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Research Article

GENE ACTION AND GENERATION MEAN ANALYSIS FOR YIELD AND ITS COMPONENT TRAITS IN INDICA RICE (*Oryza sativa* L.)

SINGH R.K.[1,2], SINGH R.P.[1], SINGH P.[1,2,3]*, VERMA R.L.[2] AND SINGH O.N.[2,4]

[1]Department of Genetics and Plant Breeding, Institute of Agriculture Sciences, Banaras Hindu University, Varanasi, 221005, Uttar Pradesh, India
[2]Crop Improvement Division, ICAR-National Rice Research Institute, Cuttack, 753006, Odisha, India
[3]Department of Plant Breeding and Genetics, VKS College of Agriculture, Dumraon, Buxar, 802119, Bihar Agricultural University, Sabour, 813210, Bihar, India
[4]Plant Variety Protection Appellate Tribunal, Intellectual Property Appellate Board, Guna Complex Annex-I, Anna Salai, Teynampet, Chennai, 600018, India
*Corresponding Author: Email - prakash201288@gmail.com

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Abstract: Blast disease of rice (*Oryza sativa* L.), caused by the fungal pathogen *Pyricularia oryzae* (synonym of *Magnaporthe grisea*) is a serious threat to rice production. Six generations including three segregating populations *viz*., F_2, B_1 and B_2 of cross between a popular high-yielding blast susceptible cultivar *i.e*., HUR 4-3 with Tetep (blast resistant genes *Pi1* and *Pi54*) were used during 2014-15 and 2015-16 for the study the nature and magnitude of gene action for disease reaction and yield attributing traits through generation mean analysis. The mean performances of the six generations (*viz*., P_1, P_2, F_1, F_2, B_1 and B_2) on 11 quantitative and four qualitative traits were used for the analysis of scaling test and generation mean. In scaling test, the values of scale A and B were showed significance for most of traits which will indicate the non-allelic interaction. The complementary interaction was showed for plant height, spikelet fertility, grain yield per plant and head rice recovery. While, the remaining other traits were showed duplicate epistasis. Among the genotypes tested under epiphytotic conditions, lines may be carried of resistant genes were highly resistant to blast disease as compared to individuals with single and/or minor or absence of both resistance genes. It indicates the non-allelic gene interaction and has a duplicate effect when both resistant genes present together. The information on epistatic interaction of various yield contributing traits and disease resistance will further assist rice plant breeders for choosing appropriate breeding strategy for blast resistance and yield enhancement.

Keywords: *Blast, Epistasis, Disease resistance, Rice and Quantitative traits*

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Introduction

Rice (*Oryza sativa* L.) is second most important staple food crop of the world feeding over half of the populations, providing 20-80 percentage of the dietary energy in the daily intake of people in Asia, and also 90 percent of rice produced and consumed in the continent being [1]. Rice crop is more resilient because it is grown in various diverse ecological condition *i.e*., rainfed low land, rainfed upland and flood prone and/ or deep-water environment. It is due to wide range of adoptability and hardiness in different agro-climatic zone [2-4].

Asia occupies an area of 137 m ha of rice cultivation wherein India has a lion's share of 44.6 m ha (23.3% of gross cropped area of the country) with an annual production of 115.6 m t (next to China, 141.6 m t) with an average productivity of 2.59 t/ha [5]. However, the cultivated area of rice during 2018-19 in Uttar Pradesh is only 5.67 m ha with total production of 13.65 m t and an average productivity of 2.40 t / ha [6]. It is estimated that demand for rice is expected to be 130 m t by 2025 in the country to maintain the present level of self-sufficiency. Therefore, the major concern in coming year is to increase the productivity and for which the losses due to various biotic and abiotic stresses have to be tackled.

The global rice production of up-to 52% are lost annually owing to the damage caused by various biotic stress factors [7]. Among the various biotic stresses, blast disease caused the fungus *Magnaporthe grisea* play an important and crucial role in decreasing the productivity of rice in many Asian countries. The fungus *Magnaporthe grisea* is a hemi biotrophic, heterothallic, ascomycetous fungus which potentially can occur in all stage of growth and causing heavy and total loss [2,3].

More than 100 blast resistance genes have been described and mapped by preceding workers but a partial number of reports are obtained on the genetics of blast resistance in rice in rice varieties [8]. In rice varieties, the blast disease resistance is mostly governed by dominant or major genes, but in few cases, recessive genes are also responsible for resistance [9,10]. Both major (dominant) and minor (recessive) genes can contribute to durable resistance against rice blast disease [11]. Therefore, an attempt has been made to study the inheritance of various kinds of genic effects and their importance in the grain yield and its component traits which also controlling the blast disease resistance in rice. However, the grain yield is a complex polygenic trait and is dependent on the combination of its component traits *viz*., number of filled grains, test weight, panicle length, panicle width and effective tillers per plant. Hence, this study is focused to elucidate the gene action associated with various yield contributing traits along with blast resistance attributes through generation mean analysis. The information about the nature and magnitude of gene action existing in the breeding material would be a valuable tool for selecting breeding system and hence to achieve the preferred genetic enhancement through correlated response of selection.

Material and methods

The experiments were conducted during *Kharif* season in 2014-15 and 2015-16 at the experimental form of Department of Genetics and Plant Breeding Institute of Agricultural Sciences, Banaras Hindu University, Varanasi and Off-season

Table-1 *Mean performance of the six generations (P_1, P_2, F_1, F_2, B_1 and B_2) of the cross HUR 4-3 ×Tetep for fifteen qualitative and quantitative traits*

SN	Generations/Traits	P_1	P_2	F_1	F_2	B_1	B_2
1	Days to first panicle emergence	90.78± 0.006	82.33± 0.007	88.09 ± 0.013	86.10 ± 0.025	87.56 ± 0.009	82.84 ± 0.014
2	Days to 50 percent flowering	96.67± 0.013	86.33 ± 0.011	92.56 ± 0.007	91.04 ± 0.029	91.43 ± 0.013	87.27 ± 0.008
3	Days to maturity	127.67± 0.007	113.67 ± 0.004	119.67 ± 0.003	124.00 ±0.037	121.71 ± 0.011	117.67 ± 0.004
4	Plant height per plant(cm)	111.11± 0.039	157.53 ± 0.028	122.30 ± 0.048	99.01 ± 0.059	94.41 ± 0.025	124.92 ± 0.032
5	Effective tillers per plant	16.62± 0.027	14.78 ± 0.034	19.80 ± 0.027	17.63 ± 0.019	17.31 ± 0.032	15.27 ± 0.045
6	Panicle length per plant (cm)	28.29± 0.027	24.80 ± 0.008	29.77 ± 0.019	24.83 ± 0.029	26.70 ± 0.038	25.92 ± 0.056
7	Number of grains per panicle	155.23± 0.012	117.21 ± 0.008	175.78 ± 0.022	167.23 ± 0.057	160.60 ± 0.015	135.41 ± 0.049
8	Spikelet fertility per plant (%)	85.58± 0.016	77.49 ± 0.014	87.81 ± 0.017	83.23 ± 0.013	84.66 ± 0.016	79.19 ± 0.010
9	Test weight per plant (g)	19.23± 0.021	18.33 ± 0.025	21.96 ± 0.027	20.29 ± 0.039	19.83 ± 0.015	18.75 ± 0.033
10	Grain yield per plant (g)	33.59± 0.051	19.35 ± 0.054	39.68 ± 0.028	31.34 ± 0.058	30.35 ± 0.048	22.96 ± 0.042
11	Disease severity per plant (%)	53.14± 0.028	5.63 ± 0.126	9.75 ± 0.039	16.90 ± 0.275	26.10 ± 0.096	10.20 ± 0.109
12	Head rice recovery (%)	58.23± 0.013	68.23 ± 0.004	68.61 ± 0.018	61.18 ± 0.031	59.50 ± 0.014	64.10 ± 0.019
13	Kernel Length (mm)	6.46± 0.021	4.56 ± 0.021	6.67 ± 0.029	6.03 ± 0.059	6.26 ± 0.015	5.05 ± 0.024
14	Kernel Breath (mm)	1.93± 0.009	2.01 ± 0.008	2.00 ± 0.013	1.94 ± 0.013	1.91 ± 0.008	1.96 ± 0.009
15	Kernel length breath ratio (%)	3.35± 0.027	2.27 ± 0.018	3.33 ± 0.040	3.10 ± 0.047	3.28 ± 0.07	2.57 ± 0.023

Whereas, P_1: HUR 4-3; P_2: Tetep; F_1: P_1 x P_2; F_2: Selfed F_1s hybrid; B_1: F_1's hybrid (P_1 × P_2) x P_1; B_2: F1's hybrid (P_1 × P_2) × P_2

(*Rabi* season) in 2014-15 at Indian Council of Agricultural Research (ICAR) - National Rice Research Institute (NRRI), Cuttack, Odisha. The Banaras Hindu University, Varanasi is situated in the North-East plain Zone of the Eastern Uttar Pradesh, India at 25º18'0' north latitude and 83º03 East longitude at an altitude of 128.93 meter above the mean sea level (MSL) in Northern Gangetic alluvial plain. The experimental material for this investigation is two rice varieties namely, HUR 4-3 (popular high yielding blast susceptible cultivar of rice), used as a recurrent parent and Tetep (blast resistant variety of rice carrying blast resistance genes *Pi1* and *Pi54*), used as a donor parent. The HUR 4-3, is one of the most widely grown rice cultivar in eastern Uttar Pradesh owing to its high yield, short duration and acceptable grain quality and it is very popular among the farmers of this area.

Creation of evaluation of segregating population

The experimental materials (HUR 4-3 and Tetep) were evaluated in the field condition for disease severity during *Kharif*, 2014-15 and further crosses were made to generate the F_1's hybrids. The F_1's hybrids along with recurrent and donor parents were grown at ICAR-NRRI, Cuttack during Off-season in 2014-15. The hybridity test was performed to test the true F_1's hybrids. The 10-15 plants of true F_1's hybrids were backcrossed with each recurrent and donor parents to generate the backcross progenies (B_1 and B_2) and remaining plants of F_1's hybrids were selfed to generate the F_2 populations. All the six generations (P_1, P_2, F_1, F_2, B_1 and B_2) of the cross HUR 4-3 × Tetep along with the recurrent and donor parents were evaluated in three replications during *Kharif* season, 2015-16 at the experimental form of Banaras Hindu University, Varanasi. All the cultural practices were adequate to grow the healthy crop except for the control of blast disease control. The blast inoculum LB-TN-2 isolate of *Magnaporthe grisea* was inoculated in the field conditions at tillerring stage to both the parents as well as segregating populations *i.e.*, F_1, F_2, B_1 and B_2.

Observation recorded

The observations were recorded at the time of maturity, for 15 agro-morphological traits on randomly selected five plants for parents and F_1's hybrid and 20 plants for segregating generations under epiphytotic condition. The agro-morphological parameters were days to first panicle emergence (days), days to 50 % flowering (days),days to maturity (days), plant height (cm), number of effective tillers per plant (nos.), panicle length per plant (cm), number of filled grains per panicle (nos.), spikelet fertility (%), grain yield per plant (gm),1000-seed weight (gm), head rice recovery (%), kernel lengths per plant (mm), kernel breadths per plant (mm) and kernel length/ breadth ratio. However, the data on disease screening or scoring and severity of disease were recorded at seven days interval adopting standard evaluation system (SES) for rice following [2,12].

Statistical analysis

The means were computed for each generation of P_1, P_2, F_1, F_2, B_1 and B_2. The variance and corresponding standard errors of the means were computed from the deviations of the individual values from the pooled mean for each of the generation in each cross. The generation mean analysis was performed according to Hayman [13] and Jinks and Jones [14] for the estimation of genetic components of variation, epistasis model and Scaling test for A, B,C and D scales as suggested by Hayman and Mather [15] and Mather and Jinks [16] was applied to test the adequacy of simple additive-dominance model. Utilizing the means of different generations, the values of A, B, C and D scales were calculated. The standard errors of A, B, C and D were obtained as square root of the variances V_A, V_B, V_C and V_D, respectively and utilized for testing the significance of the deviations of the respective scales from zero. To test the significance of the scales, the 'Student's t' values for each of these quantities were calculated. The generation means were used to estimate the six genetic parameters *viz.*, *m, d, h, i, j* and *l* of digenic interaction model representing mean (*m*), additive genetic effect (*d*), dominance genetic effect (*h*), additive × additive gene interaction effect (*i*), additive × dominance interaction (*j*) effect and dominance × dominance *(l)* gene effects, respectively assuming that no linkage and no higher order gene interaction exists.

Results and Discussion

Progenies of the cross between HUR 4-3 (recurrent) × Tetep (donor) to developed F_1's hybrid and were advanced to get segregating generations *i.e.*, F_2, B_1 (HUR 4-3 × F_1) and B_2 (HUR 4-3 × F_1). It segregates to high yielding segregants with or without blast resistance genes. To reveal the nature of gene action for yield traits and blast resistance, generation mean analysis was carried out using the data recorded from six generations including three segregating generations of the cross combination *i.e.*, HUR 4-3 × Tetep. The mean performances of the six generation materials P_1, P_2, F_1, F_2, B_1 and B_2 for 15 quantitative traits are presented in [Table-1]. The values of individual scaling tests (A, B, C and D) and estimates of gene effects *viz.*, *m, d, h, i, j* and *l* for 15 different characters were estimated and presented in [Table-2]. Any one of the scaling tests was found to be significant in all traits indicating the presence of epistasis. The types of epistasis were determined as complementary when dominance (*h*) and dominance × dominance *(l)* gene effects have same sign and duplicate epitasis when the sign was different [17, 22].

Days to first panicle emergence

The P1 (parent : HUR 4-3) was recorded highest mean value for this trait among the segregating generations and Tetep (P_2) showed the lowest value among all the generations in the cross HUR 4-3 × Tetep. The scale B was significant indicating the presence of dominance effect indicated that selection alone may not yield desirable progenies and dominance (*h*) and dominance × dominance *(l)* gene effects have opposite sign will indicate the presences of duplicate epitasis. Similar results were also reported by Shrivastava *et al.* [18]. The improvement of this trait should be based on simultaneous exploitation of additive, dominance and epitasis mainly of additive × additive type.

Days to 50 percent flowering

The maximum (96.67 days) and minimum (86.33 days) mean values for this trait was observed, respectively in P_1 and P_2 for this cross.

Table-2 *Estimation of scaling test (Hayman 1958) and gene effect based on performance of six generations viz., P_1, P_2, F_1, F_2, B_1 and B_2 of the cross HUR 4-3 ×Tetep for fifteen qualitative and quantitative traits*

Traits/ Parameters	Scaling test				Generation mean analysis						Epistasis
	A	B	C	D	*m* (Hayman)	*d* (Hayman)	*h* (Hayman)	*i* (Add × Add)	*j* (Add × Dom)	*l* (Dom × Dom)	
Days to first panicle emergence	-2.50	-2.62**	-0.76	0.55	56.20**	4.78**	-0.314	-0.571	0.487	1.60	*D*
Days to 50 percent flowering	-3.23**	-3.28**	-0.52	0.87	48.68**	4.21**	-0.735	-0.88	-0.88	2.04	*D*
Days to maturity	-1.96	2.45	1.188	1.33	38.58**	4.11**	-1.40	-1.33	-2.81**	1.42	*D*
Plant height per plant(cm)	-15.24**	-3.40**	-7.15**	-2.34	24.90**	-6.91**	1.67	2.63**	-1.64	1.33	*C*
Effective tillers per plant	-1.81	-4.03**	-0.16	1.75	24.07**	4.43**	-0.40	-1.79	2.124	2.99**	*D*
Panicle length per plant (cm)	-3.20**	-1.48	-6.84**	-2.41	73.73**	0.77	3.58**	3.17**	-0.86	-0.32	*D*
Number of grains per panicle	1.04	-2.01	2.95**	3.90**	47.40**	3.66**	-1.87	-4.59**	0.87	3.46**	*D*
Spikelet fertility per plant (%)	-1.68	-3.97**	-1.43	1.33	104.46**	4.82**	0.256	-1.39	1.103	2.681**	*C*
Test weight per plant (g)	-2.30	-2.70**	-0.13	1.63	36.06**	2.22	-0.33	-1.74	1.18	2.66**	*D*
Grain yield per plant (g)	-5.04**	-6.01**	-0.96	3.39**	24.37**	6.02**	-0.96	-3.38**	-0.19	5.99**	*D*
Disease severity per plant (%)	-2.89**	3.02**	-0.81	-0.37	5.15**	8.25**	-1.07	0.36	-3.90**	0.05	*C*
Head rice recovery (%)	-4.98**	-4.42**	-3.35**	-0.43	46.06**	-4.44**	1.36	0.46	0.37	1.99	*C*
Kernel Length (mm)	-2.82**	-4.90**	-0.23	1.45	24.14**	11.04**	-0.32	-1.49	2.13	2.86**	*D*
Kernel Breath (mm)	-3.56**	-2.67**	-2.13	0.35	110.18**	-3.20**	0.08	-0.36	-0.72	2.15	*D*
Kernel length breath ratio (%)	-1.00	-2.86**	3.52**	0.28	30.06**	15.97**	-0.43	-1.69	2.96**	2.59**	*D*

Scales A and B were significant indicating the presence of all the three types of epistatic interaction. The dominance (*h*) and dominance × dominance *(l)* gene effects have different sign will further indicate the presences of duplicate epitasis and which may indicate the dominance of resistant parent (P_2). Similar trends were also observed by earlier workers by Paul *et al*. [19] Thirugnanakumar *et al*. [20] and Li *et al*. [21] which explained dominance genetic effect in yield and stress related traits in rice.

Days to maturity

The recurrent (P_1) and donor (P_2) parents were recorded highest and lowest mean value among the all six generations for this trait in the cross HUR 4-3 × Tetep, respectively. The generation mean scales m, d and j were significant indicating the presence of additive and additive × dominance *(l)* gene interaction effects indicated that selection alone may not yield desirable progenies. However, the dominance (*h*) and dominance × dominance *(l)* gene effects have opposite sign will indicate the presences of duplicate epitasis. Similar results were confirmed by Srivastava *et al*. [18], Kumar *et al*. [24] and suggested that the improvement of this character should be based on simultaneous exploitation of additive, dominance and epitasis mainly of additive × additive type.

Plant height per plant (cm)

In this trait, P_2 (parent Tetep) exhibited higher mean value than the all six generations including parents in cross HUR 4-3 × Tetep. The scales A, B and C were significant indicating the presence of dominance effect (h) and dominance × dominance *(l)* gene interaction effects indicated that selection alone may not yield desirable progenies and the sign of dominance (h) and dominance × dominance *(l)* gene effects have similar sign which will indicate the presences of complementary gene interaction. However, significant value of additive × additive (i) gene effects for this trait indicates that selection breeding for this trait more suitable. This results in the good agreement with the Thirugnanakumar *et al*. [20] and Li *et al*. [21]

Effective tillers per plant

The F_1's hybrid and parent Tetep (P_2) recorded highest and lowest mean value among all the generations for this character in the cross HUR 4-3 × Tetep. The scale B was significant indicating non-allelic interaction and significance of additive effect (*d*) and dominance × dominance *(l)* interaction effects indicated that selection alone may not yield desirable progenies, and dominance (*h*) and dominance × dominance *(l)* gene effects have opposite sign will indicate the presences of duplicate epitasis. Significant value of dominance × dominance *(l)* for this trait indicate that heterosis breeding for this trait more suitable and desirable and are in good agreement with the finding of earlier workers, Shrivastava *et al*. [18], Thirugnanakumar *et al*. [20] and Prabhu *et al*. [22].

Panicle length per plant (cm)

The F_1's hybrid recorded highest value among the generations and the Tetep (P_2) registered the lowest value for this character in the cross HUR 4-3 × Tetep. The mean value of F_2 (24.83) was less than of F_1's hybrid (29.77) for this cross. The scales A and C were significant indicating the presence of non-allelic interactions and dominance (*h*) and dominance × dominance *(l)* gene effects have opposite sign will indicate the presences of duplicate epitasis. Significant value of dominance × dominance *(l)* for this trait indicate that heterosis breeding for this trait more suitable, Similar results were reported by Shrivastava *et al*. [18] and Prabhu *et al*. [22, 24].

Number of grains per panicle

The F_1's hybrid and parent Tetep (P_2) recorded highest and lowest value among all the generations tested for this character in the cross HUR 4-3 × Tetep, respectively. The scales C and D were significant indicating the presence of additive × additive (*i*) and dominance × dominance *(l)* gene interaction effects which showed that the selection alone may be yield desirable progenies. The sign of dominance (*h*) and dominance × dominance *(l)* gene effects have opposite sign will indicate the presences of duplicate epitasis. Significant value of additive × additive (*i*) and dominance × dominance *(l)* for this trait which also indicate the combination breeding for this trait is more suitable as reported be several workers Shrivastava *et al*. [18], Prabhu *et al*. [22] and Kumar *et al*. [24, 26].

Spikelet fertility per plant (%)

The highest mean value of spikelet fertility was recorded in F_1's hybrid (87.81 %) and the lowest in parent P_2 (77.41). Significance of scales B was detected in this cross indicating the presence of non-allelic type of gene interactions. The additive (d), dominance (h) and dominance × dominance *(l)* type of interaction effects have similar sign which will indicate the presences of complementary gene interaction. Improvement of this trait therefore can be achieved through recurrent selection [20, 22, 24].

Test or 1000-seed weight (g)

The maximum and minimum values were recorded by F_1's hybrid (21.96 g) and donor parents P_2 (18.33 g) respectively. Significance of A and B scale indicates the presence of non-allelic interaction. The dominance (*h*) and dominance × dominance type gene effects have different sign exhibited the duplicate epistasis. The dominance × dominance type of interaction was significant for this trait. This agrees with the findings of Prabhu *et al*. [22] and Kumar *et al*. [24, 26]. Which means, pre-dominance of dominance effect was observed in the inheritance of this trait. For exploiting of this type of gene effects, the appropriate breeding method would be heterosis breeding.

Grain yield per plant (g)

The highest and lowest value of average grain yield was recorded by F_1's hybrid progeny (39.68 g) and donor parents P_2 (19.35g). Significance of scales A, B and D were detected in this cross indicating the presence of additive × additive and dominance × dominance type of gene interactions.

Pre-dominance of dominance effect was observed in the inheritance of this trait. However, the dominance (*h*) and dominance × dominance *(l)* type of gene interaction have opposite sign means duplicate epistasis is observed. For exploiting, this type of gene effects the appropriate breeding method would be heterosis breeding. It is concluded that these characters are governed by non-additive gene action; it is also evident from the superior performance of F_1's hybrid than advanced lines by earlier workers [18, 22-27].

Disease severity per plant (%)

The maximum and minimum disease severity was recorded by P_1 (53.14) and P_2 (5.63) parents, respectively. Significance of scales A and B were detected in this cross indicating the presence of additive × additive and dominance × dominance type of gene interactions. Significant value of additive (*d*) and additive × dominance type of interaction is associated with homozygosity and hence it is fixable in nature and selection for these characters will be very effective. The opposite sign of '*h*' and '*l*' indicated the presence dominance towards the resistant parent (P_2). The epistatic effects among resistance genes have been reported earlier in several gene combinations during pyramiding process [3, 10, 21, 25-30].

Head rice recovery (%)

The highest average head rice recovery percentage recorded by F_1's hybrid (68.61%) and the lowest recurrent parents P_1 (58.23). Significance of scales A, B and C were detected in this cross indicating the presence of additive × additive and dominance × dominance type of gene interactions. The high magnitude of non – additive gene effects, low magnitude of additive gene effects suggested that, heterosis breeding or combination breeding is the appropriate method for improving this trait. The similar sign of '*h*' and '*l*' indicated the presence complementary gene interactions which showed the dominance towards the resistant parent (P_1). The epistatic effects among resistance genes have been reported earlier in several gene combinations during pyramiding process [20-26, 29, 31].

Kernel length/ breath ratio

The recurrent (3.35) and donor (2.27) parent of cross HUR 4-3 × Tetep expressed the maximum and minimum value and for this character, respectively. The scales B, C and I (dominance × dominance) were significant for both traits. Significance of the scaling test was indicating the presence of non-allelic gene interaction. The magnitude of additive (*d*) and dominance × dominance *(l)* gene effects were found to be greater than additive gene effect in this cross and opposite sign indicates the duplicate epistasis. The high magnitude of non – additive gene effects, low magnitude of additive gene effects suggested that, heterosis breeding or combination breeding is the appropriate method for improving of both traits. This results in confirmation of earlier findings [20, 24, 26, 29].

Conclusion

Dominance gene effects played major role in controlling the genetic variance in most of the traits studied. However, additive gene effects were also found to be important for inheritance of plant heights, panicle length, number of grains per panicle and yield per plant. Bi-parental mating might be useful in exploiting both additive and non-additive gene actions to obtain desirable recombinants.

Application of research: The characters for which additive and dominance gene actions were observed recurrent selection breeding techniques may be appropriate. With regard to the negative values observed in most cases either with main effects *'d'* and *'h'* or epistatic interaction effects *'i', 'j'* and *'l'*, these might indicate that preponderance was towards the less value trait and alleles responsible for less value of traits were over-dominant over the alleles controlling high value.

Research Category: Plant Breeding & Plant Pathology

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***Principal Investigator or Chairperson of research: Prof Ravi P Singh**
University: Banaras Hindu University, Varanasi, 221005, Uttar Pradesh, India
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