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Generation Mean Analysis for Yield and Yield Component Traits in Inter-specific Cross of Rice (*Oryza sativa* L.)

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ABSTRACT

Background: Information on gene action governing yield and yield component traits need to be studied for adoption of effective breeding procedure to wards development and isolation of high yielding promising lines from the cross with resistant to bacterial leaf blight, blast and tolerance to low soil phosphorous. The present investigation was taken up in this context to estimate the gene effects for yield and yield components of the cross, YH3 × AKDRMS 21-54, using five parameter model of generation mean analysis.

Methods: The experimental material, P_1, P_2, F_1, F_2 and F_3 generations, for the investigation was generated from *Kharif* 2019 onwards and evaluated at Agricultural College, Bapatla during *Rabi* 2021-22. Gene effects for grain yield and yield attributing traits were studied.

Result: Mean effects of all traits studied were significant indicating the presence of sufficient variation for the traits. Significance of scaling tests revealed additive-dominant model as inadequate, indicating the presence of epistasis. Digenic non-allelic interaction model with five parameters, namely, *m, d, h, i* and *l* revealed that the epistatic interaction model was adequate to explain the gene action for the traits studied in the present investigation. Dominance × dominance gene interaction was pre-dominant for grain yield per plant and majority of yield component traits studied coupled with duplicate epistasis, indicating the importance of population improvement approaches, such as bi-parental mating and recurrent selection, followed by isolation of purelines in later generations of the cross for effective improvement of yield and majority of the yield component traits.

Key words: Additive, Dominance, Epistasis, Five parameter model, Gene-action, Scaling test, Quantitative traits.

INTRODUCTION

Rice (*Oryza sativa* L., $2n = 2\times = 24$) is the primary food source for billions of people in Asia and Africa, accounting for half of the world's population (Chukwu *et al.,* 2019) and also the principal source of income for unprivileged rural people. India occupies the world's largest area under rice with 42.5 million ha. and is the second highest producer with 106.65 million tonnes followed by China, contributing to 21 per cent of global rice production. It has a vital role in the food and livelihood security of the country. However, productivity of rice is only 2.54 tonnes ha^{-1} as against the global average productivity of 3.28 tonnes ha^{-1} due to cultivation of rice under wide range of ecological situations coupled with high pressure of biotic and abiotic stresses particularly bacterial leaf blight, blast and low soil Phosphorous situations (Kumar *et al*., 2017). Considering the current growth rate in population, the supply projection falls short of expected demand of 121.6 m tons by the year 2030 and 137.3 m tons by the year 2050. This is far below the current growth rate of production (0.36%) in comparison to population growth rate of 1.63 per cent. In order to achieve this target, the productivity of rice has to be brought to the level of 3.3 tons ha^{-1}, from the present scenario (IIRR, 2015). To reach the desired production level, rice varieties must be created that have a yield advantage of about 20% over commonly cultivated varieties (Kumar *et al.,* 2017). To obtain the desired genetic improvement towards the development of better lines, it is crucial to collect information about genetic architecture of quantitative traits having wider adaptability contributing to grain yield and quality (Barhate *et al.,* 2016).

Rice yield is the outcome of multiplicative interaction of several component characters. Therefore, while breeding of high yielding varieties, breeders usually face the problem of selection of desirable parents. In general, parents are

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selected on the basis of their *per se* performance, but many times high yielding genotype may/may not transmit its superiority to progeny. Hence, critical choice of parents is most important, particularly for improvement of complex quantitative characters such as yield and its components (Kacharabhai, 2015). Partitioning of genetic variance into its all the probable components *i.e,* additive, dominance and all types of epistasis with regard to individual cross therefore assumes immense value in formulating an effective and sound breeding programme (Alvarez-Castro and Le Rouzic, 2015). Among the common approaches followed to understand the nature of gene effect, generation mean analysis using first degree statistics is an accurate one and gives detailed account of various gene effects and also the quality of the genes carried by the parents (Pujar *et al.* 2022). It is also an important statistical tool for identification of epistasis using various basic generations from a cross between two parents (Bano *et al.* 2017). An earlier study showed that understanding the inheritance pattern of the genes involved in desirable traits in cereal crops, including rice, is essential for efficient breeding approaches to genetically boost yield potential (Askander, 2020; Ganapati *et al.* 2020 and Sharma *et al.* 2022). The present study was carried out in this context to estimate different gene effects in the inheritance of yield and its related traits through generation mean analysis.

MATERIALS AND METHODS

Plant material and experimental design

The present study was carried out from *Kharif* 2019 to *Rabi* 2021-22 at Agricultural College Farm, Agricultural College, Bapatla, Acharya N G Ranga Agricultural University (ANGRAU), Guntur. The experimental material was generated from the cross between the rice genotypes, namely, YH3 and AKDRMS 21-54. The female parent, YH3 is improved MTU 1121 (Sri Druthi), a high yielding and popular *Rabi* rice variety of ANGRAU, by the incorporation of tolerance to low soil phosphorus, through introgression of pup1 gene, while the male parent, AKDRMS 21-54 is improved Akshayadhan through the introgression of *Xa21 and Pi54* genes for bacterial leaf blight and blast tolerance. Five generations (P_1, P_2, F_1, F_2 and F_3) were developed from the cross, YH3 × AKDRMS 21-54 as detailed in Fig 1 and were evaluated during *Rabi* 2019-20. The crossing was initiated during *Kharif* 2019, between the female parent YH3 (possessing *Pup1*) and male parent AKDRMS 21-54 (possessing *Xa21 and Pi54)* for development of F_1's. True F_1's were identified with the help of gene-specific markers and advanced to F_2 during *Rabi* 2019-20 by selfing. F_2 plants, homozygous and positive for the target traits, were advanced to F_3 generations through selfing.

The experiment was laid in a randomized complete block design with six replications during *Rabi* 2021-22. The parental lines and F_1's, F_2's and F_3's were planted in 2 rows and 4 rows each of 4m length at a spacing of 25 cm × 10 cm. Data were recorded on 10 plants in case of parents and F1's 50 plants of F_2's and F_3's per replication.The phenotypic traits were assessed on randomly selected plants from each individual entry in the segregating generations for 12 quantitative traits namely, days to 50 per cent flowering (days), shoot length (cm), plant height (cm), productive tillers per plant, flag leaf length (cm), flag leaf width (cm), panicle length (cm), filled grains per panicle, total grains per panicle, spikelet fertility (%), test weight (g) and grain yield per plant (g).

Statistical analysis

The morphological data recorded was subjected to statistical analysis using R software (R Core team, 2013). Different statistical tests like co-efficient of variation (CV), standard error (SE), critical difference (CD) and analysis of variance (ANOVA).

Adequacy of scale was tested to fulfil the conditions, namely, additivity of gene effects and independence of heritable components from non-heritable ones. The test of first condition gives information about absence or presence of gene interactions. The test of adequacy of scales is essential because in most of the cases the estimation of additive and dominance components of variances is made assuming the absence of gene interaction. The generation mean analysis was performed according to Hayman (1958) and Jinks and Jones (1958) for the estimation of genetic components of variation, epistasis model and gene effects in two steps (i) testing for epistasis to determine the presence or absence of inter-allelic interaction and (ii) estimation of gene effects, variances and the type of epistasis involved.

Scaling test for A, B, C and D scales as suggested by Hayman and Mather (1955) and Mather and Jinks (1971) was applied to test the adequacy of simple additive-dominance model but since, back cross is absent, only C and D scales were computed as follows:

Scale C = $4F_2 - 2F_1 - P_1 - P_2 = 0$

Scale D = $4F_3 - 2F_2 - P_1 - P_2 = 0$

When the scale is adequate, the values of C and D should be zero within the limit of their respective Standard Errors.

Variances of above scales:

$VC = 16V(\overline{F_2}) + 4V(\overline{F_1}) + V(\overline{P_1}) + V(\overline{P_2}) = 0$

$VD = 16V(\overline{F_3}) + 4V(\overline{F_2}) + V(\overline{P_1}) + V(\overline{P_2}) = 0$

Standard errors of the above scale:

S.E for C scale = $\sqrt{VC}$

S.E for D scale = $\sqrt{VD}$

The 't' values were calculated as follows:

t cal for C-test = Scale C/S.E of C scale

t cal for D-test = Scale D/S.E of D scale

The calculated value of 't' was compared with tabulated value of 't' at 5% level of significance (Singh and Chaudhary. 1985). In each test, the degree of freedom is sum of the degrees of freedom of various generations (total number of observations-total number of replications) involved.

RESULTS AND DISCUSSION

The analysis of variance revealed very significant genotype differences for each of the twelve quantitative traits, indicating that the presence of sustainable amount of variability for these yield attributing traits (Table 1).

Mean performance of traits in different generations

The character wise mean performances of the five generation materials P_1, P_2, F_1, F_2 and F_3 for 12 traits were presented in Table 2. F_1 along with two segregating populations (F2 and F3) flowered and matured earlier compared to P_1 parent, which is desirable for further

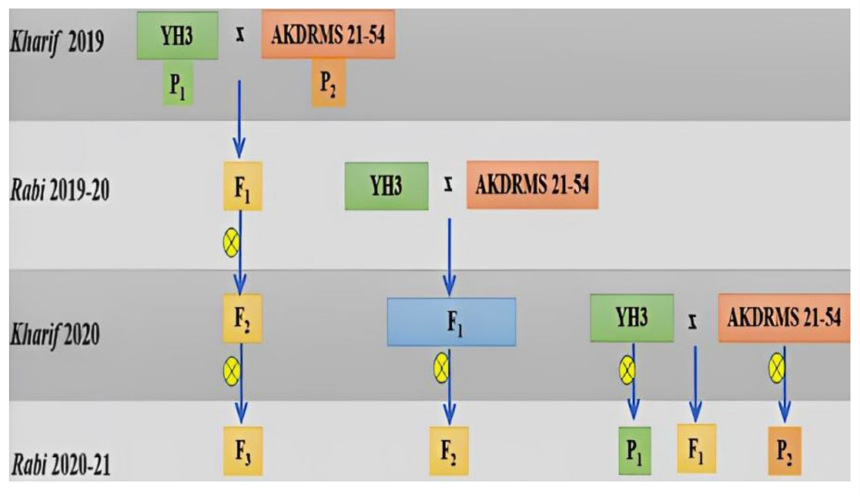

Fig 1: Generation of experimental material for generation mean analysis.

Table 1: Analysis of variance for 10 rice grain quality traits.

Characters	Source of variation (mean sum of squares)		
	Replication	Treatment	Error
Days to 50 per cent flowering	63.43	274.96**	41.51
Shoot length	20.97	114.05**	3.79
Plant height	17.19	259.12**	6.26
Productive tillers per plant	3.81	64.50**	0.77
Flag leaf length	2.53	55.76**	1.30
Flag leaf width	0.01	0.10*	0.00
Panicle length	2.98	9.51**	0.98
Filled grains per panicle	148.60	1798.65**	104.53
Total grains per panicle	386.07	1373.91**	271.89
Spikelet fertility	7.29	92.62**	11.37
Test weight	1.32	44.75**	1.46
Grain yield per plant	98.29	693.86**	30.51

*and ** Significant at 5% and 1% levels of probability, respectively.

Table 2: Estimates of generation means and standard errors of YH3 x AKDRMS 21-54 for yield and yield components.

Characters	P_1	P_2	F_1	F_2	F_3
	Mean±SEm	Mean±SEm	Mean±SEm	Mean±SEm	Mean±SEm
Days to 50 per cent flowering	92.66±0.28	87.16±0.47	75.00±1.34	90.08±0.57	88.13±0.77
Shoot length	78.29±0.69	90.03±1.00	82.76±0.85	82.97±0.48	86.24±0.67
Plant height	101.19±0.90	118.86±1.01	107.85±1.24	106.03±0.60	111.13±0.85
Productive tillers per plant	10.55±0.40	14.40±0.46	18.51±0.58	11.09±0.12	11.84±0.28
Flag leaf length	32.60±0.76	24.68±0.88	29.86±0.64	31.31±0.38	30.76±0.31
Flag leaf width	1.47±0.03	1.14±0.02	1.40±0.02	1.39±0.02	1.33±0.01
Panicle length	25.68±0.39	23.34±0.25	26.66±0.44	25.38±0.20	26.07±0.23
Filled grains per panicle	168.51±5.29	148.55±4.07	186.50±5.30	193.11±4.03	174.64±3.43
Total grains per panicle	185.50±5.60	180.99±5.59	203.53±5.49	215.99±4.23	208.99±3.20
Spikelet fertility	90.75±0.62	83.49±1.51	91.48±0.62	89.08±0.37	83.39±0.55
Test weight	26.18±0.43	20.63±0.55	28.05±0.47	25.35±0.39	24.84±0.14
Grain yield per plant	34.72±2.50	23.19±1.43	43.97±3.30	37.57±0.26	35.59±0.82

selections. Shoot length and plant height of F_2 and F3 were observed to be intermediate to the parents. These findings are in agreement with earlier reports of Singh *et al.* (2015a) for plant height. The number of productive tillers per plant, flag leaf length and width in segregating populations (F_2 and F_3) was intermediate to the parents. The less difference for panicle length was observed between parents. Among all generation materials panicle length was comparable to both parents. The F_2 and F_3 segregants possessed higher number of filled and total grains per panicle than parents. The number of filled grains, total grains per panicle and spikelet fertility in F_1 was higher than both parents. The test weight of segregating generations was intermediate to the parents and desirable for consumer preference. Most of the above results of present investigation are conformity with the findings of Ghritlahre *et al.* (2018). The YH3 parent (P_1) had recorded higher grain yield per plant compared with AKDRMS 21-54, while the F_1 yielded more grain yield compared with the parents, but the two segregating populations (F_2 and F_3), grain yield per plant were lesser than F_1 generation.

Estimates from scaling tests

Scaling tests were performed to understand the adequacy of simple additive dominance model (Table 3). The scaling test showed significance for both C and D scales for grain yield and all yield component traits studied, indicating the presence of epistasis, The significance of C scale suggests [dd] type of epistasis. The significance of D scale reveal [aa] type of epistasis, significance of C and D scales indicate presence of both [aa] and [dd] type of epistasis (Kearsey and Pooni, 1996). The results are in broad agreement with the reports of Ghritlahre *et al.* (2018).

Estimation of gene effects based on five generation means

Digenic non-allelic interaction model with five parameters namely, *m, d, h, i* and *l* revealed that the epistatic interaction model was found adequate to explain the gene action in the traits studied in the present investigation. The estimates of gene effects clearly illustrate high variation in the observed traits (Table 3 and Fig 2-3). The dominance (*h*) and dominance × dominance (*l*) gene effects displayed opposite signs for the traits *viz.*, shoot length, plant height, flag leaf length, flag leaf width, panicle length, filled grains per panicle, total grains per panicle and spikelet fertility indicating duplicate epistasis. The results are in agreement with the findings of Sudeepthi (2020) for shoot length; Ghritlahre *et al.* (2018) for plant height; Muthuvijayaragavan and Murugan (2019) and Jondhale *et al.* (2018) for flag leaf length and flag leaf width; Palaniraja (2017) for panicle length; Divya *et al.* (2014) for filled grains per panicle; Subbulakshmi *et al.* (2016) for total grains per panicle and Sand and Lal (2014) for spikelet fertility. In contrast, days to 50 per cent flowering, productive tillers per plant, test weight and grain yield per plant reported same sign for (*h*) and (*l*), indicating complementary epistasis. The results are in agreement with the findings of Savitha and Kumari (2015) for days to 50 per cent flowering;

Table 3: Estimates of genetic factors for yield and yield components in YH3 × AKDRMS 21-54.

Characters	Scaling test		Estimation of genetic factors					Epistasis
	C	D	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	[l]	
Days to 50 per cent flowering	30.5**	-7.46*	90.08**±0.58	2.75**±0.28	-4.86*±2.52	15.56**±2.29	-50.62**±7.13	Complementary
Shoot length	-1.94*	10.71**	82.98**±0.48	-5.87**±0.61	-8.86**±2.11	-19.2**±2.07	16.88**±5.74	Duplicate
Plant height	-11.61**	12.37**	106.04**±0.61	-8.83**±0.68	-12.36**±2.72	-27.85**±2.64	32.00**±7.47	Duplicate
Productive tillers per plant	-17.62**	0.22*	11.09**±0.12	-1.93**±0.31	2.95**±0.88	-6.94**±0.90	23.80**±2.37	omplementary
Flag leaf length	8.24**	3.14*	31.31**±0.38	3.96**±0.59	0.50*±1.21	7.20**±1.54	-6.80*±3.88	Duplicate
Flag leaf width	0.15*	-0.09*	1.40**±0.01	0.17**±0.02	0.19**±0.05	0.42**±0.06	-0.33*±0.14	Duplicate
Panicle length	-0.81*	4.5**	25.39**±0.21	1.17**±0.24	-0.99*±0.8	-0.80*±0.88	7.10**±2.38	Duplicate
Filled grains per panicle	82.39**	-4.72*	193.12**±4.03	9.98**±3.34	44.84**±12.70	36.84**±13.94	-116.15**±39.70	Duplicate
Total grains per panicle	90.42**	37.5*	216.00**±4.24	2.26*±3.96	10.36*±12.58	-5.42*±14.42	-70.57*±40.68	Duplicate
Spikelet fertility	-0.86*	-18.84**	89.09**±0.37	3.63**±0.82	16.77**±1.70	19.68**±1.79	-23.97**±4.52	Duplicate
Test weight	-1.52*	1.85*	25.35**±0.4	2.77**±0.35	3.15**±0.94	4.05**±1.21	4.51*±3.50	Complementary
Grain yield per plant	-44.59**	12.29**	37.57**±0.27	6.27**±1.44	6.89*±3.16	-3.10*±4.16	75.85**±10.09	Complementary

Subbulakshmi *et al.* (2016) for productive tillers per plant; Rani *et al*. (2015) for test weight and Krishna *et al*. (2018) grain yield per plant. On contrary, Singh *et al*. (2015b) had reported opposite sign for days to 50 per cent flowering, test weight and yield per plant, indicating duplicate epistasis.

The classification of gene interactions depends on the magnitudes and signs of the estimates of dominance and dominance × dominance effects, when there are many pairs of interacting genes (Mather and Jinks, 1982). The sign associated with the estimates of (*d*) and (*h*) indicates the parent that concentrates the highest number of genes for increasing the trait (Falconer, 1964). The positive sign for (*d*) was observed in the traits, days to 50 per cent flowering, flag leaf length, flag leaf width, panicle length, filled grains per panicle, total grains per panicle, spikelet fertility, test weight and grain yield per plant, indicating that YH3 contributed positively to these traits, as compared to AKDRMS 21-54. Further, the negative sign for (*h*) was

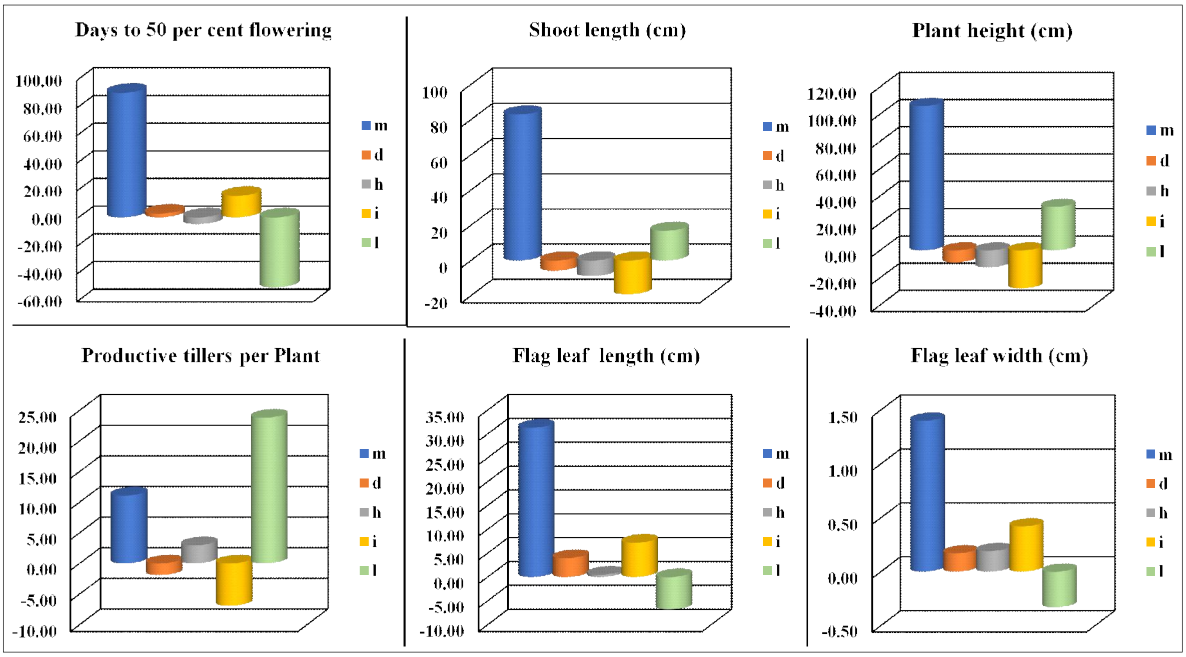

Fig 2: Genetic components of YH3 × AKDRMS 21-54 cross for morphological traits.

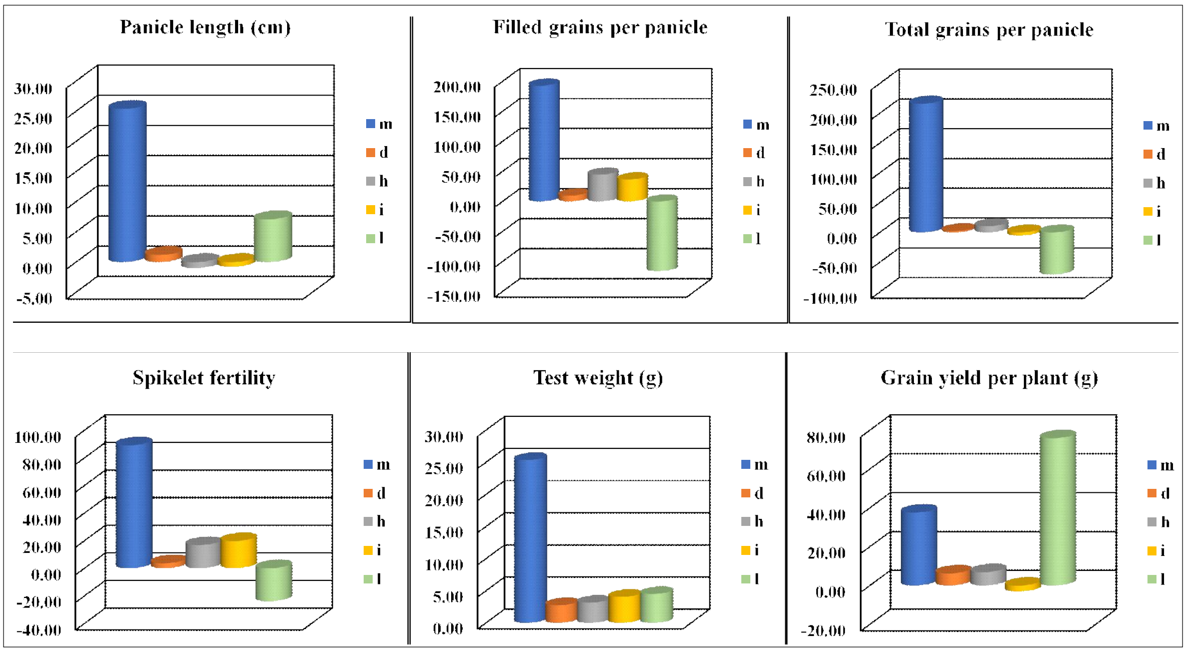

Fig 3: Genetic components of YH3 × AKDRMS 21-54 cross for grain yield and yield component trait.

observed in the traits, days to 50 per cent flowering, shoot length, plant height and panicle length indicating that the dominance was towards the resistant parent AKDRMS 21-54 as observed earlier by Ghritlahre *et al*. (2018).

In general, the choice of an appropriate breeding method for improvement of quantitative characters largely depends on the nature of gene action. Knowledge of the way genes act and interact will determine which breeding system can optimize gene action more efficiently and will help to elucidate the role of breeding systems (Hallauer and Miranda, 1988). Hayman's generation mean analysis is considered as the best method to obtain information on the nature and magnitude of gene action (Gunasekar *et al*. 2018).

CONCLUSION

The generation mean for most of the characters showed the importance of both additive and dominance type of gene effects. Among the epistatic gene effects, the additive × additive gene interaction was predominant for shoot length, flag leaf length and flag leaf width. The gene interaction is associated with homozygosity and hence is fixable in nature and therefore, selection for these traits will be very effective in early generations and breeding procedures, such as pedigree method of breeding may be adopted for isolation of desirable lines, while for all other traits, including grain yield per plant, dominance x dominance gene interaction was found to be pre-dominant. The gene interaction is not fixable and hence, population improvement approaches, such as bi-parental mating and recurrent selection, followed by isolation of purelines in later generations would be effective.

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