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Gene effect estimation in elite rice (*Oryza sativa* L.) crosses using generation mean analysis

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Abstract
At the Zonal Agricultural Research Station in Mandya, an experiment was conducted to investigate the gene action governing yield and its attributing traits for two crosses using three different rice genotypes. To explore the generation mean analysis for yield and yield attributing features, the experimental material comprised of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) obtained from two crossings employing three parents. The presence of epistasis in the expression of grain yield and its components was revealed by the Generation mean analysis. The presence of significant additive effects in the crosses KMP149 x IC2 and KMP149 x IC10, demonstrated that direct selection for yield improvement was beneficial. Given the great variability of the interaction components, a cross and trait specific breeding strategy, such as direct selection and generation of pure lines, is recommended for yield improvement.

Keywords: Gene, estimation, rice, crosses, *Oryza sativa* L.

Introduction
Any breeding program's effectiveness hinges on a detailed grasp of the genotypes' genetic architecture and the nature of gene activation. The component variance is estimated using generation mean analysis, which offers information on the prevalent kind of gene activity for the various features (Hayman, 1958; Jinks & Jones, 1958) [3, 4]. Apart from genetic components of variance, generation mean analysis can reveal the nature of inter-allelic interaction. Generation mean analysis is a tool for designing the most appropriate breeding approaches to develop crop varieties with desired traits and is commonly used in studies on the inheritance of quantitative traits (Uzokwe *et al*., 2017) [20].

This sort of analysis reveals the relative relevance of the genes' average effects, such as additive effects (d), dominance deviations (h), and non-allelic gene interactions, such as additive x additive (i) additive x dominance (j), and dominance x dominance (k) (Subbalaxmi *et al.,* 2016; Uzokwe *et al*., 2017) [20]. The goal of this work was to use generation mean analysis to better understand the gene action of yield and its attributing features in rice, which aids in determining an appropriate strategy for improving various traits.

Materials and Methods
Three rice genotypes *viz.* IC2, IC10 and KMP149 were selected based on contrasting characters *viz.,* grain size and flowering duration and developed material (F_1, F_2, BC_1 and BC_2) from two independent crosses (KMP149 x IC2, KMP149 x IC10) during *Rabi*, 2019, *kharif* 2019-20 and *Rabi* 2020 at Zonal Agricultural Research Station, V. C. Farm, Mandya, to study the gene action governing yield and its attributing traits. Generation Mean Analysis was carried out for traits *viz.,* plant height (cm), No. of tillers (Nos.), Days to maturity (days), Panicle length (cm), No. of grains per panicle (Nos.), Weight of panicle (gm), Test weight (gm), Grain yield per plant (gm), Grain length (mm), Grain width (mm) and L/B ratio.
Variation for kernel dimensions such as medium slender x short bold (cross 1) and medium slender x long bold (cross 2) and flowering duration was used as a criterion for choosing parents for the generation mean analysis. The entire work (crossing and evaluation) was taken up at Zonal Agricultural Research Station (ZARS), V. C. Farm, Mandya.
During *Rabi*, 2019 crossing programme was taken up to get F_1 seed from these two crosses. During *Kharif* 2019-20, these F_1s were raised to get F_2 seed and simultaneous these F_1s were mated with their respective parents to get BC_1 and BC_2 seed of two crosses in the same season. Thus, seed of six basic generations, P_1, P_2, F_1, F_2, BC_1 and BC_2 was in hand for these two crosses at the end of the season *Kharif* 2019-20.

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During *Rabi*, 2020 P_1, P_2, F_1, F_2, BC_1 and BC_2 of both the crosses were raised to study the generation mean analysis. The material was sown in augmented design. Recommended cultural practices were adopted. The total number of populations raised were, 20 for each parent, 50 for F_1s, 100 for back cross generations and 200 for F_2s.

Statistical analysis

To confirm the data adequacy, Mather's (1949) [8] scaling test (A, B, C, and D) was performed for confirmation of additive-dominance model, as reported by Singh and Chaudhary (2012).

$A = P_1 + F_1 - 2BC_1 = \frac{1}{2} ([i] - [j] + [l])$
$B = P_2 + F_1 - 2BC_2 = \frac{1}{2} ([i] + [i] + [l])$
$C = P_1 + P_2 + 2F_1 - 4F_2 = 2[i] + [l]$
$D = 2F_2 - BC_1 - BC_2$

Estimates of various gene effects, allelic interaction, and their test of significance were computed by a six-parameter model of Hayman (1958) [3] and Jinks and Jones (1958) [4] by the following equations:

$m = \text{Mean} = F_2$
$d = \text{Additive effect} = BC_1 - BC_2$
$h = \text{Dominance effect} = 2BC_1 + 2BC_{2} + F_1 - 4F_2 - (1/2) P_1 - (1/2) P_2$
$i = \text{Additive} \times \text{Additive genetic interaction}$
$= 2BC_1 + 2BC_2 - 4F_2$
$j = \text{Additive} \times \text{Dominance genetic interaction}$
$= 2BC_1 - P_1 - 2BC_2 + P_2$
$l = \text{Dominance} \times \text{Dominance genetic interaction}$
$= P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$

Results and Discussion

All four scaling tests (A, B, C, and D) were extremely significant for all of the characters in this study, demonstrating that the additive-dominance model is inadequate to explain the inheritance of yield and its contributing characters. Table 1, 2 and 3 show the results of individual scaling tests as well as estimates of mean (m), additive gene effect (d), dominance gene effect (h), and epistatic interactions, such as additive x additive (i) additive x dominance (j), and dominance x dominance (l).

For all the characters in the two crosses, the A, B, C, and D scaling tests revealed that at least one, two, or all four scales were significant, demonstrating the presence of non-allelic interaction in the inheritance of the characters under consideration. Weight of panicle, grain width, L/B ratio of cross 1 and test weight, grain length, grain width, L/B ratio of cross II, on the other hand, had non-significant values for all four scales, showing that inheritance is non-interacting. In all the features showing epistasis, either one or both scaling tests were found to be significant.

When the simple additive-dominance model failed to explain variation in generation means, a six-parameter model with three digenic interaction parameters was developed, proposed by Hayman (1958) [3] was applied.

In cross-I, the results revealed that, in addition to the significance of the mean (m), additive (d), and dominance (h) effects, all three digenic interactions additive x additive (i) additive x dominance (j), and dominance x dominance (l) were significant for plant height, days to maturity, panicle length, number of grains/panicle, and grain yield per plant and

in cross-II for no. of tillers, days to maturity, no. of grains/panicle, panicle weight, and grain yield per plant. These findings are consistent with those obtained by Kumar *et al.* (2017) [5].

When there are several pairs of interacting genes, the magnitudes and signs of the estimations of dominance and dominant effects determine the classification of gene interactions (Mather and Jinks 1982) [9]. The parent with the highest number of genes for increasing the trait is indicated by the sign linked with the estimates of (d) and (h) (Falconer 1989) [2]. In cross-I, the additive (d) impact was shown to be substantial and positive for the number of tillers, days to maturity, panicle length, number of grains/panicle, panicle weight, grain yield per plant, grain length and L: B ratio; in the case of cross-II for the number of tillers, days to maturity, panicle length, number of grains/panicle, panicle weight and grain yield/plant.

Similarly, in cross-I for plant height, test weight, and grain width, the additive (d) effect was significant and negative; in cross-II for plant height, test weight, grain length, grain width, and L: B ratio, the additive (d) effect was significant and negative (Paul *et al.* 2003; Thirugnanakumar *et al.* 2007; Li *et al.* 2010) [12, 19, 6] which explained dominance genetic effect in yield related traits in rice. On the contrary, Ray and Islam (2008) and Sharifi *et al.* (2011) [13, 15] have reported the importance of additive effects. Simple pedigree selection can take use of the additive component of variation. The cheapest and quickest technique would be mass selection for multiple early generations targeted at improving heterozygous populations by adjusting the frequencies of desirable genes, followed by single plant selection in the resulting material. However, the presence of non-fixable (h, j, and l) components, as well as duplicate types of epistasis, may create a delay in early generations in the development of this feature through selection. Progeny may be produced in this condition, and selection would be deferred to later generations. For days to blooming, plant height, and productive tillers per plant, these findings match those of Kumar *et al.* (2017) [5].

For plant height, days to maturity, no. of grains and grain yield per plant, the dominance (h) effects were positive and significant; for cross-II, the dominance (h) effects were positive and significant for no. of tillers, days to maturity, weight of panicle, test weight, and grain width. These findings corroborate those of Nayak *et al.* (2007) [10] for grains per panicle and 100 seed weight; Patel *et al.* (2015) [11] for productive tillers per plant, grains per panicle, 100 seed weight, grain yield per plant, straw yield per plant, harvest index, Sultana *et al.* (2016) [18] for grains per panicle, 100 seed weight.

In cross-I, there was a significant and negative dominance (h) effect for panicle length, test weight, grain length, and L: B ratio; in cross-II, there was a significant and negative dominance (h) impact for panicle length, no. of grains/panicle, and grain yield/plant.

For panicle length, weight of panicle, test weight, grain length, and L: B ratio in cross-I, the sign of dominance x dominance (l) effect was positive; and also in cross II, for panicle length, no. of grains/panicle, grain yield/plant, and L: B ratio, the sign of dominance x dominance (l) impact was positive. In these crosses, the sign of the dominance x dominance (l) component was positive, indicating that they had a favourable effect on the expression of that trait in both

the crosses. The importance of non-fixable gene effects in the expression of these traits in these crosses could be exploited by bi-parental mating of recurrent selection or the use of the population improvement concept as an alternative to the usual technique.

The sign of dominance x dominance (l) effect was negative for plant height, no. of tillers, days to maturity, panicle length, no. of grains/panicle and grain yield per plant in cross-I; for plant height, no. of tillers, days maturity, weight of panicle, test weight, grain length and grain width, indicating the reducing effect in the expression of these characters, while negative sign of dominance x dominance (l) component for days to maturity in cross-I and cross-II suggesting the beneficial effect for early flowering of this crop. The sign of the dominance x dominance (l) component was positive in the other characters, indicating that they had a favourable effect on their expression in both rice crosses. In comparison to additive x dominance (j) and dominance x dominance (l) the additive x additive (i) interaction had a bigger effect.

The additive x additive (i) effect found significant and positive for plant height, days to maturity, no. of grains/panicle and grain yield per plant in cross-I; for plant

height, days to maturity in cross-II. This suggested that these traits had a better response to population selection pressure. Improvements could be made in these crossings using a cyclic breeding strategy, in which desirable recombinants are selected and intercrossed to pool the favourable genes for synthesising the elite population. Similar results were obtained by Sabesan (2005), Mahalingam Nadarajan (2010) and Chamundeswari *et al*. (2013) [14, 7, 1].

In cross-I and cross-II, significant additive (d) and additive x additive (i) epistasis was detected for days to maturity, number of grains per panicle, and grain yield per plant. For grains per panicle and 100 seed weight, these results are consistent with those found by Nayak *et al*. (2007) [10].

Duplicate epistasis was detected in almost all traits except panicle weight in cross I and L: B ratio in cross II, making it difficult to fix genotypes with elevated levels of character manifestation because one parameter's opposite effect would be balanced out by the negative influence of another parameter. In cross-I, complimentary epistasis was detected for panicle weight, suggesting that early generation selection might be successful.

Table 1: Scaling tests of generation means for the cross KMP-149 x IC2 for different traits

	KMP-149 X IC2			
	Scales			
SL No.	Characteristics Yield traits	A	B	C	D
1	Plant height	17.711**±2.673	21.943**±2.138	-29.168**±29.168	-12.468**±1.818
2	No. of tillers	-3.800** ±0.578	2.490**±0.575	-3.230**±1.186	-0.960±0.371
3	Days to maturity	-19.390**±2.644	40.930**±2.020	-10.400**±3.643	-15.970**±-15.970
4	Panicle length	-3.638** ±0.374	1.555**±0.323	1.173±0.722	1.628**±0.279
5	No. of grains /panicle	-72.9 10** ±14.580	74.080**±12.097	-142.770**±22.860	-71.970**±9.865
6	Weight of panicle	-1.025±0.592	1.525±0.821	-1.288±0.841	-0.894±0.650
8	Test weight (g)	1.364*±0.586	-2.711**±0.637	1.165±1.198	1.256**±0.420
9	Grain yield/plant	-26.555**±1.275	21.010**±1.307	-25.359**±2.408	-9.907**±0.592
10	Grain length	-0.704**±0.101	-0.136±0.103	0.384±0.200	0.612**±0.088
11	Grain width	0.555±0.068	-0.357±0.078	0.142±0.261	-0.028±0.130
12	L/B ratio	-0.844±0.071	0.273±0.083	-0.312±0.139	0.129±0.066

Table 2: Scaling tests of generation means for the cross KMP-149 x IC10 for different traits

	KMP-149 X IC10			
	Scales			
SL No.	Characteristics Yield traits	A	B	C	D
1	Plant height	16.967**±1.641	-7.255**± 2.391	3.945** ± 3.325	-2.883* ± 1.014
2	No. of tillers	114.080**±13.268	163.290**±11.756	356.810**±23.617	39.720**±12.318
3	Days to maturity	-124.350**±0.770	-89.786**±0.565	-213.008**±0.969	0.564±0.115
4	Panicle length	-16.880**±0.410	-11.160**±0.413	-26.640**±0.673	0.700±0.300
5	No. of grains /panicle	-248.550**±2.591	-54.860**±3.350	-279.230**±5.415	12.090**±1.756
6	Weight of panicle	15.665**±0.238	18.385**±0.234	35.314**±0.434	0.632±0.195
8	Test weight (g)	5.078±0.340	-1.097±0.242	2.511**±0.524	-0.735±0.284
9	Grain yield/plant	-38.121**±0.774	8.305**±0.951	-16.758**±2.436	6.529**±1.169
10	Grain length	0.962±0.095	-0.692±0.095	0.018±0.169	-0.124±0.080
11	Grain width	0.497±0.070	0.071±0.063	0.425±0.120	-0.072±0.057
12	L/B ratio	-0.115±0.094	-0.377±0.084	-0.364±0.161	0.063±0.077

Table 3: Estimates of main genetic and digenic-epistatic effects for which additive-dominance model was inadequate in the inheritance of seed yield and its attributing traits in two crosses of rice

Trait	Crosses	$[\hat{m}]$	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	$[\hat{j}]$	[l]	χ^2 Statistic	Types of epistasis
Plant height	C_1	75.79**±3.71	-4.95**±0.72	48.19**±9.08	24.94**±3.64	39.65**±2.55	-20.71**±6.25	269.357	Duplicate
	C_2	98.27**±2.31	-8.25**±1.11	14.26±6.06	5.77**±2.03	24.22**±2.56	-15.48**±4.21	144.954	Duplicate
No. of tillers	C_1	7.51**±0.75	1.68**±0.14	1.37±1.81	1.92±0.74	-6.29**±0.46	-0.61±1.39	195.514	Duplicate
	C_2	88.57**±24.64	1.98**±0.16	429.73**±60.01	-79.44**±24.64	-49.21**±15.03	-197.93**±38.23	326.501	Duplicate

Days to maturity	C₁	129.56**±2.99	11.15**±1.09	84.26**±7.93	31.94**±2.79	-60.32**±2.96	-53.48**±5.39	628.790	Duplicate
	C₂	134.34**±4.33	17.35**±1.02	106.14**±9.72	26.76**±4.21	-67.50**±2.64	-116.44**±5.64	1937.291	Duplicate
Panicle length	C₁	25.55**±0.57	1.10**±0.13	-7.79**±1.34	-3.26**±0.56	-5.19**±0.37	5.34**±0.89	243.425	Duplicate
	C₂	23.60**±0.62	1.20**±0.17	-42.78**±1.58	-1.40±0.59	-5.72**±0.52	29.44**±1.04	2338.337	Duplicate
No. of grains /panicle	C₁	121.69**±19.78	52.73**±1.47	224.61**±51.14	143.94**±19.73	-146.99**±14.16	-145.11**±38.41	208.296	Duplicate
	C₂	259.51**±4.07	83.01**±2.07	-455.39**±9.53	-24.18**±3.51	-193.69**±4.20	327.59**±5.64	9440.058	Duplicate
Weight of panicle	C₁	2.49±1.30	0.39**±0.04	2.96±3.44	1.79±1.29	-2.55±1.01	2.29±2.18	8.774	Complementary
	C₂	5.42**±0.39	0.50**±0.06	50.29**±0.97	-1.26**±0.39	-2.72**±0.27	-32.79**±0.65	9289.126	Duplicate
Test weight (g)	C₁	19.35**±0.84	-1.07**±0.06	-4.85**±2.09	-2.51±0.89	4.07**±0.52	3.86±1.56	66.308	Duplicate
	C₂	15.26**±0.57	-0.96**±0.08	6.01**±1.41	1.47±0.57	6.18**±0.38	-5.45**±0.88	296.143	Duplicate
Grain yield/plant	C₁	20.99**±1.21	13.27**±0.25	26.65**±3.28	19.81**±1.18	-47.57**±0.96	-14.27**±2.91	2871.105	Duplicate
	C₂	56.31**±2.36	10.84**±0.33	-50.23**±5.15	-13.06**±2.34	-46.43**±1.07	42.87**±2.95	2883.488	Duplicate
Grain length	C₁	6.79**±0.18	0.03±0.03	-2.72**±0.44	-1.22**±0.18	-0.57**±0.12	2.06**±0.28	81.559	Duplicate
	C₂	5.64**±0.16	-0.29**±0.02	0.54±0.40	0.25±0.16	1.66**±0.11	-0.51±0.27	228.440	Duplicate
Grain width	C₁	2.41**±0.26	-0.42**±0.02	0.51±0.56	0.06±0.26	0.91**±0.09	-0.25±0.31	118.953	Duplicate
	C₂	2.0**±0.12	-0.09**±0.02	0.99**±0.29	0.14±0.11	0.43**±0.08	-0.71**±0.19	52.855	Duplicate
L/B ratio	C₁	2.59**±0.13	0.40**±0.02	-1.09**±0.33	-0.26±0.13	-1.12**±0.09	0.83**±0.22	204.378	Duplicate
	C₂	2.88**±0.16	-0.02±0.02	-0.99±0.38	-0.13±0.15	0.26±0.10	0.62±0.25	20.869	Complementary

*, ** Significant at 5% and 1% levels, respectively
Cross-I: KMP-149 × IC2, Cross-II: KMP-149 × IC10,

Conclusions

The generation mean analysis was performed by analysing grain yield and contributing attributes in six basic populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of two cross combinations (KMP149 x IC2, KMP149 x IC10). All two crosses were subjected to A, B, C, and D scaling tests to sort out the model (interacting crosses) for the characters in question, and then to six parameter models to estimate the main gene effects (m), (d), and (h), as well as their interactions (i), (j), and (l) involved in the cross for the expression of the respective trait under study. The inadequacies of the additive-dominance model was tested using a scaling test (A, B, C, and D). The presence of epistatic interaction in corresponding crossings is shown by a significant divergence of the scale (s) from zero. It's worth noting that both crossing had substantial values for all six gene effect components for grain yield and quality parameters.

The outcome of the six-parameter model revealed that, in addition to the significance of mean (m), additive (d) and dominance (h) effects and all the three digenic interactions additive x additive (i), additive x dominance (j) and dominance x dominance (l) were significant for plant height, days to maturity, panicle length, no. of grains/panicle and grain yield per plant in cross-I; for panicle length, no. of tillers, days to maturity, no. of grains/panicle, weight of panicle and grain yield per plant in cross-II. Because the sign of dominance (h) and dominant dominance (l) for most features in these four crosses was opposite, the nature of epistasis in these crosses was determined to be duplication. As a result of the observed duplicate epistasis, single plant selection may be postponed, and biparental or diallel selective mating could be used, with a few cycles of crossing promising segregants in F_2 and subsequent generations to aid in the incorporation of desirable genes into a single genetic background. In other words, this sort of epistasis tends to cancel or decrease each other's influence in hybrid combinations, obstructing selection progress. As a result, selection would have to be delayed until later generations of segregation, when dominance effects are diminished. Crosses that indicate complementing interactions, on the other hand, could be used in pedigree approaches. Biparental mating, recurrent selection, and the diallel selective mating system may be useful in obtaining desirable recombinants by leveraging both additive and non-additive gene action.

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