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Research Article

Generation mean analysis for yield and quality traits in basmati rice (*Oryza sativa* L.)

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Abstract
The present study explicates the genetics of 15 (eight yield traits and seven quality traits) basmati traits by employing generation mean analysis in six crosses of basmati rice crosses. Generation mean analysis is a biometrical tool which not only can identify presence of epistasis but also explain its types and role in inheritance of traits. Simple and Joint scaling test indicated role of epistasis in inheritance all the six crosses except for alkali spread value in the cross HUBR10-9 x PuB-1509, which showed dominance gene action. 90 individual tests each of simple and joint scaling tests divulged role of one or the other type of epistasis in inheritance of different traits in all the six crosses except for alkali spread value in cross HUBR10-9 x PuB-1509, which showed dominance gene action. Complementary digenic interaction were observed for yield per plant trait; however, other traits showed equal importance of complementary and duplicate digenic interaction in inheritance of different traits examined in the present study. Most of the traits were governed by epistatic gene action which suggested that traits of such population can be improved when the selection process is delayed. However, selection can be practiced at early stage of breeding program in such traits which were governed by additive gene action.

Keywords: Basmati, complementary and duplicate interaction, epistasis, generation mean analysis

INTRODUCTION

Basmati is an important crop in India as it one of the major agriculture-based export commodities fetching billions of dollars every year. In year 2022-23 India exported 4.6 million MT of basmati and gained 4.79 billion US dollars, which is the second highest among any agriculture commodity exported from the country, following buffalo meat (APEDA, 2022-23). However, the quantity of non-basmati exported was approximately 3.9 times less than basmati. Besides its economic importance, basmati is famous among its consumers, every other person prefers basmati over non-basmati rice. Few of the many reasons behind the consumers enamor towards basmati are slender kernel, increased length after cooking, cooked rice texture and aroma.

There are 34 basmati varieties available in India among which only few are exported *viz*., Tarori Basmati, PuB-1, PuB-1121 and PuB-1509. A crop which affects socio-economic structure of India so magnanimously demands more variety to be developed. A rice variety can be called as basmati only when it meets all the standards stipulated by Export of Basmati Rice (Quality Control and Inspection) Rules, 2003 (Sharma *et al*., 2021). Besides this, a rice variety can be called as basmati variety only when one of the parents used in breeding program is a traditional basmati variety (Jaiswal and Sharma, 2022). Basmati Rules 2003 define two types basmati varieties *viz*., traditional and evolved (Sharma *et al*. 2021). In general, traditional basmati possess excellent quality traits but

gives poor yield (Ahuja *et al*. 1995, Nagaraju 2002 and Siddiq *et al*. 2012), poor general combining ability (Ahuja *et al*. 1995), scarce genetic variability (Siddiq *et al*. 2012). Poor general combining ability in traditional basmati varieties have been reported by Kour *et al*. (2019) and Sharma and Jaiswal (2020a).

Basmati breeding program is a complex task. Its intricacy can be worked out by decerning the nature of gene action and gene interaction which governs inheritance of different traits of basmati rice. Hence, a study was undertaken using six best performing F_1s of diallel mating design conducted in previous season which further were advanced to obtain F_2, B_1 and B_2 to study gene action of yield and quality traits by employing Generation Mean Analysis

MATERIALS AND METHODS

Generation of experimental material for the present study was carried out with the help of nine Basmati varieties in two cropping season *Kharif* 2016 and 2017 at Agriculture Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh. In *Kharif* 2016, nine varieties of Basmati namely, Type-1(T-3), Basmati-370, Taraori Basmati (TB), Ranbir Basmati, Pusa Basmati (PuB-1), CSR-30, Pusa Basmati-1121 (PuB-1121), HUBR 10-9 and Pusa Basmati 1509 (PuB-1509) were subjected to diallel mating design (without reciprocals) which resulted in 36 F_1s. In *Kharif* 2017, nine parents and single lines of 10 plants each of 36 F1s were raised in a separate crossing block. In *Kharif* 2017, work plan was done in two phases. In the first phase, 6 F_1s out of 36 F_1s were selected at early stage of plant growth based on number of tillers. F_2 seeds of these selected 6 F_1s were harvested separately. In the second phase: B_1, B_2 were developed of the six selected crosses; by crossing the F_1 with P_1 and P_2 respectively. And at the same time, fresh F_1s were also developed in the crossing block. Thus, by the end of *kharif* , 2017, six generations of each of the six selected crosses (Cross I-VI) constituting of P_1, P_2, F_1, F_2, B_1 and B_2 were obtained.

During *Kharif* 2018, P_1, P_2, F_1s, F_2s, B_1s and B_2s of the six selected crosses namely: T-3 x PuB-1 (**Cross I**); T-3 x PuB-1121 (Cross II); PuB-1 x HUBR10-9 (Cross III), CSR-30 x HUBR10-9 (Cross IV), PuB-1121 x HUBR10-9 (Cross V) and HUBR10-9 x PuB-1509 (Cross VI) were raised in Compact Family Block Design in three replications. Plant to plant and row to row distance was kept 10 x15 cm and all package of practice for Basmati rice was followed to raise a healthy crop and a better crop stand. Observations were recorded on eight yield traits (days to 50 percent flowering, days to maturity, plant height, panicle length, number of panicles per plant, number of grains per panicle, 100-grain weight, yield per plant) and seven grain quality traits (kernel length, kernel breadth, kernel length after cooking, kernel breadth after cooking, alkali spreading value, aroma and amylose content). From each cross, data was collected on 30 P_1, P_2 and F_1; 60 B_1 and B_2; and 150 F_2 plants from all the three replications. The traits were evaluated following guidelines and standard protocol given in **S**tandard Evaluation System, IRRI, 2013.

Aroma was tested by five-member panel. To measure the presence or absence of aroma in the experimental material, the polished rice kernels were kept in 1.7% KOH solution in a petri dish for 10 minutes at 25-30°C. After ten minutes, the panel members smelled and assessed the strength of aroma in comparison to aroma of Taraori basmati. Taraori basmati was taken as standard to compare the strength of aroma present in each sample and were scaled in order of 1to3, where 1= non aromatic, 2= slightly aromatic and 3= strongly aromatic. The average of five panel members for each sample was taken as final reading of aroma.

ANOVA for Compact Family Block Design were carried out by following Panse and Sukhatme (1967). Further, ANOVA of each of the six crosses were calculated separately (Panse and Sukhatme). Presence of epistasis in the inheritance of traits was examined by using simple (Marther, 1949) and Joint Scaling tests (Cavalli, 1952). Accordingly, the genetics of traits which showed allelic interaction were studied by using 6-parameter model (Hayman, 1958), while, the inheritance of traits which showed non-allelic interaction were studied by applying 3-paramter model proposed by Jinks and Jones (1958).

Estimation of presence of epistasis: To observe presence of epistasis in governance of different traits, two scaling tests were used *viz*., simple scaling tests and Joint scaling tests. A, B and C scaling tests, and Chi-square tests were employed to assess the role of epistasis in simple and Joint scaling tests respectively. Values of A, B and C scales were calculated by using following formula

Scales	Variance of scales
$A = 2\,\bar{B}_1 - \bar{P}_1 - \bar{F}_1$	$VA = 4V(\bar{B}_1) + V(\bar{P}_1) + V(\bar{F}_1)$
$B = 2\,\bar{B}_2 - \bar{P}_2 - \bar{F}_1$	$VB = 4V(\bar{B}_2) + V(\bar{P}_2) + V(\bar{F}_1)$
$C = 4\,\bar{F}_2 - 2\,\bar{F}_1 - \bar{P}_1 - \bar{P}_2$	$VC = 16\,V(\bar{F}_2) + 4V(\bar{F}_1) + V(\bar{P}_1) + V(\bar{P}_2)$

Where, A, B and C are the scales and $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\bar{B}_1$ and $\bar{B}_2$ are generation means for a particular character. $V\bar{A}$, $V\bar{B}$, and $V\bar{C}$ are corresponding variances of the scales and $V(\bar{P}_1)$, $V(\bar{P}_2)$ etc. are the variance of the sample means of respective generations.

RESULTS AND DISCUSSION

ANOVA was conducted at two levels *viz*., for each of the six cross generations following Compact Family Block Design and for each trait within a cross following Randomized Block Design. Compact Family Block Design ANOVA illustrated significant results in all the six

cross generations (**Table 1**). In case of ANOVA results of Randomized Block Design within each cross for different traits, all crosses manifested significant results except for one trait, *viz*., number of panicles per plant in Cross I (T-3 x PuB-1) (**Table 2**). Similar findings have been recorded by Ramli *et al.* (2016), Sravan and Jaiswal (2017a) and Kour *et al.* (2019) in aromatic rice crop.

Detection of epistasis by applying scaling tests : Presence of epistasis was examined by following simple and Joint scaling tests for the inheritance of 15 traits studied in the experiment. Sravan and Jaiswal (2017a), and Krishna *et al.* (2018) have also employed both scaling tests to discern the presence of epistasis in inheritance of different traits. In the present study, backcross population

Table 1. ANOVA of compact family block design of six crosses of basmati rice

Traits	Source of variation				
	Replication	Cross	Error A	Progeny within cross	Error B
	df =2	df =5	df =10	df =30	df =60
Days to 50 percent flowering	2.60	75.58***	1.50	22.42***	2.37
Days to maturity	1.09	63.01***	1.80	24.29***	2.21
Plant height (cm)	29	1489.42***	6.95	306.94***	7.33
Panicle length (cm)	3.75	11.28***	0.59	3.59***	0.83
Number of panicles per plant	1.59	25.64***	1.23	12.51***	2.70
Number of grains per panicle	723.06	6364.85***	124.43	1486.10***	100.03
100-grain weight (g)	0.001	0.62***	0.001	0.11***	0.001
Yield per plant (g)	13.42	443.20***	10.07	105.33***	6.75
Kernel length (mm)	0.001	1.26***	0.001	0.51***	0.01
Kernel breadth (mm)	0.001	0.02***	0.001	0.01***	0.001
Kernel length after cooking (mm)	0.00	24.76***	0.18	10.46***	0.28
Kernel breadth after cooking (mm)	0.005	0.03***	0.003	0.02***	0.003
Alkali spreading value (scale 1-7)	1.27	9.93***	0.24	1.44***	0.22
Aroma (scale 1-3)	0.01	0.19***	0.02	0.15***	0.01
Amylose content (%)	0.81	1.70***	0.29	3.19***	0.25

Significance Levels *** = <.001

Table 2. Mean sum of square of progenies of six crosses of basmati rice

Traits	Mean Sum of Square of progenies (df=5)					
	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
Days to 50 percent flowering	19.15**	23.69*	12.66**	53.85**	33.79**	33.79**
Days to maturity	17.89**	33.01**	19.45**	65.06**	30.40**	30.40**
Plant height (cm)	1321.16**	450.77**	380.81**	594.14**	55.30**	55.30**
Panicle length (cm)	17.75**	9.02**	8.53**	7.06**	12.18**	12.18**
Number of panicles per plant	3.04	18.27**	4.29*	48.84**	6.77**	6.09*
Number of grains per panicle	1313.58**	619.60**	808.35**	2151.61**	3472.11**	3472.11**
100-grain weight (g)	0.02**	0.31**	0.06**	0.11**	0.20**	0.20**
Yield per plant (g)	101.88**	121.53**	570.83**	634.05**	505.47**	505.47**
Kernel length (mm)	0.22**	1.41**	0.22**	0.18**	0.84**	0.84**
Kernel breadth (mm)	0.02**	0.00**	0.00**	0.01**	0.00**	0.00**
Kernel length after cooking(mm)	6.74**	23.18**	5.65**	1.20**	17.84**	17.84**
Kernel breadth after cooking (mm)	0.06**	0.04**	0.03**	0.02*	0.07**	0.07**
Alkali spreading value (scale 1-7)	4.37**	3.54**	0.90**	0.01**	2.77**	2.77**
Aroma (scale 1-3)	1.15**	0.97**	0.19**	0.33**	0.26**	0.26**
Amylose content (%)	4.46**	3.99**	5.55**	7.17**	5.39**	5.39**

Significance Levels * = <.05, and ** = <.01

were used and hence only A, B C simple scaling tests were performed. Joint scaling tests were performed using chi square test (χ^2). Simple scaling tests and joint scaling tests were in congruence with each other in all the 90 cases. Since, there were 15 traits and six crosses hence 90 tests were performed to know the presence of epistasis (**Table 3-5**). Here, term "case" represents as one test conducted either for simple or joint scaling tests. However, contradictory results of simple and Joint scaling tests were reported by Divya *et al.* (2014) in 5 out of 20 cases, Krishna *et al.* (2018) four out of 70 cases. Presence of epistasis was observed in all cases, except for one trait of Cross VI (HUBR10-9 x PuB-1509). For the traits which showed epitasis, six parameter model was used to further decipher which type of non-allelic gene interaction is governing the inheritance of those traits. Similarly, trait, alkali spreading value in **Cross VI** did not show epistasis in scaling test hence three parameter model was applied to estimate type of gene action in the trait. It was observed that, dominance [$\hat{h}$] gene action was governing the trait inheritance. Similarly, Ganapati *et al.* (2020) found one trait, namely 1000-grain weight which showed absence of epistasis in its inheritance. Except for one case, traits were governed by both allelic and non-allelic interactions. However, many authors have reported that traits were governed by epistasis only. In the present findings, traits which did not fit into additive dominance model *i.e*., which showed presence of epistasis in scaling tests were further examined to elucidate which type of epistasis were controlling the traits.

Assessment of Gene effects and gene interaction yield attributing traits: Traits which are negatively correlated yield *viz*., days to 50 percent flowering, days to maturity and plant height showed dominance gene effects, additive x additive and dominance x dominance types of epistasis. Similar findings have been recorded by authors *viz*., Sravan and Jaiswal (2017a) and Bano *et al*. (2017). Panicle length showed dominance and dominance x dominance (l) type of gene interaction (**Table 4**). Hasib *et al*. (2002) recorded additive and dominance gene action and Krishna *et al*. (2018) observed all type of gene interaction in their studies. Panicles per plant directly contribute to the increase in yield, this trait showed d, h, i and l type of epistasis. However, authors *viz*., Murugan and Ganesan (2006) and Krishna *et al*. (2018) observed additive [$\hat{d}$] and dominance [$\hat{h}$] type of gene action all types inter-allelic interaction effects. Number of seed per panicle and 100-grain weight are positively correlated with yield per plant traits (Sharma and Jaiswal, 2020) and these traits were controlled by h and l type of epistasis (**Table 5**). Similar findings have been recorded by Krishna *et al*. (2018), and Bano *et al*. (2017) in aromatic rice.

Among digenic interaction in which the direction of h and l type of epitasis are considered and accordingly termed as complementary when h and l have same direction either positive or negative. In same way, if h and l show contrasting direction of gene interaction then it is called as duplicate epistasis (Hayman and Mather, 1955). In the present findings, yield attributing traits showed equal importance of both complementary and duplicate epistasis. Though, yield per plant traits showed only complementary epistasis. Aforementioned experimental findings have been also recorded by Gopikanan and Ganesh (2014), Rani *et al.* (2015), and Ganapati *et al.* (2020) in rice crop.

Organoleptic traits: Among organoleptic traits, slender kernel astounds rice consumers, hence, rice kernel dimension plays an important role in breeding for basmati rice variety. Kernel dimension related traits *viz*., length and breadth before and after cooking were found to be controlled by mostly both, gene effects (additive and dominance) and epistasis (additive x additive and dominance x dominance) (**Table 5**). Similar findings have been recorded by rice workers *viz*., Sravan and Jaiswal (2017a) in aromatic rice and by Bano *et al*. (2017) in basmati rice varieties for rice kernel related traits. Alkali spreading value gives an indirect explanation of amylose content present in rice kernel based on spreading of polished kernels in 1-7% KOH solution. The alkali spreading value showed dominance type of gene effect, and additive x additive, dominance x dominance type of gene interaction. However, in one Cross VI (HUBR10-9 x PuB-1509) the trait did not show significant value neither in simple scaling tests nor in joint scaling test and hence Jinks and Jones three parameter model was used to discern the gene effect and it was found that the trait showed dominance type of gene effect. Aroma and amylose content showed presence of dominance x dominance type of gene interaction (**Table 6**). For aroma, Sravan and Jaiswal (2017a) recorded all types of gene effects and interaction in their study in aromatic rice. For amylose content, additive and dominance gene action,

Table 3. Estimates of genetic parameter in non-interacting trait following Jinks and Jones

Alkali spreading value	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	Simple scaling test (A, B and C)	Joint scaling test
HUBR10-9 x PuB-1509	6.3***±0.13	-0.31±0.18	-1.37*±0.64	NS	NS

Significance Levels * = <.05, ** = <.01 & *** = <.001

Table 4. Estimates of gene effects following Hayman's six parameter model for yield traits of basmati rice

CROSS	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	$[\hat{j}]$	$[\hat{l}]$	Type of interactions	Simple scaling test			Joint scaling test
								A	B	C	χ2
Days to fifty percent flowering											
T-3x PuB-1	105.03*** ±2.15	1.52** ±0.08	-15.25***±2.15	-12.3*** ±2.15	-0.47 ± 0.55	3.7 ±2.9	--	**	**	**	**
T-3x PuB-1121	106.63***±0.45	-1.78*±0.77	-17.23***±2.35	-11.83***±2.35	-1.18±0.77	1.8±3.56	--	**	**	**	**
PuB-1 x HUBR10-9	103.61***±0.37	-1.22±0.65	-6.09**±1.97	-4.33*±1.96	-0.28±0.65	-8.37**±3	C	**	**	**	**
CSR-30 x HUBR10-9	106.59***±0.46	-0.4±0.82	-3.29±2.47	-2.97±2.47	-6.95±0.82	9.81**±3.76	--	**	**	**	**
PuB-1121 x HUBR10-9	102.85***±0.38	-3.3***±1	-3.24±2.53	3.68±2.53	-4.98±1	-21.18***±4.31	--	**	**	**	**
HUBR10-9 x PuB-1509	105.87***±0.35	0.07±0.79	-13.48***±2.13	-6.09**±2.12	3.55±0.8	-8.27*±3.48	C	**	**	**	**
Days to maturity											
T-3x PuB-1	134.94*** ±0.49	1.62** ±0.63	-21.29*** ±3.06	-19.66***±2.31	-2.32 ±2.09	25.76***±5.1	D	**	NS	**	**
T-3x PuB-1121	138.79***±0.48	-1.7*±0.82	-32.56***±2.54	-26.71***±2.53	-2.25±0.82	29.54***±3.82	D	**	NS	**	**
PuB-1 x HUBR10-9	136.23***±0.42	-0.83±0.67	-24.5***±2.15	-21.53***±2.14	-1.57±0.67	18.87***±3.17	D	NS	**	**	**
CSR-30 x HUBR10-9	139.18***±0.48	0.05±0.89	-22.9***±2.63	-20.62***±2.62	-6.5±0.89	29.89***±4.06	D	**	**	**	**
PuB-1121 x HUBR10-9	132.3***±0.43	-3.07**±1	-8.58***±2.66	-1.47±2.66	-5.25±1.01	-8.03±4.39	--	NS	**	**	**
HUBR10-9 x PuB-1509	134.81***±0.38	-0.22±0.83	-18.49***±2.27	-9.35***±2.26	3.05±0.84	-2.01±3.69	--				
Plant height											
T-3x PuB-1	132.39***±1.36	-8.17*** ±3.51	45.12 ***±8.89	-3.27±1.35	-0.19 ±0.48	20.69 ±15.08	--	**	**	**	**
T-3x PuB-1121	136.79***±1.41	-11.41**±3.63	-19.24*±9.22	-18.02±9.2	-29.63±3.65	32.33*±15.62	--	**	**	NS	**
PuB-1 x HUBR10-9	122.87***±1.39	10.51***±2.74	2.39±7.84	2.97±7.81	18.9±2.76	-72.69***±12.37	--	**	**	**	**
CSR-30 x HUBR10-9	122.79***±1.3	-3.25±2.45	51.6***±7.17	41.65***±7.14	-22.74±2.84	-18.57±11.16	--	**	**	**	**
PuB-1121 x HUBR10-9	123.79***±1.15	4.56±2.53	5.05±6.87	-2.72±6.84	2.93±2.57	-10.78±11.18	--	**	**	**	**
HUBR10-9 x PuB-1509	117.01***±1.11	-1.83±2.51	67.42***±6.71	46.84***±6.7	-9.33±2.53	-97.72***±11.02	D	NS	NS	**	**
Panicle length											
T-3x PuB-1	27.76***±0.25	-0.25±0.45	0.31±1.39	-3.27*±1.35	-0.19±0.48	21.55*** ±2.17	--	**	**	**	**
T-3x PuB-1121	28.11***±0.22	-1.76***±0.5	-2.06±1.35	-5.0***±1.33	-2.79±0.53	13.89***±2.23	--	**	**	**	**
PuB-1 x HUBR10-9	29.31***±0.20	0.89±0.45	6.63***±1.22	2.5*±1.2	-0.08±0.47	1.29±2.01	--	**	**	**	**
CSR-30 x HUBR10-9	26.67***±0.20	-1.41***±3.89	6.28***±1.14	3.1**±1.1	-1.21±0.44	4.15*±1.84	C	**	**	**	**
PuB-1121 x HUBR10-9	28.00***±0.20	0.55±0.61	3.97**±1.47	-1.14±1.46	1.22±0.63	9.28***±2.58	C	**	**	**	**
HUBR10-9 x PuB-1509	28.16***±0.21	0.29±0.44	3.64**±1.23	-1.36±1.22	-0.18±0.45	9.61***±1.99	C	**	**	**	**
No. of panicles/plant											
T-3x PuB-1	8.89**±0.28	-1.32 *±0.67	6.67*** ±1.77	4.42* ±1.75	-1.27 ±0.69	-4.09 ±2.94	--	NS	NS	**	**
T-3x PuB-1121	10.8***±0.24	-6.35***±0.86	8.67***±2.02	5.83**±1.96	-5.48±0.91	-10.53**±3.7	D	**	**	NS	**
PuB-1 x HUBR10-9	10.68***±0.29	1.43±0.76	6.43***±1.95	5.21**±1.92	2.22±0.79	-11.58***±3.34	D	**	NS	NS	**
CSR-30 x HUBR10-9	10.2***±0.25	-0.05±0.61	10.18***±1.67	0.70±1.58	-0.37±0.7	20.43***±2.86	C	**	**	**	**
PuB-1121 x HUBR10-9	10.27***±0.31	-1.40±0.77	10.82***±2.05	7.77***±1.96	-1.28±0.81	-8.74*±3.52	D	NS	**	**	**
HUBR10-9 x PuB-1509	10.98***±0.38	-4.00***±1.00	11.83**±4.14	4.81±2.51	-2.35±1.04	9.35±7.86	--	**	**	**	**

Significance Levels * = <.05, ** = <.01 & *** = <.001; NS=not significant

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Table 5. Estimates of gene effects following Hayman's six parameter model for yield and quality traits of basmati rice

CROSS	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}\hat{i}]$	$[\hat{j}]$	$[\hat{l}]$	Type of interactions	Simple scaling test			Joint scaling test
								A	B	C	χ2
Number of grains/plant											
T-3x PuB-1	83.37*** ±2.16	-53.47***±4.22	32.5**±12.37	18.53±12.08	-44.4 ±4.55	54.06**±19.69	C	**	NS	**	**
T-3x PuB-1121	85.57***±2.34	-1.57±4.83	-45.03***±13.55	-69.09***±13.44	-15.67±4.91	85.36***±21.73	D	**	NS	**	**
PuB-1 x HUBR10-9	118***±3.11	-15.12*±6.65	39.48*±18.48	20.31**±18.22	4.15±7.02	34.85***±30	--	**	**	**	**
CSR-30 x HUBR10-9	89.32***±2.16	-48.62***±5.84	42.09**±14.94	41.89**±14.53	-28.05±6.6	70.15**±25.87	C	**	**	**	**
PuB-1121 x HUBR10-9	83.09***±2.64	3.37±5.79	63.82***±15.98	38.79*±15.66	52.43±6.12	36.95±26.21	--	**	**	**	**
HUBR10-9 x PuB-1509	91.19***±2.74	31.08***±5.82	24.82±16.26	-4.58±15.97	-10.32±6.13	130.68***±26.43	--	**	**	**	**
100-Grain weight (g)											
T-3x PuB-1	2.27***±0.02	0.04±0.03	-0.16±0.09	-0.32***±0.09	-0.05±0.03	0.64***±0.14	--	**	**	NS	**
T-3x PuB-1121	2.27***±0.02	-0.4***±0.04	1.23***±0.1	0.88***±0.1	-0.06±0.04	0.010±0.16	--	**	**	**	**
PuB-1 x HUBR10-9	2.27***±0.01	-0.13***±0.02	0.17**±0.07	-0.02±0.07	0.04±0.02	0.45***±0.10	C	**	**	**	**
CSR-30 x HUBR10-9	2.4***±0.02	0.003±0.04	0.43***±0.12	0.22*±0.11	-0.16±0.04	0.82***±0.18	C	**	**	**	**
PuB-1121 x HUBR10-9	2.59***±0.02	0.4***±0.05	-0.27*±0.13	-0.52***±0.13	0.17±0.05	1.82***±0.21	D	**	**	**	**
HUBR10-9 x PuB-1509	2.58***±0.02	-0.25***±0.04	0.5***±0.1	0.24*±0.1	-0.008±0.04	0.5**±0.16	C	**	**	**	**
Yield per plant (g)											
T-3x PuB-1	8.4***±0.37	-5.34***±1.05	24.46***±2.65	18.73***±2.57	-6.11±1.14	14.3**±4.64	C	**	**	**	**
T-3x PuB-1121	14.33***±0.57	-6.57***±1.24	5.0±3.45	-5.68±3.63	-5.53±1.29	47.59***±5.68	--	**	**	**	**
PuB-1 x HUBR10-9	16.77***±0.63	-1.84±1.81	39.92***±4.52	13.44**±4.42	5.96±1.84	61.07***±7.9	C	**	**	**	**
CSR-30 x HUBR10-9	14.23***±0.52	-7.65***±1.36	31.15***±3.63	8.36*±3.42	-3.74±1.44	87.17***±6.32	C	**	**	**	**
PuB-1121 x HUBR10-9	14.53***±0.65	0.84±1.58	37.12***±4.19	14.49***±4.09	7.68±1.62	60.95***±7.1	C	**	**	**	**
HUBR10-9 x PuB-1509	18.18***±0.91	-1.82±1.99	20.78***±5.51	2.75±5.4	-4.9***±2.02	75.55***±9.04	C	**	**	**	**
Kernel length (mm)											
T-3x PuB-1	7.03***±0.04	-0.39***±0.08	1.54***±0.23	1.12***±0.22	-0.44±0.09	-2.36***±0.38	D	NS	**	NS	**
T-3x PuB-1121	7.08***±0.03	-0.81***±0.09	2.24***±0.23	1.89***±0.23	0.10±0.10	-1.17**±0.41	D	NS	**	**	**
PuB-1 x HUBR10-9	7.55***±0.03	0.07±0.06	-0.14±0.18	-0.27±0.18	0.36±0.06	-0.98***±0.28	C	**	**	**	**
CSR-30 x HUBR10-9	7.41***±0.03	0.28***±0.06	0.59***±0.18	0.40*±0.18	0.47±0.07	-1.67***±0.29	D	**	**	**	**
PuB-1121 x HUBR10-9	7.83***±0.06	0.89***±0.09	-1.82***±0.31	-1.86***±0.3	0.34±0.1	4.18***±0.44	D	**	NS	**	**
HUBR10-9 x PuB-1509	7.86***±0.04	-0.68***±0.1	-0.11±0.25	0.24±0.24	-0.31±0.1	-1.64***±0.43	--	**	**	NS	**
Kernel breadth (mm)											
T-3x PuB-1	1.84***±0.01	0.05*±0.02	-0.6***±0.07	-0.54***±0.07	-0.01±0.02	0.87***±0.1	D	**	**	**	**
T-3x PuB-1121	1.85***±0.00	-0.06***±0.01	-0.08±0.05	-0.04±0.04	-0.02±0.02	-0.08±0.07	--	NS	**	**	**
PuB-1 x HUBR10-9	1.72***±0.00	-0.04*±0.02	-0.01±0.05	0.04±0.05	0.002±0.02	0.09±0.08	--	**	**	**	**
CSR-30 x HUBR10-9	1.83***±0.01	-0.07***±0.02	-0.006±0.06	0.08±0.06	-0.16±0.02	-0.25**±0.09	--	NS	**	**	**
PuB-1121 x HUBR10-9	1.79***±0.01	-0.02±0.02	-0.06±0.05	-0.02±0.05	-0.07±0.02	0.03±0.09	--	**	**	NS	**
HUBR10-9 x PuB-1509	1.82***±0.01	-0.03±0.02	-0.06±0.05	-0.04±0.05	0.01±0.02	-0.1±0.08	--	**	NS	NS	**

Significance Levels * = <.05, ** = <.01 & *** = <.001; NS=not significant

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Table 6. Estimates of gene effects following Hayman's six parameter model for quality traits of basmati rice

CROSS	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}\hat{i}]$	$[\hat{j}]$	$[\hat{l}]$	Type of interactions	Simple scaling test			Joint scaling test
								A	B	C	χ2
Kernel length after cooking (mm)											
T-3x PuB-1	12.53***±0.17	0.43±0.36	-1.71±0.99	1.42±0.97	1.31±0.36	-9.59***±1.6	--	**	**	**	**
T-3x PuB-1121	13.06***±0.17	-3.34***±0.47	4.61***±1.18	2.93*±1.16	0.06±0.49	6.25**±2.05	C	**	**	**	**
PuB-1 x HUBR10-9	14.8***±0.26	-0.75*±0.37	0.205±1.28	-3.21*±1.26	-1.27±0.39	4.19*±1.84	--		NS		
CSR-30 x HUBR10-9	11.92***±0.17	0.06±0.24	6.51***±0.85	6.08***±0.84	0.15±0.26	-9.66***±1.22	D				
PuB-1121 x HUBR10-9	15.19***±0.22	1.48***±0.36	-8.9***±1.14	-7.73***±1.13	-1.99±0.4	13.08***±1.72	D		NS		
HUBR10-9 x PuB-1509	15.54***±0.18	-2.01***±0.38	2.46*±1.06	2.82**±1.04	0.51±0.4	-11.61***±1.7	D	**	**	**	**
Kernel breadth after cooking(mm)											
T-3x PuB-1	2.24***±0.02	0.12**±0.05	-0.5***±0.13	-0.7***±0.13	0.02±0.05	1.65***±7.96	D	**	**	**	**
T-3x PuB-1121	2.33***±0.02	-0.24***±0.04	0.27**±0.10	0.09±0.10	-0.26±0.04	0.36*±0.17	C		NS		
PuB-1 x HUBR10-9	2.26***±0.02	-0.08±0.04	-0.23*±0.11	-0.39***±0.11	-0.04±0.04	1.14***±0.18	D	**	**	**	**
CSR-30 x HUBR10-9	2.34***±0.02	-0.03±0.04	-0.20±0.12	-0.10±0.12	0.01±0.04	0.47*±0.19	--	**	**	**	**
PuB-1121 x HUBR10-9	2.3***±0.02	0.01±0.05	0.02±0.12	-0.26*±0.12	0.03±0.05	1.34***±0.2	--				
HUBR10-9 x PuB-1509	2.35***±0.02	-0.09**±0.03	-0.31**±0.1	-0.28**±0.1	-0.18±0.03	0.72***±0.16	D		NS	NS	
Alkali spreading value (scale 1-7)											
T-3x PuB-1	4.07***±0.1	0.1±0.25	0.62±0.64	3.61***±0.64	0.65±0.25	-8.13***±1.06	D	**	**	**	**
T-3x PuB-1121	4.01***±0.09	-0.07±0.23	3.27***±0.58	4.85***±0.58	1.18±0.23	-6.37***±0.99	D		NS		
PuB-1 x HUBR10-9	5.64***±0.09	-0.13±0.11	1.75***±0.4	2.83***±0.4	0.28±0.11	-5.02***±0.55	--	**	**	**	**
CSR-30 x HUBR10-9	3.78***±0.09	-0.97***±0.19	-0.16±0.53	2.73***±0.53	-0.83±0.19	-0.2±0.84	--		NS		
PuB-1121 x HUBR10-9	5.53***±0.12	-0.52±0.28	-2.98***±0.73	-2.81***±0.73	-0.62±0.28	10.24***±1.23	D	**	**	**	**
Aroma (scale 1-3)											
T-3x PuB-1	1.36***±0.04	-0.02±0.1	-0.11±0.24	0.4±0.24	-0.52±0.1	2.77***±0.4	--	**	**	**	**
T-3x PuB-1121	1.44***±0.04	-0.02±0.09	0.11±0.25	0.61*±0.25	-0.52±0.09	2.03***±0.41	--	**	**	**	**
PuB-1 x HUBR10-9	1.56***±0.04	0.17±0.09	-0.04±0.24	-0.04±0.24	0.17±0.09	1.84***±0.4	--	**	**	**	**
CSR-30 x HUBR10-9	1.51***±0.05	-0.05±0.1	-0.6*±0.27	-0.59*±0.27	-0.05±0.1	3.16***±0.44	D	**	**	**	**
PuB-1121 x HUBR10-9	1.45***±0.04	0.12±0.09	0.11±0.25	0.11±0.25	0.12±0.09	1.99***±0.4	--	**	**	**	**
HUBR10-9 x PuB-1509	1.34***±0.04	0.03±0.09	0.17±0.25	0.17±0.25	0.03±0.09	2.29***±0.4	--	**	**	**	**
Amylose content (%)											
T-3x PuB-1	23.38***±0.19	-3.07***±0.2	-0.43±0.86	0.21±0.86	-3.0±0.22	2.62*±1.13	D	**	**	**	**
T-3x PuB-1121	24.02***±0.22	0.73±0.55	-6.12***±1.41	-7.21***±1.41	-0.47±0.55	12.73***±2.37	D			NS	
PuB-1 x HUBR10-9	23.5***±0.2	-1.73***±0.41	0.02±1.15	-2.18±1.41	-2.54±0.42	10.06***±1.83	--	**	**	**	**
CSR-30 x HUBR10-9	23.47***±0.2	0.2±0.29	1.39±0.1	-2.33*±0.99	0.32±0.31	10.67***±1.44	--	**	**	**	**
PuB-1121 x HUBR10-9	23.38***±0.19	0.91**±0.28	8.85***±0.96	6.11***±0.95	1.4±0.29	-10.31***±1.37	D		NS		
HUBR10-9 x PuB-1509	23.66***±0.2	-3.32***±0.26	2*±0.95	-0.51±0.94	-3.38±0.27	3.34*±1.32	C	**	**	**	**

Significance Levels * = <.05, ** = <.01 & *** = <.001; NS=not significant

and all the three types of gene interaction was reported by Bano *et al*. (2017) and Sravan and Jaiswal. Whereas, Srivastava *et al*. (2012) observed additive, dominance additive x additive, dominance x dominance type of gene interaction.

Digenic studies revealed that both complementary and duplicate epistasis were contributing to inheritance of organoleptic traits among different generations of six crosses. Ramli *et al.* (2015), Sravan and Jaiswal (2017a), and Kour *et al.* (2019) have recorded similar findings for different quality traits of rice. However, duplicate digenic interaction were recorded more than complementary among organoleptic traits. Similar findings have been reported by Kacharabhai (2015) in rice crop for kernel length and breadth.

Yield and quality traits of basmati rice were found to be predominantly controlled by epistasis. In such situation, the traits improvement *viz*., increase in yield or tweaking the amylose content, increase in aroma, slender kernel before and after cooking can be achieved by heterosis breeding. Generous amount of genetic variability was present which was evident from the significant ANOVA results both between and within cross generations used in the experiment. Along with heterosis breeding, pedigree breeding method can be also used to improve quality or yield traits of the experimental material of the present study. Eventually, the breeder has to take into consideration the digenic interaction too. The traits which showed complementary epistasis can be used as a parameter to assess the genetic worth of the selected plant for further improvement. However, in view of trait improvement, if selection is practiced for such plants which show duplicate epistasis or large number of epistasis for that trait. Then in such case, selection practices will be inefficient.

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