variation among parents for general combining ability. The analysis of variance for combining ability revealed highly significant differences among the genotypes in respect of most of the studied traits (Table 1). The significance differences among the lines (females) and testers (males) indicated the prevalence of additive variance for most of grain yield and quality traits. Significance differences among line × tester for all studied traits revealed that non-additive variance was important for all traits except PL, confirming the earlier finding of Panwar (2005).

3.2. Estimates of gene action

The predominance of SCA variance for all the traits suggested that dominance and epistatic gene interactions controlled these traits (Table 1). High dominance of genetic variance (σ^2D)was obtained for all traits except PL than the additive genetic variance (σ^2A) indicating the predominance of non-additive gene action, hence PL was controlled through additive gene action. The ratio of variances due to general combining ability (σ^2GCA) to specific combining ability (σ^2SCA)was less than unity which indicated that the gene effect was predominantly non-additive for all the traits. Average degree of dominance was more than unity indicating the preponderance of non-additive type of gene action. Hence, the heterosis breeding will be more effective in improvement of such characters. The present results were advocated with earlier studies for PL, EBT, PL, GY (Karthikeyan *et al.,* 2009; Suvathipriya and Kalaimagal, 2018; Kour *et al.,* 2019 and Nagamani *et al.,* 2022).

3.3. Association analysis for trait improvement

The correlation analysis was performed using "Correlogram" to assess the relationship among the agronomic and grain quality traits in parental genotypes and hybrids (Fig 1). The correlogram analysis showed scatter plots, variable distribution, boxplots and correlation coefficients for hybrids and parents. The correlation due to parental genotypes and hybrids was denoted with "P" and "H", respectively whereas, overall correlation was represented by "Corr" (Fig 1). The overall Grain yield had positive and significant correlation with PH, EBT, PL, GP, SF, HP, MP and HRR indicating that enhancement in the grain yield was highly driven by improved tillering ability, panicle architecture and superior milling quality traits. In parental genotypes (P), GY showed significant negative association with DFF, GL and L:B ratio, suggesting that early flowering and moderate grain size favored higher productivity. However GY was positively associated with GP and SF, indicating the importance of grain number and fertility percentage in yield determination. Head rice recovery had significant negative correlation with DFF and it was positively correlated with PH, GP,

Table 1: Analysis of variance for combining ability, and gene action for agronomic and grain quality traits

Source of variance/ Traits	Rep	Genotypes	Parent	Parent vs. Crosses	Crosses	Line	Tester	Line × Tester	Error	σ2 GCA	σ2 SCA	σ2 GCA / σ2 SCA	σ2A	σ2D	Average degree dominance
df	1	31	11	1	19	9	1	9	19						
DFF	1.6	91.38*	111.65*	77.63*	80.37*	137.40*	10.00*	31.17*	0.44	1.67	15.36	0.11	3.34	15.36	0.22
PH	6.02	859.45*	616.74*	8554.47*	594.97*	874.86*	206.48*	358.25*	10.46	8.03	173.89	0.04	16.06	173.89	0.092
EBT	0.26	2.75*	1.97*	13.74*	2.62*	3.48*	0.02	2.06*	0.58	0.019	0.73	0.03	0.04	0.74	0.05
PL	11.24	32.61*	25.62*	263.71*	24.49*	46.19*	1.76	5.31	5.9	0.65	-0.29	-2.21	1.3	-0.29	-4.42
GP	1.94	3044.00*	2170.29*	32961.33*	1975.25*	2381.45*	29.58	1785.23*	74.58	6.44	855.32	0.01	12.89	855.32	0.02
SF	5.01	97.10*	118.13*	495.16*	63.97*	76.07*	157.41*	41.49*	15.51	0.76	12.99	0.06	1.53	12.99	0.12
TSW	0.05	19.81*	32.52*	37.68*	11.51*	12.27*	11.91*	10.70*	0.02	0.027	5.34	0.01	0.06	5.34	0.01
GY	0.53	73.40*	8.70*	1094.40*	57.13*	49.09*	10.40*	70.35*	1.89	-0.44	34.23	-0.01	-0.89	34.23	-0.02
HP	0.21	38.86*	28.74*	94.53*	41.79*	64.68*	74.99*	15.21*	2.59	0.9	6.31	0.14	1.8	6.31	0.29
MP	0	36.50*	31.02*	115.14*	35.53*	50.73*	57.10*	17.95*	2.09	0.6	7.93	0.075	1.194	7.927	0.151
HRR	0.22	23.58*	20.33*	169.62*	17.77*	28.26*	5.99	8.59*	1.84	0.31	3.37	0.09	0.62	3.37	0.19
GL	0.11	1.17*	2.05*	3.97*	0.52*	0.90*	0.78*	0.11*	0.04	0.01	0.03	0.39	0.03	0.04	0.78
GB	0.01	0.03*	0.03*	0.04*	0.03*	0.04*	0	0.01*	0	0	0.01	0.07	0	0	0.14
L:B	0	0.54*	0.90*	2.65*	0.23*	0.29*	0.13*	0.17*	0.02	0	0.08	0.02	0	0.08	0.05
AP	2.2	5.33*	3.12*	9.50*	6.39*	7.50*	6.44*	5.28*	0.74*	0.04	2.27	0.02	0.08	2.27	0.03
PP	0.02	1.55*	2.30*	0.54*	1.17*	1.36*	0	1.11*	0.12*	0	0.49	0	0	0.49	0.01

Here, df: Degree of freedom, Rep: Replication, σ2 GCA: Variance due to general combining ability, σ2 SCA: Variance due to specific combining ability, σ2A: Additive genetic variance, σ2D: Dominance genetic variance, DFF: Days to 50% flowering, PH: Plant height, EBT: Ear bearing tillers, PL: Panicle length, GP: Grains per panicle, SF: Spikelet fertility %, TSW: 1000 seed weight, GY: Grain yield per plant, HP: Hulling %, MP: Milling %, HRR: Head rice recovery %, GL : Grain length, GB: Grain breadth, L:B: L:B ratio, AP: Amylose %, PP: Protein % and * mean Significant at p=0.05.

SF, GY, HP and MP suggesting that vigorous and high yielding genotypes also exhibited better milling quality. Additionally, the boxplots analysis revealed that early flowering in hybrids with higher number of EBT, PL, SF, TSW, HP, MP, HHR and AP compared to parents, demonstrated superior hybrid vigor (Fig 1). These results suggested the predominance of non-additive gene action and highlighted the potential of hybrids for simultaneous improvement of grain yield and quality traits.

3.4. Clustering pattern of lines, testers and hybrids

Principal component analysis was performed to determine variability among the lines, testers and hybrids based on PC's values. The variation explained by PC1 (39.20%) and PC2 (14.91%) was 54.11% inferring that more than half of the total phenotypic variation among the genotypes was explained by first two PCs (Fig 2). The grouping pattern showed that mostly hybrids were distributed positive side of PC1 and clustering was towards GY, EBT, PL, PH, GP, SF, HP, MP, HRR, GB and TSW which indicated strong association of hybrids with agronomic and grain quality enhancing traits (Fig 2). These findings also reflected the presence of non-additive gene action (SCA effect) that contributed to superior hybrid performance. Whereas, lines mainly distributed on the negative side of PC1 and associated with GL, L:B ratio and amylose %, indicated that parental lines contributed strongly towards grain quality traits due to reflection of additive gene action (GCA effects). Both the testers were positioned near the origin with moderate dispersion suggesting a balanced combining ability. Tester HPR 2795 appeared closer to productive hybrids that indicated it to be a good general combiner in a series of crosses.

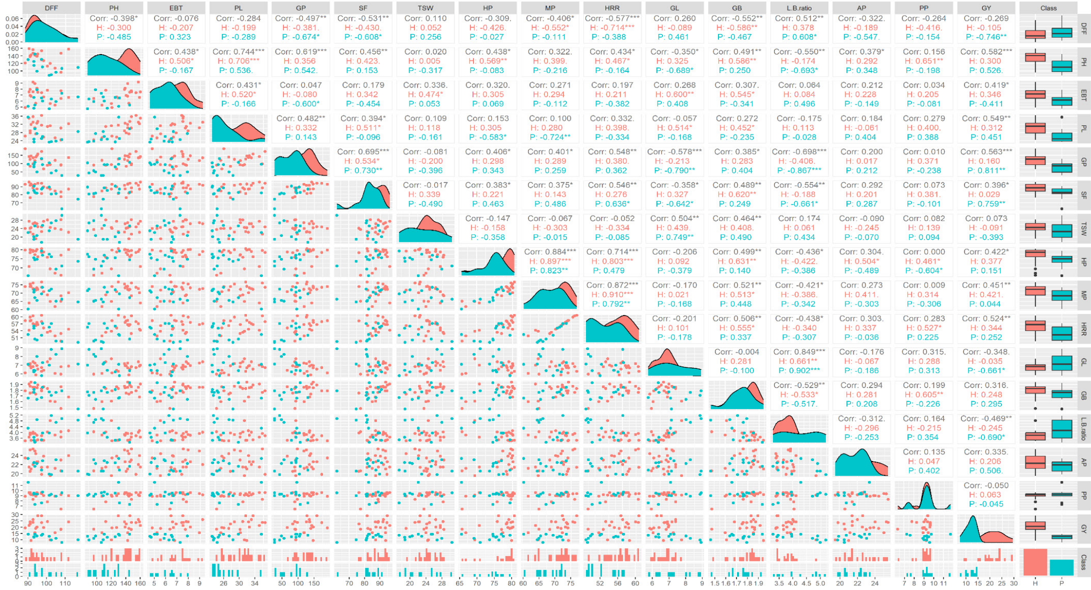

Fig 1: Correlation analysis among the agronomic and grain quality traits. Here, P indicates correlation due to parents, H represents correlation due to hybrids and Corr indicates overall correlation. The reddish-pink and bluish-green shaded distribution curves due to hybrids and parents for each traits, respectively. The lower side of correlation matrix showed scattering of hybrids and parents in reddish-pink and bluish-green shaded dots respectively for each traits.

3.5. Estimates of GCA effects

The negative GCA effects for earliness and plant height are desirable, whereas positive effect are desirable for other grain yield and quality. In the present investigation, on the basis significant GCA effect, three potential lines were identified viz., "Kasturi" for PL, GP, SF, GY, TSW, DFF, GB, PP ; "RYT 3178" for PL, GY, DFF, HP, MP, HRR and AP, and "Pusa Basmati 1121" for EBT, GY, TSW, GL and L:B (Table 2). Similarly, significant GCA effects were estimated for testers,and tester "HPR 2795" was observed to be the best general combiner for various traits viz., PL, SF, TSW, DFF and GL (Table 2). Hence there is a possibility of elucidating desirable progenies and fixing them in the early generation. Good general combiner for grain yield and quality traits was also reported by earlier workers also (Saleem*et al.,* 2010; Devi *et al.,* 2017; Suvathipriya and Kalaimagal, 2018 and Nagamani *et al.,* 2022).

3.6. Estimates of SCA effects

Among the twenty hybrids, the cross combination Lakha Mandal × HPR 2720 exhibited significant and desirable SCA effect values for EBT, GP, GY, TSW, DFF, HP, MP, GB and AP (Table 3). Three more crosses viz., HPR 2800-2 × HPR 2795, Super Basmati × HPR 2720 and HPR 3003 × HPR 2720 had significant and desirable SCA effect for grain yield and earliness traits. Six cross combinations viz., HPR 2800-2 × HPR 2795, Lakha Mandal × HPR 2722, Super Basmati × HPR 2720, HPR 3003 × HPR 2720, RYT 3178 × HPR 2720 and HPR 2590 × HPR 2795 exhibited positive significant SCA effect for GY, these results are in agreement with the earlier finding (Devi *et al.* 2017; Suvathipriya and Kalaimagal 2018). Three cross combinations namely, Lakha Mandal × HPR 2720, HPR 3003 × HPR 2795 and RYT 3178 × HPR 2795 exhibited desirable significant SCA effect value for amylose percent. The cross combinations *viz.,* Pusa Basmati 1509 × HPR 2795, Pusa Basmati 1121 × HPR 2720 and RYT 3178 × HPR 2795 showed positive significant SCA effect for protein percent (Table 3). These results are corroborated by the findings of various workers (Durai*et al.,* 2009; Saleem *et al.,* 2010; Sanghera and Hussain, 2012; Bhatti *et al.,* 2015 and Devi *et al.,* 2017).

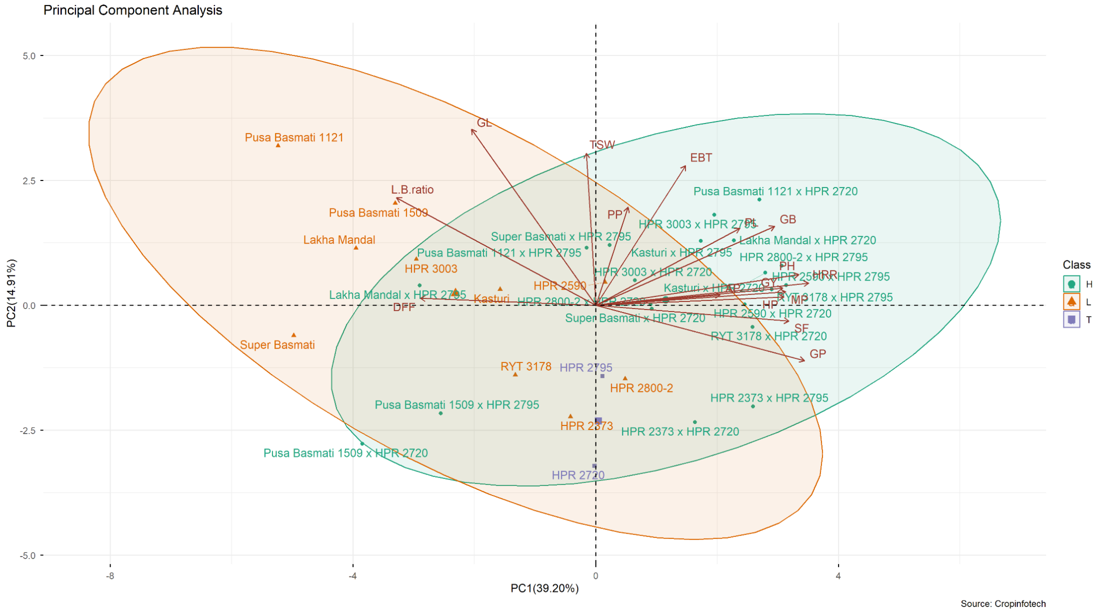

Fig 2: Clustering of parents and hybrids based on principal component analysis. Here, Hybrids represented with green color, Lines with orange and Testers with purple color.

3.7. Estimates of heterosis

Parent lines with high GCA effects for grain yield and quality are more likely to formed hybrids with satisfactory performance. The effects of both GCA and SCA are able to produce hybrids with better heterosis. Significant and desirable heterosis over the better parent and standard variety Kasturi were observed in the hybrid HPR 2800 × HPR 2795 for nine traits viz., GP (17.76, 30.57), GY (67.59, 69.75), HP (5.88, 21.70), MP (4.93, 24.81), HRR (6.87, 14.27) and AP (12.69, 8.13)(Table 4-5; Fig 3-4). In addition of this, four crosses viz., Pusa Basmati 1121 × HPR 2720, RYT 3178 × HPR 2720, HPR 2590 × HPR 2795 and Pusa Basmati 1121 × HPR 2795 showed desirable and significant heterosis for both heterobeltiosis and standard heterosis towards grain yield, quality and earliness traits. More than 25 % significant positive heterobeltiosis and standard heterosis was observed for grain yield in sixteen cross combinations viz., HPR 2590 × HPR 2795 (101.03, 103.63), RYT 3178 × HPR 2720 (115.24, 102.24), Pusa Basmati 1121 × HPR 2720 (93.31, 81.63), Pusa Basmati 1121 × HPR 2795 (67.93, 70.10), Super Basmati × HPR 2720 (79.93, 69.05), HPR 2800-2 × HPR 2795 (67.59, 69.75), RYT 3178 × HPR 2795 (63.45, 66.56), Kasturi × HPR 2720 (64.51, 64.51), HPR 3003 × HPR 2720 (67.29, 57.18), Kasturi × HPR 2795 (46.90, 48.79), Lakha Mandal × HPR 2720 (49.44, 40.41), HPR 2800-2 × HPR 2720 (46.47, 37.62), HPR 2373 × HPR 2795 (34.48, 36.22), HPR 2373 × HPR 2720 (41.26, 32.73), Super Basmati × HPR 2795 (25.86, 27.49), Pusa Basmati 1509 × HPR 2795 (36.06, 27.84), respectively (Table 4-5; Fig 3-4). Interestingly, the

Table 2: Estimates of GCA effects of parents for agronomic and grain quality traits

Parents	DFF	PH	EBT	PL	GP	SF	TSW	GY	HP	MP	HRR	GL	GB	L:B	AP	PP
Lines																
HPR 2800-2	-2.35 **	-3.63 *	0.27	-3.26 *	-26.41 **	2.7	0.28 **	1.34	2.72 **	2.15 **	1.39	0.04	0.08 **	-0.15 *	2.10 **	0.19
HPR 2373	-5.60 **	-3.80 *	-1.79 **	-3.71 **	40.19 **	-0.52	-2.99 **	-1.41	2.87 **	1.92 *	1.15	-0.75 **	-0.03	-0.38 **	1.47 **	-0.12
Lakha Mandal	1.15 **	-6.78 **	-0.19	1.39	-3.41	-1.03	0.80 **	-5.69 **	-1.86 *	-1.96 *	-0.5	0.59 **	-0.06 *	0.51 **	-1.35 **	0.38 *
Super Basmati	12.15 **	16.12 **	0.12	0.74	-9.11 *	-2.81	0.62 **	0.56	1.86 *	-1.68 *	-2.45 **	0.11	-0.02	0.1	1.05 *	0.11
Kasturi	-3.10 **	19.92 **	0.42	5.19 **	33.14 **	6.91 **	1.50 **	1.77 *	-2.01 *	-2.22 **	-0.12	0.1	0.06 *	-0.09	-1.77 **	0.62 **
HPR 3003	-4.60 **	4.77 **	0.88 *	-1.46	-22.21 **	-3.3	0.81 **	-1.66 *	1.14	2.06 *	1.3	0.33 **	0.01	0.14	0.33	0.53 **
RYT 3178	-2.10 **	1.97	-0.03	3.14 *	-10.76 *	-3.02	-2.68 **	5.66 **	3.42 **	5.32 **	4.34 **	-0.18	0.01	-0.12	1.00 *	-0.16
HPR 2590	-3.60 **	7.12 **	0.1	2.14	27.99 **	5.77 **	-0.03	-1.39	1.3	2.19 **	1.42 *	-0.14	0.13 **	-0.34 **	-0.61	0.3
Pusa Basmati 1509	8.65 **	-34.03 **	-1.20 **	-5.61 **	-18.41 **	-6.97 **	-0.90 **	-3.71 **	-10.18 **	-7.54 **	-5.53 **	-0.73 **	-0.25 **	0.12	-1.51 **	-1.34 **
Pusa Basmati 1121	-0.6	-1.68	1.45 **	1.44	-11.01 *	2.28	2.58 **	4.52 **	0.73	-0.24	-1	0.63 **	0.05	0.22 **	-0.7	-0.52 **
SE(gca for line)	0.33	1.62	0.38	1.21	4.32	1.97	0.07	0.69	0.8	0.72	0.67	0.09	0.03	0.07	0.43	0.17
SE(bet gca of lines)	0.47	2.29	0.54	1.72	6.11	2.78	0.1	0.97	1.13	1.02	0.95	0.13	0.04	0.1	0.61	0.24
CD(0.05%)	0.98	4.78	1.13	3.59	12.76	5.82	0.22	2.03	2.38	2.13	2	0.28	0.08	0.21	1.27	0.52
Testers																
HPR 2795	-0.50 **	-2.27 **	0.02	0.21	-0.86	1.98 *	0.55 **	-0.51	-1.37 **	-1.19 **	-0.39	0.14 **	0.01	0.06	0.4	0
HPR 2720	0.50 **	2.27 **	-0.02	-0.21	0.86	-1.98 *	-0.55 **	0.51	1.37 **	1.19 **	0.39	-0.14 **	-0.01	-0.06	-0.4	0
SE(gca for tester)	0.15	0.72	0.17	0.54	1.93	0.88	0.03	0.3	0.36	0.32	0.3	0.04	0.01	0.03	0.19	0.08
SE(bet gca of tester)	0.21	1.02	0.24	0.77	2.73	1.24	0.05	0.43	0.51	0.45	0.43	0.06	0.01	0.04	0.27	0.11
CD(0.05%)	0.43	2.14	0.5	1.6	5.71	2.6	0.1	0.91	1.06	0.95	0.89	0.12	0.03	0.09	0.57	0.23

Here, DFF: Days to 50% flowering, PH: Plant height, EBT: Ear bearing tillers, PL: Panicle length, GP: Grains per panicle, SF: Spikelet fertility %, TSW: 1000 seed weight, GY: Grain yield per plant, HP: Hulling %, MP: Milling %, HRR: Head rice recovery %, GL : Grain length, GB: Grain breadth, L:B: L:B ratio, AP: Amylose %, PP: Protein % and * mean Significant at p=0.05, ** mean Significant at p=0.01.

Table 3: Estimates of SCA effects of hybrids for agronomic and grain quality traits

Cross	DFF	PH	EBT	PL	GP	SF	TSW	GY	HP	MP	HRR	GL	GB	L:B	AP	PP
HPR 2800-2×HPR 2795	-3.00 **	7.52 **	0.6	1.34	29.71 **	-1.19	-3.05 **	2.81 **	2.01	3.50 **	2.70 *	0.24	-0.01	0.14	0.3	0.16
HPR 2800-2×HPR 2720	3.00 **	-7.52 **	-0.6	-1.34	-29.71 **	1.19	3.05 **	-2.81 **	-2.01	-3.50 **	-2.70 *	-0.24	0.01	-0.14	-0.3	-0.16
HPR 2373×HPR 2795	-2.25 **	-9.05 **	-0.38	-0.81	25.91 **	3.54	1.91 **	0.76	1.62	2.26 *	1.45	-0.02	0.02	-0.05	-0.87	-0.03
HPR 2373×HPR 2720	2.25 **	9.05 **	0.38	0.81	-25.91 **	-3.54	-1.91 **	-0.76	-1.62	-2.26 *	-1.45	0.02	-0.02	0.05	0.87	0.03
LakhaMandal×HPR 2795	4.00 **	-6.83 **	-1.30 *	-0.81	-25.29 **	-2.08	-1.46 **	-4.61 **	-3.96 **	-2.96 **	-1.55	0.25	-0.13 **	0.45 **	-1.91 **	-0.22
LakhaMandal×HPR 2720	-4.00 **	6.83 **	1.30 *	0.81	25.29 **	2.08	1.46 **	4.61 **	3.96 **	2.96 **	1.55	-0.25	0.13 **	-0.45 **	1.91 **	0.22
Super Basmati×HPR 2795	-1.50 **	-3.23	0.53	-1.26	-20.39 **	-3.65	2.48 **	-2.46 *	-0.15	0.28	-0.53	-0.18	0.08	-0.27 *	-0.88	0.11
Super Basmati×HPR 2720	1.50 **	3.23	-0.53	1.26	20.39 **	3.65	-2.48 **	2.46 *	0.15	-0.28	0.53	0.18	-0.08	0.27 *	0.88	-0.11
Kasturi×HPR 2795	-2.75 **	5.17 *	0.03	-0.91	-14.04 *	-1.12	0.77 **	-0.62	-2.50 *	-3.53 **	-1.48	0	0.05	-0.11	0.39	-0.01
Kasturi×HPR 2720	2.75 **	-5.17 *	-0.03	0.91	14.04 *	1.12	-0.77 **	0.62	2.50 *	3.53 **	1.48	0	-0.05	0.11	-0.39	0.01
HPR 3003×HPR 2795	1.75 **	3.32	0.97	1.04	17.61 **	6.39 *	0.77 **	-2.99 **	0.87	0.39	-0.41	0.02	0.04	-0.08	1.81 **	-0.1
HPR 3003×HPR 2720	-1.75 **	-3.32	-0.97	-1.04	-17.61 **	-6.39 *	-0.77 **	2.99 **	-0.87	-0.39	0.41	-0.02	-0.04	0.08	-1.81 **	0.1
RYT 3178×HPR 2795	-1.75 **	11.02 **	0.5	1.84	-13.64 *	1.47	-1.15 **	-2.12 *	0.93	0.9	0.31	0.14	-0.05	0.19	1.60 *	-0.57 *
RYT 3178×HPR 2720	1.75 **	-11.02 **	-0.5	-1.84	13.64 *	-1.47	1.15 **	2.12 *	-0.93	-0.9	-0.31	-0.14	0.05	-0.19	-1.60 *	0.57 *
HPR 2590×HPR 2795	2.25 **	3.77	0.33	0.54	6.31	-1.44	-0.30 *	10.38 **	-0.46	0.26	-0.54	-0.2	-0.04	-0.04	0.37	0.07
HPR 2590×HPR 2720	-2.25 **	-3.77	-0.33	-0.54	-6.31	1.44	0.30 *	-10.38 **	0.46	-0.26	0.54	0.2	0.04	0.04	-0.37	-0.07
Pusa Basmati 1509×HPR 2795	-1.00 *	7.72 **	-0.57	0.29	15.01 *	1.66	-0.32 **	-0.84	1.91	-0.44	1.53	-0.1	0.05	-0.17	-0.13	1.27 **
Pusa Basmati 1509×HPR 2720	1.00 *	-7.72 **	0.57	-0.29	-15.01 *	-1.66	0.32 **	0.84	-1.91	0.44	-1.53	0.1	-0.05	0.17	0.13	-1.27 **
Pusa Basmati 1121×HPR 2795	4.25 **	-19.43 **	-0.72	-1.26	-21.19 **	-3.56	0.35 **	-0.32	-0.27	-0.68	-1.48	-0.14	-0.02	-0.04	-0.67	-0.68 *
Pusa Basmati 1121×HPR 2720	-4.25 **	19.43 **	0.72	1.26	21.19 **	3.56	-0.35 **	0.31	0.27	0.68	1.48	0.14	0.02	0.04	0.67	0.68 *
SE(sca effects)	0.47	2.28	0.53	1.71	6.1	2.78	0.1	0.97	1.13	1.02	0.95	0.13	0.03	0.1	0.6	0.24
SE(bet sca effects)	0.66	3.23	0.76	2.42	8.63	3.93	0.14	1.37	1.61	1.44	1.35	0.18	0.05	0.14	0.86	0.35
CD (0.05%)	1.38	6.75	1.59	5.07	18.04	8.23	0.31	2.87	3.36	3.02	2.83	0.39	0.11	0.3	1.79	0.73

Here, DFF: Days to 50% flowering, PH: Plant height, EBT: Ear bearing tillers, PL: Panicle length, GP: Grains per panicle, SF: Spikelet fertility %, TSW: 1000 seed weight, GY: Grain yield per plant, HP: Hulling %, MP: Milling %, HRR: Head rice recovery %, GL : Grain length, GB: Grain breadth, L:B: L:B ratio, AP: Amylose %, PP: Protein % and * mean Significant at p=0.05, ** mean Significant at p=0.01.

Table 4: Estimates of heterobeltiosis for agronomic and grain quality traits

CROSS	DFF	PH	EBT	PL	GP	SF	TSW	GY	HP	MP	HRR	GL	GB	L:B	AP	PP
HPR 2800-2×HPR 2795	-2.66 **	-4.77	20.45	-3.36	17.76 *	0.96	-11.23 **	67.59 **	5.88 **	4.93 *	6.87 **	12.45 **	-3.37	11.59 **	12.69 **	-1.42
HPR 2800-2×HPR 2720	1.03	-2.79	1.52	2.39	-47.46 **	-0.79	36.43 **	46.47 **	-0.74	-1.49	-1.37	2.96	2.76	-1	6.39	-4.91
HPR 2373×HPR 2795	-5.32 **	-16.34 **	-7.81	-12.08	76.45 **	9.09	-4.53 **	34.48 **	5.86 **	4.71 *	6.04 *	-4.52	-7.25 *	-6.29	4.32	-5.05
HPR 2373×HPR 2720	-3.08 **	9.73 **	-13.94	9.16	6.69	-5.82	1.88 *	41.26 **	-0.07	1.7	2.18	-8.33 *	-1.71	-6.57	8.51 *	-4.51
LakhaMandal×HPR 2795	-2.86 **	-16.86 **	-5.34	5.03	-12.15	4.75	-11.74 **	-32.07 **	-6.79 **	-3.55	6.69 *	-6.18 *	-16.84 **	2.55	-15.13 **	2.81
LakhaMandal×HPR 2720	-9.52 **	5.76 *	24.58 *	29.48 **	12.54	0.06	-5.20 **	49.44 **	1.01	5.35 **	10.56 **	-15.52 **	4.56	-19.15 **	-2	7.81 *
Super Basmati×HPR 2795	-7.73 **	1.45	15.3	1.34	-12.9	0.72	12.02 **	25.86 **	3.33	1.67	4.85	-4.34	-3.89	-24.25 **	6.29	2.39
Super Basmati×HPR 2720	-4.29 **	20.50 **	-1.19	13.57	4.38	-0.19	17.53 **	79.93 **	0.9	1.09	4.87	-3.22	0.9	-15.42 **	15.28 **	-0.11
Kasturi×HPR 2795	-3.19 **	9.88 **	41.49 **	-1.41	32.52 **	15.47 **	8.75 **	46.90 **	-5.01 *	-4.79 *	3.44	-1.41	-1.04	-14.57 **	-8.08 *	-17.31 **
Kasturi×HPR 2720	0	16.99 **	13.63	2.54	32.00 **	8.07	12.10 **	64.51 **	-1.02	5.81 **	10.55 **	-5.28	7.21 *	-12.12 **	-14.84 **	-17.22 **
HPR 3003×HPR 2795	-1.05	-1.87	12.97	1.68	10.37	12.23 *	6.02 **	6.9	3.56	7.40 **	12.50 **	-9.26 **	-4.15	-19.67 **	12.26 **	1.51
HPR 3003×HPR 2720	-6.15 **	6.83 *	-12.22	1.09	-34.92 **	-12.27 *	16.62 **	67.29 **	-1.3	6.31 **	11.84 **	-13.26 **	4.8	-18.55 **	-7.63 *	3.61
RYT 3178×HPR 2795	-8.37 **	1.52	41.86 **	19.80 **	-8.13	-1.11	-15.45 **	63.45 **	2.75	6.44 **	8.82 **	-1.93	-9.07 **	-0.88	17.53 **	-8.94 *
RYT 3178×HPR 2720	-3.94 **	-1.19	-0.46	25.90 **	-2.08	-8.83	-1.76 **	115.24 **	1.5	7.26 **	9.09 **	-9.86 **	3.68	-13.11 **	3.08	3.59
HPR 2590×HPR 2795	-2.55 **	0.07	25.00 *	12.08	46.73 **	6.58	-2.59 **	101.03 **	-1.05	-1.63	-0.97	-10.14 **	-2.33	-12.12 **	-1.03	-3.8
HPR 2590×HPR 2720	-6.12 **	8.28 **	4.13	22.22 *	12.38	5.36	-4.53 **	-34.59 **	0.59	0.91	2.28	-8.36 *	5.15	-13.01 **	-7.83 *	-5.24
Pusa Basmati 1509×HPR 2795	1.95 **	-25.64 **	-16.27	-14.77	11.5	2.11	-10.12 **	7.59	-12.03 **	-14.63 **	-9.27 **	-31.04 **	-17.36 **	-26.23 **	-2.08	-3.88
Pusa Basmati 1509×HPR 2720	4.88 **	-26.16 **	-1.99	-2.79	-30.00 **	-11.06 *	-11.81 **	36.06 **	-16.90 **	-10.11 **	-13.27 **	-32.01 **	-13.20 **	-21.68 **	-0.7	-31.21 **
Pusa Basmati 1121×HPR 2795	-6.94 **	-22.05 **	7.07	3.69	-15.42 *	6.95	-7.04 **	67.93 **	1.65	2.39	5.82 *	-16.79 **	-5.18	-18.81 **	-0.86	-18.60 **
Pusa Basmati 1121×HPR 2720	-13.89 **	19.28 **	26.29 *	31.47 **	3.54	5.55	-12.94 **	93.31 **	-0.39	4.54 *	9.48 **	-16.68 **	3.36	-19.32 **	5.82	-4.39

Table 5: Standard heterosis for agronomic and grain quality traits

CROSS	DFF	PH	EBT	PL	GP	SF	TSW	GY	HP	MP	HRR	GL	GB	L:B	AP	PP
HPR 2800-2×HPR 2795	-2.66 **	-4.77	20.45	-3.36	17.76 *	0.96	-11.23 **	67.59 **	5.88 **	4.93 *	6.87 **	12.45 **	-3.37	11.59 **	12.69 **	-1.42
HPR 2800-2×HPR 2720	1.03	-2.79	1.52	2.39	-47.46 **	-0.79	36.43 **	46.47 **	-0.74	-1.49	-1.37	2.96	2.76	-1	6.39	-4.91
HPR 2373×HPR 2795	-5.32 **	-16.34 **	-7.81	-12.08	76.45 **	9.09	-4.53 **	34.48 **	5.86 **	4.71 *	6.04 *	-4.52	-7.25 *	-6.29	4.32	-5.05
HPR 2373×HPR 2720	-3.08 **	9.73 **	-13.94	9.16	6.69	-5.82	1.88 *	41.26 **	-0.07	1.7	2.18	-8.33 *	-1.71	-6.57	8.51 *	-4.51
LakhaMandal×HPR 2795	-2.86 **	-16.86 **	-5.34	5.03	-12.15	4.75	-11.74 **	-32.07 **	-6.79 **	-3.55	6.69 *	-6.18 *	-16.84 **	2.55	-15.13 **	2.81
LakhaMandal×HPR 2720	-9.52 **	5.76 *	24.58 *	29.48 **	12.54	0.06	-5.20 **	49.44 **	1.01	5.35 **	10.56 **	-15.52 **	4.56	-19.15 **	-2	7.81 *
Super Basmati×HPR 2795	-7.73 **	1.45	15.3	1.34	-12.9	0.72	12.02 **	25.86 **	3.33	1.67	4.85	-4.34	-3.89	-24.25 **	6.29	2.39
Super Basmati×HPR 2720	-4.29 **	20.50 **	-1.19	13.57	4.38	-0.19	17.53 **	79.93 **	0.9	1.09	4.87	-3.22	0.9	-15.42 **	15.28 **	-0.11
Kasturi×HPR 2795	-3.19 **	9.88 **	41.49 **	-1.41	32.52 **	15.47 **	8.75 **	46.90 **	-5.01 *	-4.79 *	3.44	-1.41	-1.04	-14.57 **	-8.08 *	-17.31 **
Kasturi×HPR 2720	0	16.99 **	13.63	2.54	32.00 **	8.07	12.10 **	64.51 **	-1.02	5.81 **	10.55 **	-5.28	7.21 *	-12.12 **	-14.84 **	-17.22 **
HPR 3003×HPR 2795	-1.05	-1.87	12.97	1.68	10.37	12.23 *	6.02 **	6.9	3.56	7.40 **	12.50 **	-9.26 **	-4.15	-19.67 **	12.26 **	1.51
HPR 3003×HPR 2720	-6.15 **	6.83 *	-12.22	1.09	-34.92 **	-12.27 *	16.62 **	67.29 **	-1.3	6.31 **	11.84 **	-13.26 **	4.8	-18.55 **	-7.63 *	3.61
RYT 3178×HPR 2795	-8.37 **	1.52	41.86 **	19.80 **	-8.13	-1.11	-15.45 **	63.45 **	2.75	6.44 **	8.82 **	-1.93	-9.07 **	-0.88	17.53 **	-8.94 *
RYT 3178×HPR 2720	-3.94 **	-1.19	-0.46	25.90 **	-2.08	-8.83	-1.76 **	115.24 **	1.5	7.26 **	9.09 **	-9.86 **	3.68	-13.11 **	3.08	3.59
HPR 2590×HPR 2795	-2.55 **	0.07	25.00 *	12.08	46.73 **	6.58	-2.59 **	101.03 **	-1.05	-1.63	-0.97	-10.14 **	-2.33	-12.12 **	-1.03	-3.8
HPR 2590×HPR 2720	-6.12 **	8.28 **	4.13	22.22 *	12.38	5.36	-4.53 **	-34.59 **	0.59	0.91	2.28	-8.36 *	5.15	-13.01 **	-7.83 *	-5.24
Pusa Basmati 1509×HPR 2795	1.95 **	-25.64 **	-16.27	-14.77	11.5	2.11	-10.12 **	7.59	-12.03 **	-14.63 **	-9.27 **	-31.04 **	-17.36 **	-26.23 **	-2.08	-3.88
Pusa Basmati 1509×HPR 2720	4.88 **	-26.16 **	-1.99	-2.79	-30.00 **	-11.06 *	-11.81 **	36.06 **	-16.90 **	-10.11 **	-13.27 **	-32.01 **	-13.20 **	-21.68 **	-0.7	-31.21 **
Pusa Basmati 1121×HPR 2795	-6.94 **	-22.05 **	7.07	3.69	-15.42 *	6.95	-7.04 **	67.93 **	1.65	2.39	5.82 *	-16.79 **	-5.18	-18.81 **	-0.86	-18.60 **
Pusa Basmati 1121×HPR 2720	-13.89 **	19.28 **	26.29 *	31.47 **	3.54	5.55	-12.94 **	93.31 **	-0.39	4.54 *	9.48 **	-16.68 **	3.36	-19.32 **	5.82	-4.39

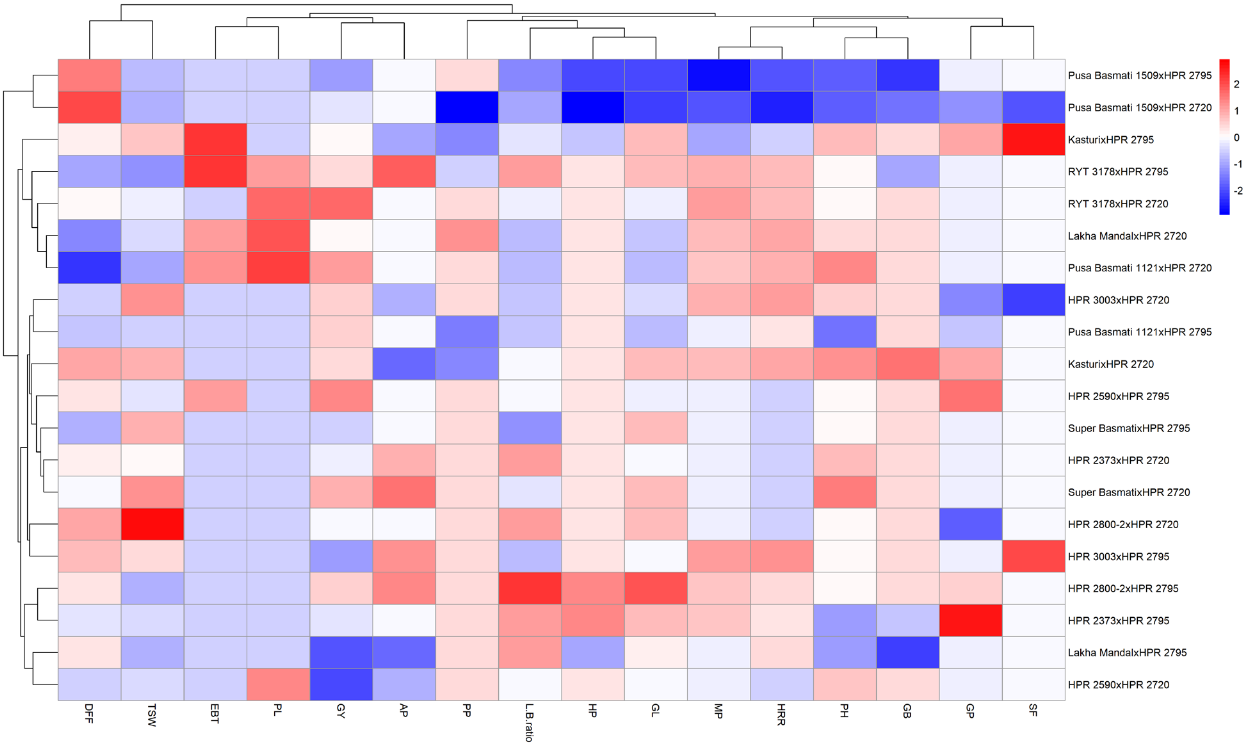

Fig 3: Estimates of better parent heterosis for agronomic and grain quality traits

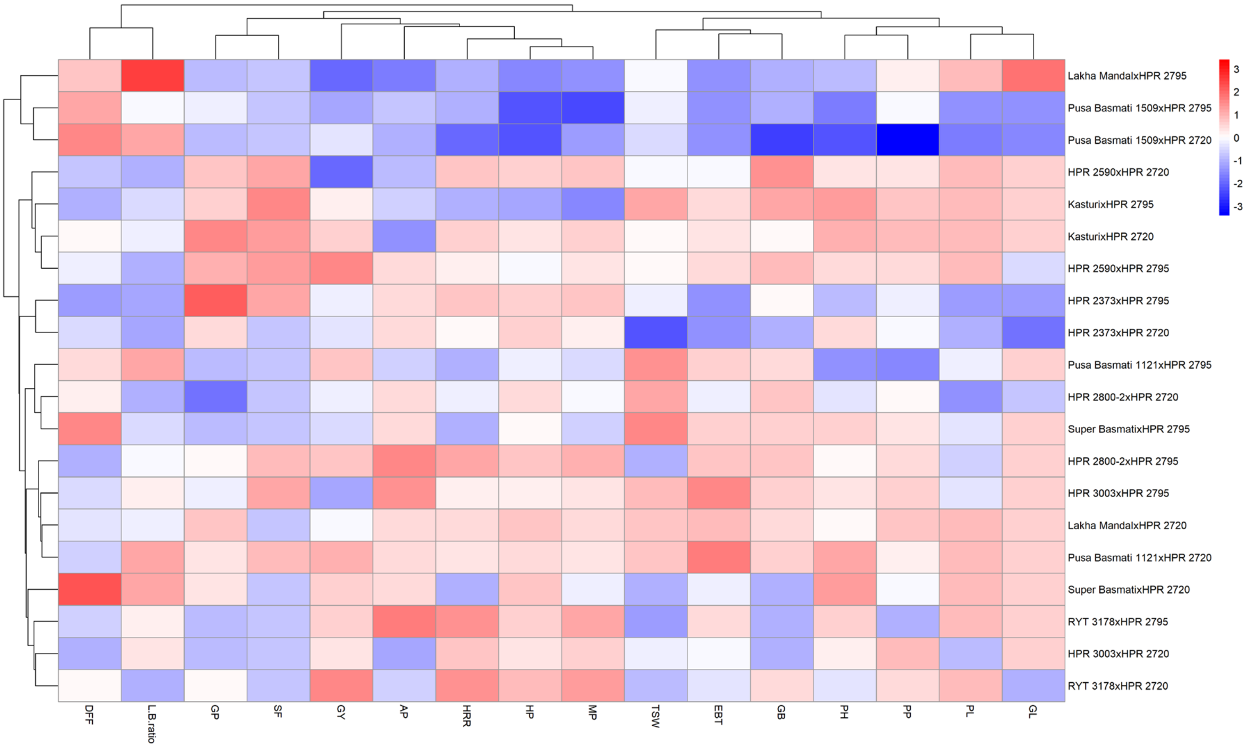

Fig 4: Estimates of standard heterosis for agronomic and grain quality traits

present results were corroborated by the earlier finding (Bhatti *et al.*, 2015 and Devi *et al.*, 2017; Kour *et al.*, 2019; Ambikabathy *et al.*, 2019). Three hybrids RYT 3178 × HPR 2795, HPR 2800-2 × HPR 2795 and HPR 3003 × HPR 2795 showed positive significant heterobeltiosis and standard heterosis for amylose per cent (Saleem *et al.*, 2010; and Devi *et al.*, 2017).

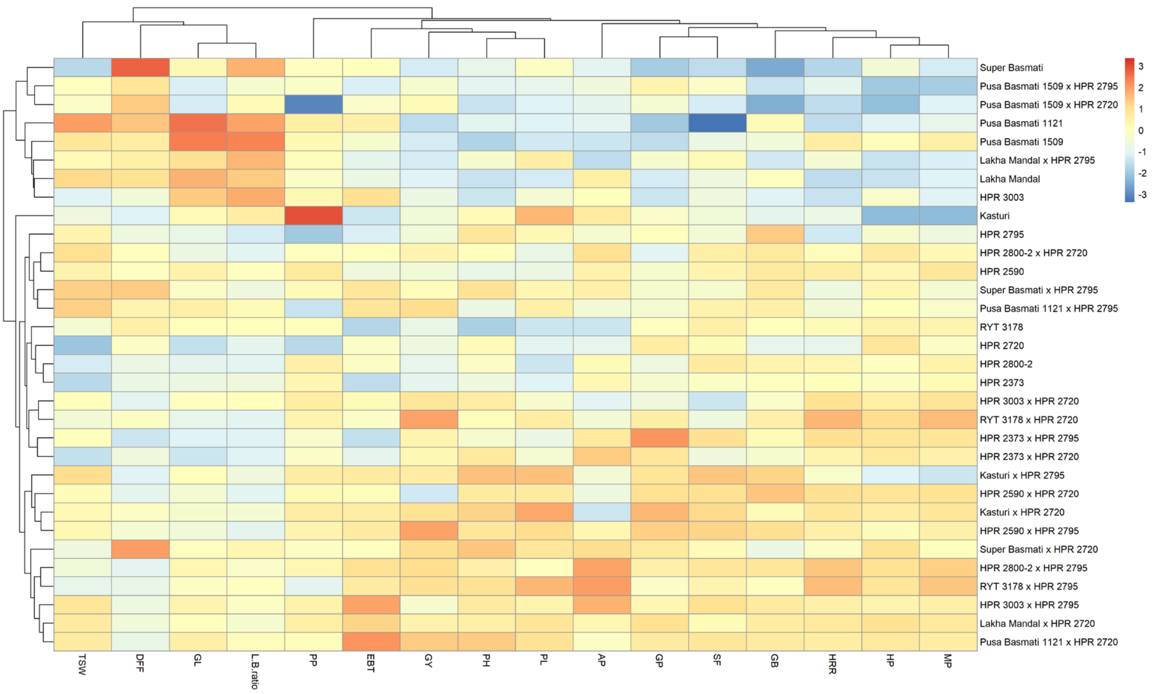

Fig 5: Mean performance of lines, testers and their hybrids for agronomic and grain quality traits

3.8. Selection of promising heterotic cross combination

The heterotic cross combinations were selected based on the mean (*per se*) performance (Fig 5), SCA effects (Table 3) and standard heterosis (Table 5). Out of twenty cross combinations only three hybrids namely HPR 2590 × HPR 2795 (29.15 g/plant), RYT 3178 × HPR 2720 (28.95 g/plant) and HPR 2800-2 × HPR 2795 (24.35 g/plant) with standard heterosis 103.63, 102.24 and 69.75%, respectively were found to be the promising heterotic combinations for grain yield and quality traits. Hence, these hybrids may be for exploited for commercial heterosis breeding in rice.

Conclusion

The analysis of variance revealed significant differences among genotypes for all the traits studied, suggesting the prevalence of wide range of genetic variability in the material. The ratio of σ^2GCA / σ^2SCA was less than unity, indicating that the gene effect was predominantly non-additive type for all the traits. The magnitude of dominance variance was higher than the additive variance for all the traits except for panicle length which indicated the preponderance of non-additive gene action suggesting the exploitation of hybrid vigor. Additionally, the performance of hybrids in boxplot analysis as well as the distribution of hybrids in PCA bi-plot strongly supported the preponderance of non-additive gene action. The association analysis revealed that grain yield improvement was primarily driven by enhanced tillering ability and panicle architectural traits. The positive association between GY and HRR suggests the feasibility of simultaneous improvement of grain yield and quality. PCA explained 54.11% of the total variation through the first two PCs, which clearly differentiated hybrids from parental line. The estimates of GCA effects revealed that the lines RYT 3178, Pusa Basmati 1121 and Kasturi had good GCA for agronomic traits, whereas the lines HPR 3003, HPR 2373, HPR 2590, HPR 2800-2 and Kasturi for earliness.

Tester HPR 2795 was found as a good general combiner for most of the agronomic traits. Moreover, SCA effects helped in the identification of best cross combinations associated with agronomic and grain quality traits. Three promising heterotic cross combinations, namely HPR 2590 × HPR 2795, RYT 3178 × HPR 2720, and HPR 2800-2 × HPR 2795 were identified based on the mean performance, significant SCA effects and high standard heterosis that can be further exploited for commercial hybrid rice breeding. The present studies demonstrated the effectiveness of Line × Tester design for identification superior heterotic cross combination and highlighted the scope of rice hybrid breeding.

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Authors' Contributions

OP, DB, AKB conceptualization and execution of research, compilation and editing of the manuscript; AM, ArK, HPS helped in the statistical analysis of the findings and in editing of the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical Approval:

The article doesn't contain any study involving ethical approval.

Use of Generative AI or AI assisted technologies:

Authors declare that no Generative AI or AI assisted technologies have been used in preparation of this manuscript.

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