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GENERATION MEAN ANALYSIS FOR YIELD AND ITS ATTRIBUTING TRAITS IN RICE (*ORYZA SATIVA* L.)

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ABSTRACT

The present investigation was started from *summer*-2022 at Main Rice Research Centre, Navsari Agricultural University, Navsari to study the genetic parameters *viz.*, gene action of three crosses through generation mean analysis (each having P_1, P_2, F_1, F_2 and F_3 generations) in a Compact Family Block Design (CFBD) with three replications. On the basis of five parameter model, main effects *viz.*, mean (m), additive (d) and dominance (h) and two digenic interactions, additive × additive (i) and dominance × dominance (l) were significant for productive tillers per plant in cross II; for panicle length (cm) in crosses II and III; for grain yield per plant (g) in crosses I and II; for kernel breadth (mm) in crosses II and III; for L:B ratio in crosses II and III and amylose content (%) in crosses I and II and for grains per panicle and 100 grain weight (g) in all the crosses indicated that involvement of additive, dominance as well as epistasis interaction for controlling these traits. The duplicate epistasis was observed for plant height (cm), grains per panicle, 100 grain weight (g), grain yield per plant (g), kernel length (mm) and kernel breadth (mm) in all the three crosses; for days to flowering in cross III; for productive tillers per plant in cross II and cross III; for panicle length (cm) in cross II; for L:B ratio in crosses II and III and amylose content (%) in cross II. While, complementary epistasis was observed for days to flowering in crosses I and II; for productive tillers per plant in cross-1; for panicle length in cross I and cross III; for L:B ratio in cross-I and for amylose content in cross I and cross III.

Keywords: Additive, Dominance, Epistasis, Generation mean analysis, Five parameter model, Gene-action, Scaling test, Rice (*Oryza sativa* L.)

Introduction

Rice is the premier food crop of the world, contributing to 73 per cent of total calorie intake of the population. Self sufficiency and stability in rice production were made possible by development of high yielding varieties (Pingali, 1990). Botanically rice (*Oryza sativa* L.) belongs to genus Oryza of the tribe Oryzae which belongs to family Poaceae (Gramineae) having 24 identified species (Khush, 1997). Further, *O. sativa* L. is grouped into three subspecies, namely Japonica, Javonica and Indica. Based on its belongness as subspecies Javonica is believed to evolve from Indonesia, Japonica from Japan and Indica from India. Rice is a vital staple food that supports over half of the world's population by providing essential carbohydrates, vitamins, and minerals. It plays a crucial economic role, offering livelihoods to millions of farmers and contributing significantly to the economies of major rice-producing countries. Culturally, rice is integral to numerous culinary traditions and rituals, symbolizing prosperity and fertility. Its cultivation is key to global food security, although it poses environmental challenges such as methane emissions and water usage. Overall, rice's

importance is reflected in its nutritional value, economic impact, cultural significance, and role in global trade and food systems.

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 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 and Ganapati *et al*., 2020). 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

The experimental material consisting of five generations (P_1, P_2, F_1, F_2 and F_3) of each of the three crosses. The material comprising of four genetically diverse parents of rice (IRBB 55, Mahisagar, GR-11 and TN-1) to develop three F_1 hybrids *i.e*., IRBB 55 × Mahisagar (Cross-I), IRBB 55 × GR-11 (Cross-II) and IRBB 55 × TN-1 (Cross-III). The F_1S were generated by crossing of above four parents during *summer*-2022. Selfing of F_1S was done in *kharif*-2022 with their respective parents. Selfing of F_2S was done during *summer*-2023 to get F_3S. The evaluation trial was conducted in *kharif*-2023 at Main Rice Research Centre, Navsari Agricultural University, Navsari. Each replication was divided in five compact blocks. Each three crosses consisting of five generations were randomly allotted to the blocks. Five generations were then randomly allotted to each plot within a block. Each plot consisted of two rows of parents and F_1S, fifteen rows of the F_3 and thirty rows of the F_2 generations of each cross. Twenty plants were planted in each row. The observation was recorded for eleven traits *viz*, days to flowering, plant height (cm), productive tillers per plant, panicle length (cm), grains per panicle, 100 grain weight (g), grain yield per plant (g), kernel length (mm), kernel breadth (mm), L:B ratio and amylose content (%). The biometrical techniques to detect and estimate the additive (d), dominance (h) and genetic interactions viz., additive × additive (i), dominance × dominance (l) from five generations have been analysed according to Mather (1949), Hayman (1958) and Jinks and Jones (1958) using Windostat.

Statistical analysis

The morphological data recorded was subjected to statistical analysis using Windostat Software at statistics department of N.M. Collage of Agriculture, Navsari Agricultural University.

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 in present investigation and follow the five parameter generation mean analysis model, only C and D scales were computed as follows:

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$$

$$D = 4\bar{F}_3 - 2\bar{F}_2 - \bar{P}_1 - \bar{P}_2$$

The variances of the estimates were computed using following formulae:

$$V_C = 16V(\bar{F}_2) + 4V(\bar{F}_1) + V(\bar{P}_1) + V(\bar{P}_2)$$

$$V_D = 16V(\bar{F}_3) + 4V(\bar{F}_2) + V(\bar{P}_1) + V(\bar{P}_2)$$

The standard error of each test was calculated as square root of variance as under:

$$S.E.(C) = \sqrt{V_C}$$

$$S.E.(D) = \sqrt{V_D}$$

The significance of each test was tested by calculating the 't' test value as follows:

$$t(C) = \frac{C}{S.E.(C)}$$

$$t(D) = \frac{D}{S.E.(D)}$$

The calculated values of 't' were compared with tabulated values of 't' at 5 % (1.960) and 1 % (2.575) levels of significance.

Result and Discussion

Estimates from scaling tests

Scaling tests were performed to understand the adequacy of simple additive dominance model (Table 1). The individual scaling tests 'C' and 'D' revealed the presence of epistasis. This indicated that the genetic variation could not be described to additive and dominance effect alone, but epistasis also plays a major role. Epistasis, or interactions between genes, has long been recognized to be fundamentally important to understand both the structure and function of genetic pathways and the evolutionary dynamics of complex genetic systems. The significance of C scale suggests (dominance × dominance) type of epistasis. The significance of D scale reveal (additive × additive) type of epistasis, significance of both C and D scales indicate presence of both (additive × additive) and (dominant × dominant) type of epistasis (Kearsey and Pooni, 1996). The results are in broad agreement with the reports of Kumar *et al*. (2023).

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 1, 2 and 3).

Table 1: Estimation of scaling tests and gene effects for days to flowering, plant height (cm), productive tillers per plant and panicle length (cm)

Crosses	Gene effect											
	Scaling test		Five parameter model					Three parameter model			χ^2 at 2 d.f.	Types of epistasis
	C	D	*m*	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	$[\hat{l}]$	*m*	$[\hat{d}]$	$[\hat{h}]$		
Days to flowering												
I	8.62**	6.84**	97.58**	2.59**	-3.53**	2.06*	-2.37	-	-	-	124.10**	C
II	8.79**	1.17	101.39**	-3.34**	2.23	-6.00**	-10.16*	-	-	-	41.17**	C
II	-2.89*	-9.46**	97.11**	-1.21**	3.73**	3.41**	-8.76*				64.00**	D
Plant height (cm												
I	25.60**	31.46**	122.36**	-4.05**	-6.35**	-24.79**	7.81	-	-	-	411.15**	D
II	-29.11**	25.45**	109.62	-12.7**	-5.46*	-47.22**	72.74**	-	-	-	195.25**	D
III	22.21**	3.20	113.77**	-2.03**	21.53**	-2.50	-25.34**				111.99**	D
Productive tillers per plant												
I	-2.96**	-0.65	10.66**	0.09	0.62	0.13	3.08**	-	-	-	28.17**	C
II	-0.81	-8.54**	10.32**	1.57**	7.56**	8.69**	-10.32**	-	-	-	521.74**	D
III	-0.98*	-1.35*	11.21**	0.41**	2.06**	1.55**	-0.48	-	-	-	13.71**	D
Panicle length (cm)												
I	-7.73**	-1.49*	23.07**	0.08	0.21	-0.12	8.32**	-	-	-	224.89**	C
II	-3.36**	-7.46**	23.02**	3.94**	8.86**	12.30**	-5.47*	-	-	-	162.34**	D
III	-7.24**	-4.01**	23.46**	1.05**	3.48**	3.58**	4.30*	-	-	-	257.02**	C

*,** significant at 5% and 1% level of significance respectively

Cross 1 : IRBB55 × Mahisagar

Cross 2 : IRBB55 × GR-11

Cross 3: IRBB55 × TN-1

Table 2: Estimation of scaling tests and gene effects for grain per panicle, 100 grain weight (g), grain yield per plant (g) and kernel length (cm)

Crosses	Gene effect											
	Scaling test		Five parameter model					Three parameter model			χ^2 at 2 d.f.	Types of epistasis
	C	D	*m*	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{l}$]	*m*	[$\hat{d}$]	[$\hat{h}$]		
Grain per panicle												
I	101.81**	50.20**	244.88**	-12.65**	27.62**	-41.8**	-68.81**	-	-	-	345.33**	D
II	-52.69**	-68.63**	167.35**	11.28**	54.65**	59.54**	-21.25*	-	-	-	7.72**	D
II	176.22**	41.06**	223.48**	30.36**	55.82**	62.71**	-180.21**	-	-	-	36.22**	D
100 grain weight (g)												
I	0.62**	-0.87**	2.58**	-0.12**	1.10**	0.44**	-1.98**	-	-	-	174.49**	D
II	-52.69**	-68.63**	167.35**	11.28**	54.65**	59.54**	-21.25**	-	-	-	310.95**	D
III	176.22**	41.06**	223.48**	30.36**	55.82**	62.71**	-180.21**	-	-	-	1076.23**	D
Grain yield per plant (g)												
I	6.48**	-5.76**	34.69**	5.10**	11.91**	15.13**	-16.34**	-	-	-	123.25**	D
II	-52.69**	-68.63**	167.35**	11.28**	54.65**	59.54**	-21.25*	-	-	-	7.72*	D
III	176.22**	41.06**	223.48**	30.36	55.82**	62.71**	-180.21**	-	-	-	1076.63**	D
Kernel length (cm)												
I	-0.21**	0.02	6.69**	-0.10**	-0.03	-0.24	0.31*	-	-	-	14.19*	D
II	1.15**	0.27**	6.67**	0.48**	0.48**	0.97	-1.17**	-	-	-	23.77**	D
III	0.27**	0.015	6.41**	0.46**	0.37**	0.96**	-0.34	-	-	-	0.029	D

*,** significant at 5% and 1% level of significance respectively

Cross 1 : IRBB55 × Mahisagar

Cross 2 : IRBB55 × GR-11

Cross 3: IRBB55 × TN-1

Table 3: Estimation of scaling tests and gene effects for kernel breadth (mm), L: B ratio and Amylose content (%)

Crosses	Gene effect											
	Scaling test		Five parameter model					Three parameter model			χ^2 at 2 d.f.	Types of epistasis
	C	**D**	***M***	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{l}$]	***m***	[$\hat{d}$]	[$\hat{h}$]		
Kernel breadth (cm)												
I	-0.21**	0.02	6.69**	-0.09**	-0.03	-0.24*	0.31	-	-	-	14.19**	D
II	1.15**	0.27**	6.67**	0.48**	0.48**	0.97**	-1.17**	-	-	-	23.77**	D
III	0.27*	0.015	6.41**	0.63**	0.37**	0.96**	-0.34*	-	-	-	12.92**	D
L:B ratio												
I	0.33**	-0.051	3.22**	-0.08**	-0.05	-0.06	-0.51**	-	-	-	24.07**	C
II	0.28**	-0.22**	3.26**	0.026*	0.32**	0.25**	-0.67**	-	-	-	25.42**	D
III	0.42**	-0.069	3.13**	0.19**	0.30**	0.50**	-0.65**	-	-	-	63.20**	D
Amylose content (%)												
I	-2.59**	0.44	24.08**	-0.49**	0.66*	-1.70**	4.04**	-	-	-	65.87**	C
II	-0.14	-2.25**	23.15**	0.36**	1.54**	2.19**	-2.80**	-	-	-	54.22**	D
III	-9.95**	-9.49**	23.10**	-1.46**	5.95**	1.76**	0.61	-	-	-	1.12	C

*,** significant at 5% and 1% level of significance respectively

Cross 1 :IRBB55 × Mahisagar

Cross 2 :IRBB55 × GR-11

Cross 3: IRBB55 × TN-1

The result obtained from five parameters model revealed that in addition to the significance of mean (m), additive (d) dominance (h) effects and the two digenic interactions additive × additive (i) and dominance × dominance (l) were significant for days to flowering in cross III; productive tillers per plant in cross II; panicle length (cm) in cross II and cross III; grains per panicle and 100 grain weight (g) in all the three crosses; grain yield per plant (g) in cross I and cross II; kernel breadth (mm) and L:B ratio in cross II and cross III and amylose content (%) in cross I and cross II. These results are in agreement with those obtained by Singh *et al.* (2007), Roy and Senapati (2011), Patel *et al.* (2015), Rani *et al.* (2015), Sultana *et al.* (2016) and Kumar *et al.* (2017).

The highly significant mean values from the generation mean analysis in all the crosses except for plant height (cm) in cross II showed that the five generations differed from each other and these all studied traits are quantitatively inherited. The additive (d) effect found significant in cross I for days to flowering; in cross II and cross III for productive tillers per plant, panicle length (cm), grains per panicle, 100 grain weight (g), kernel length (mm), kernel breadth (mm) and L:B ratio and in cross II for amylose content (%). However, the additive (d) effect found significant and negative in cross II and III for days to flowering, for plant height (cm) in all the three crosses, in cross I for grains per panicle, 100 grain weight (g), kernel length (mm), kernel breadth (mm), and L:B ratio; in cross II and III for amylose content (%).

The hybrid showing positive and significant dominance (h) effects for days to flowering in cross II; plant height (cm) in cross III; productive tillers per plant, panicle length (cm), grains per panicle, 100 grain weight (g), grain yield per plant and amylose content (%) in all the three crosses; kernel length (mm), kernel breadth (mm) and L:B ratio in cross II and cross III. These results are in agreement with those obtained by Roy and Senapati (2011), Rani *et al.* (2015) and Sultana *et al.* (2016). However, Significant and negative dominance (h) effect was observed for days to flowering and plant height (cm) in cross I and cross II; kernel length (mm), kernel breadth (mm) and L:B ratio in cross I.

The magnitude of dominance (h) component was higher than that of additive (d) effect, suggesting greater importance of dominance effect in the expression of most of the studied characters. Epistasis gene effects are known to contribute a sizable part of variation in the genetic makeup of character which shows higher estimate of dominance effects (Gamble, 1962).

Considering the contribution of epistasis gene effect for any character in relation to magnitude, dominance × dominance (l) interaction had enhancing effect as compare to additive × additive (i) in case of plant height (cm) in cross I and II; productive tillers per plant in cross I; panicle length (cm) in cross I and III; kernel length (mm) and kernel breadth (mm) in cross I and amylose content (%) in cross I. The sign of dominance × dominance (l) component was positive in these crosses indicating their enhancing effect in the expression of that character in all three crosses of rice. Non fixable gene effect was important in the expression of these traits in these crosses could be exploited by bi-parental mating of recurrent selection or the use of population improvement concept as an alternative to conventional method.

The additive × additive (i) interaction showed positive and significant value in case of days to flowering in cross I and III; productive tillers per plant, 100 grain weight (g) and grain yield per plant (g) in all three crosses; for panicle length (cm), grains per panicle, kernel length (cm), kernel breadth (mm), L:B ratio and amylose content (%) in cross II and III. This indicated better response to selection pressure in population for these characters. In these crosses, improvement could be made by cyclic method of breeding in which desirable recombinants are selected and intercrossed to pool the favorable genes for synthesizing the elite population.

The sign of dominance (h) and dominance × dominance (l) parameters in opposite directions indicates involvement of duplicate type of epistasis in the inheritance of a trait. The duplicate type of epistasis was observed for days to flowering in cross III; productive tillers per plant and L:B ratio in cross II and cross III; panicle length (cm) and amylose content (%) in cross II; plant height (cm), grains per panicle, 100 grain weight (g), grain yield per plant (g), kernel length (mm) and kernel breadth (mm) in all the three crosses. The presence of duplicate epistasis would be detrimental for rapid progress, making it difficult to fix genotypes with increased level of character manifestation because the opposite effect of one parameter would be cancelled out by the negative effect of another parameter.

The sign of dominance (h) and dominance × dominance (l) parameter being similar sign indicates the involvement of complementary epistasis in the expression of the trait. Presence of complementary effect of traits will produce new recombinants capable of improving yield. The complementary epistasis were observed for days to flowering in cross I and II; productive tillers per plant and L:B ratio in cross I ; and panicle length (mm) and amylose content (%) in cross I and III.

Additive and non-additive or additive and dominant gene actions played a major role in most of the crosses for most of the traits included in present investigation. This suggested that homozygous recombinants along with desired phenotype of trait could be developed by following reciprocal recurrent selection since it is designed to improve the frequency of favourable alleles (for the trait undergoing selection) in a population for quantitative traits, further breeding efforts are needed to release a cultivar from a recurrent selection population.

The additive component of variation can be exploited by simple pedigree selection. Mass selection for several early generation aimed at the improvement of heterozygous population by modifying the frequencies of desirable genes followed by single plant selection in the resulting material would be cheapest and quickest procedure. However, the presence of non-fixable (h, j and l) component together with duplicate type of epistasis may cause delay in the improvement in trait through selection in early generations. Under this situation, progeny could be achieved and the selection is delayed to later generations. Besides these, in case of preponderance of additive genetic variance, genetic improvement in yield would be easier through indirect selection of its component traits (Mori *et al.*, 2022).

Estimation of additive (d) and dominance (h) component varied from cross to cross and trait to trait. The variable expression of gene effect in different crosses might be due to the genetic makeup of a particular cross and the effect of environmental condition on the expression of different traits.

Conclusion

The generation mean for most of the characters showed the importance of both additive and dominance type of gene effects. In such circumstances biparental mating design or reciprocal recurrent selection can be followed for further recombination of alleles to produce desirable segregants. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages. Diallel selective mating system proposed by Jensen (1970) could also be followed to break such undesirable linkages between two or more genes and to produce desirable recombinants. Simple selection procedures or pedigree breeding method is sufficient to harness additive gene action. But the presence of dominance gene action in most of the characters warrants postponement of selection to later generations after effecting crosses. Heterosis breeding procedures are effective in harnessing dominance gene action to the full extent.

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