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Epistatic gene action of some biometric and qualitative traits in rice (*Oryza sativa* L.)

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Abstract
The success of any plant breeding programme depends to a greater extend on the nature of genetic architecture of the population handled by the breeder. In the present study, four cross combinations were chosen for generation mean analysis as they possessed high grain yield and component traits along with earliness and short stature. Four cross combinations (IR 55408-01 x IR 50, IR 55408-01 x CO 43, IR 42 x IR 50 and IR 42 x CO 43), five generations *viz.*, P_1, P_2, F_1, F_2 and F_3 were raised in RBD and gene action for various traits was studied. The scaling test revealed that simple additive-dominance model was inadequate, since any one or both the scales were significant in all the crosses for all the traits showing the existence of digenic epistatic interaction effects. Based on this, the crosses subjected to the analysis of digenic interaction model with estimates of five parameters namely, m, d, h, i and l. the results revealed that additive, dominance and two types of interactions i.e., additive x additive and dominance x dominance effects along with the complementary and duplicate interactions were found to govern yield and all its component traits.

Keywords: Rice, generation mean analysis, inheritance

Introduction
Rice is the most staple food of the world ensuring a diet fortified with 43% of calorie requirement to more than 70% of Indians to sustain them substantially than any other single crop. For increased productivity of rice to meet out the demand for the increasing population, it could be done by exploiting the variability through artificial hybridization and selection. The nature and magnitude of gene effects through simple and joint scaling tests indicated the presence of epistatic gene interaction as well as digenic interactions. The present study was undertaken with the objective to test the adequacy of additive-dominance model inheritance of various characters using simple and joint scaling tests and to study the nature and magnitude of gene effects controlling yield and yield components.

Materials and Methods
The experimental materials comprised of the parents P_1 and P_2, F_1, F_2 and F_3 generation of the four crosses *viz*., IR 55408-01 x IR 50, IR 42 x CO 43, IR 55408-01 x CO 43 and IR 42 x IR 50. Four crosses were selected based on different combination of *gca* effects of parents and *sca* effects of hybrids along with superior per se performance of yield and its component traits. The experiment was laid out in RBD design with three replications. Four selected parents were raised in a crossing block during June-September, 2009. Selfing of parents were also done to get enough seeds for generation building. Selected four hybrids were sown along with their parents to obtain F_2 population. Enough seeds were also reserved to raise the F_2 population and the harvested seeds from F_2 were also used to raise F_3 generation. Nursery sowing of all the generations was done on same day. Plants were randomly selected from each generation for data. The variances and the variance of mean were also computed for each of the five generations for all the four cross combinations studied. The adequacy of the data for a simple additive-dominance model was tested utilizing the scales, C and D as suggested by Mather (1949) [6]. Estimation of five parameters, (m), (d), (h), (i) and (l) were analysed as given by Hayman, 1958 [2]. The test of significance of the gene effects was done by 't' test.

Results and Discussion
In the present study, the scaling test revealed that simple additive-dominance model was inadequate, since any one or both the scales were significant in all the crosses for all the traits thus showing the existence of digenic epistatic interaction effects (Table 1).
In case of days to first flower, the effect of 'd' had negative and significance in crosses 2 and 3. The 'h' effect was negative and significant in crosses 1 and 3. The additive x additive 'i' effect was positive and significant in cross 2 and whereas the dominance x dominance effect

'l' was negative in cross 2 and cross 4 which indicated that selection should be postponed to later generations for improvement of this trait. This is in accordance of the results of Singh *et al*. (1996) [12] and Hasib (2004) [1]. The results indicated that the gene action is cross specific. However, as indicated by Savery (1998) [11] the 'h' and 'l' signs took opposite signs in three crosses (crosses 1, 3 and 4) indicated the presence of duplicate epistasis and same signs in cross 2, thus indicated the presence of complementary epistasis.

Table 1: Scaling tests and gene effects for different characters in rice

Components	Cross I	Cross 2	Cross 3	Cross 4
1. Days to first flower				
Scale C	-6.79* ±3.20	-15.47* ±5.10	-11.49* ±3.70	-5.53* ±2.76
D	-3.69±2.30	-16.31*±3.09	-6.11*±2.45	-7.45*±3.30
Genetic effects (m)	65.67*±0.59	63.00*±0.34	66.98*±0.28	66.23* ±0.48
(d)	0.86*±0.40	-2.40*±0.91	-1.48* ±0.49	-0.88 ±0.69
(h)	-4.77* ±2.21	-0.08 ±1.75	-2.09* ±1.02	0.28 ±1.85
(i)	1.47±2.70	3.56*±1.72	-0.79±2.16	2.37±2.95
(l)	4.13±4.50	-1.12 ±4.00	7.17 ±6.57	-2.56 ±4.92
Type of epistasis	Duplicate	Complementary	Duplicate	Duplicate
2. Plant height				
Scale C	27.5*±3.78	-8.31*±3.75	-1.81±1.79	-2.16±3.25
D	36.5*±3.45	-21.73*±3.38	-1.27±2.83	-7.50*±3.08
Genetic effects (m)	103.00*±0.80	91.50*±0.30	106.61*±0.42	73.00*±0.46
(d)	18.45*±1.46	-13.23*±1.32	-1.63±1.70	6.85*±1.08
(h)	-5.40*±2.51	5.41*±2.53	-3.38±2.38	-2.98±1.80
(i)	17.15*±3.82	-13.35*±3.39	-2.71±3.00	18.34*±4.00
(l)	12.00*±4.52	-17.89*±5.32	0.72±4.10	-7.12±4.30
Type of epistasis	Duplicate	Duplicate	Duplicate	Complementary
3. Number of productive tillers per plant				
Scale C	3.71±3.60	4.14±3.76	5.21±3.80	8.50*±3.76
D	13.67*±2.67	9.10*±3.05	9.51*±3.39	8.42*±3.30
Genetic effects (m)	22.68*±0.62	24.89*±0.60	24.00*±0.52	23.62*±0.61
(d)	1.33±0.74	-0.13±0.75	-0.80±0.63	1.99*±0.77
(h)	-1.68±2.28	-1.51±1.55	-1.01±1.74	0.77±1.78
(i)	-5.85*±2.54	-6.43*±2.78	-7.06*±3.26	-0.22±2.80
(l)	13.28*±5.70	6.61±5.19	5.73±5.78	-0.11±6.00
Type of epistasis	Duplicate	Duplicate	Duplicate	Duplicate
4. Number of grains per panicle				
Scale C	49.64*±11.46	-5.91±7.70	17.61±9.02	8.78±8.12
D	68.00*±10.36	17.29±9.60	37.23*±10.07	25.30*±8.71
Genetic effects (m)	131.62*±0.81	127.15*±0.60	125.78*±0.71	123.01*±0.63
(d)	6.34*±2.10	9.88*±1.98	-3.16±3.05	19.30*±2.67
(h)	4.52*±2.11	3.13±2.15	5.18*±2.49	3.47±2.75
(i)	-24.38*±4.86	7.24±5.90	-28.06*±7.91	23.20*±4.78
(l)	24.48*±7.05	30.93*±7.15	26.16*±8.01	22.03*±6.60
Type of epistasis	Complementary	Complementary	Complementary	Complementary
5. Thousand grain weight				
Scale C	6.99*±2.00	-1.46±2.52	4.42*±2.20	5.21*±2.30
D	2.03±1.58	1.76±1.40	0.24±1.18	3.71*±1.56
Genetic effects (m)	24.88*±0.09	23.41*±0.14	25.90*±0.10	23.93*±0.08
(d)	1.81*±0.75	-0.54±0.60	-0.09±0.14	1.36*±0.18
(h)	1.87±1.30	-0.96±1.10	2.17*±0.96	0.34±0.70
(i)	3.42*±1.58	-2.49±1.50	0.40±1.09	1.10±0.98
(l)	-6.61*±2.75	4.29*±2.12	-5.57*±2.42	-2.00±1.91
Type of epistasis	Duplicate	Duplicate	Duplicate	Duplicate
6. Grain length				
Scale C	-0.32±0.30	1.46*±0.50	0.60±0.33	-0.14±0.35
D	0.40±0.25	0.78*±0.29	0.70*±0.25	-0.80*±0.30
Genetic effects (m)	8.90*±0.04	9.10*±0.04	9.00*±0.04	8.88*±0.05
(d)	-0.01±0.09	0.38*±0.08	0.40*±0.16	-0.03±0.08
(h)	-0.16±0.18	0.25±0.16	0.35±0.17	0.58*±0.19
(i)	-0.34±0.24	0.48*±0.21	0.43*±0.21	0.45*±0.20
(l)	0.96*±0.47	-0.91*±0.45	0.13±0.36	-0.88±0.50
Type of epistasis	Duplicate	Duplicate	Complementary	Duplicate
7. Grain breadth				
Scale C	0.27±0.21	0.09±0.19	0.86*±0.24	-0.42*±0.18
D	0.83*±0.18	-0.13±0.14	0.34*±0.16	-0.10±0.14
Genetic effects (m)	2.96*±0.02	2.30*±0.06	3.01*±0.03	2.08*±0.05
(d)	0.23*±0.04	-0.13±0.08	0.19*±0.06	-0.09±0.07
(h)	0.11±0.09	-0.22*±0.10	0.27*±0.12	-0.17±0.10

(i)	-0.06±0.14	-0.42*±0.16	0.30*±0.14	-0.18±0.12
(l)	0.75*±0.32	0.24±0.30	-0.69*±0.26	0.43±0.28
Type of epistasis	Complementary	Duplicate	Duplicate	Duplicate
8. Grain L/B ratio				
Scale C	-0.69*±0.29	0.42±0.27	-0.70*±0.30	0.74*±0.37
D	-0.43*±0.20	0.26±0.19	-0.33±0.24	0.44*±0.21
Genetic effects (m)	3.20*±0.04	3.96*±0.04	3.00*±0.03	4.28*±0.02
(d)	-0.34*±0.08	0.36*±0.09	-0.11±0.08	0.13±0.07
(h)	-0.03±0.13	0.19±0.14	-0.04±0.12	-0.02±0.10
(i)	-0.50*±0.18	0.62*±0.20	-0.11±0.17	-0.15±0.15
(l)	0.35±0.26	-0.21±0.22	0.48*±0.23	0.24±0.20
Type of epistasis	Duplicate	Duplicate	Duplicate	Duplicate
9. Grain yield per plant				
Scale C	14.94*±4.90	9.35*±4.15	4.38±4.30	11.45*±5.09
D	16.10*±4.50	8.79*±3.38	1.38±3.28	13.01*±4.67
Genetic effects (m)	39.76*±0.72	38.00*±0.68	36.01*±0.80	35.16*±0.62
(d)	2.79*±1.56	-1.25±0.92	0.30±1.10	1.02±1.00
(h)	0.71±2.00	2.17±1.52	2.52*±2.25	-0.64±1.75
(i)	-2.66±2.78	-4.26*±2.10	0.41±3.00	-4.74*±2.35
(l)	1.55±4.01	-0.74±4.38	-4.00±3.98	2.08±4.72
Type of epistasis	Complementary	Duplicate	Duplicate	Duplicate

Cross 1=IR 55408-01 x IR 50 Cross 3 = IR 55408-01 x CO 43 * significant at 5% level
Cross 2=IR 42 x CO 43 Cross 4 = IR 42 x IR 50

For plant height, the additive effect 'd' was positive and significant for two crosses (cross 1 and cross 4) while it was negative and significant in cross 2.The cross 2 showed positive and significant dominance effect 'h' and cross 1 recorded negative significance for this trait. The additive x additive 'i' effect was positive and significant in the crosses 1 and 4, whereas the dominance x dominance effect 'l' was positive and significant in cross 1. whereas, the cross 2 showed negative significance. The results indicated that gene action is cross specific. The 'h' and 'l' signs took opposite signs in three crosses (crosses 1, 2 and 3) indicated the presence of duplicate epistasis and same signs in one cross (cross 4) thus indicated the presence of complementary epistasis. This is in accordance with the findings of Vivekanandan (1993) [14] and Nayak *et al*. (2007) [7].

For number of productive tillers per plant, the additive 'd' effect was positive and significant in cross 4 and non significant in cross 1 and the dominance effect 'h' was positive in cross 4 and negative in all other crosses. This indicated that gene action is cross specific. The additive x additive 'i' effect was negative and significant in cross 1, 2 and 3 whereas, the dominance x dominance effect 'l' was positive and significant in cross 1. This indicated the predominance of additive gene action and selection could be done in the immediate segregating generation for this trait. Similar findings were done by Kumaravelu (1992) [4] and Saleem *et al*. (2005) [10] in rice. The 'h' and 'l' effects revealed unlike sign in all the four crosses thus indicated the presence of duplicate epistasis.

The effect of 'd' was positive and significance in crosses 1, 2 and 4. The 'h' effect was also positive in all the crosses but significant in crosses 1 and 3 which denoted that additive gene effect seemed to be unidirectional for number of grains per panicle. The additive x additive 'i' effect was negative and significant in the crosses 1 and 2, whereas the dominance x dominance effect 'l' was positive and significant in all the crosses which indicated that selection should be postponed to later generations for improvement of this trait. This is in accordance of the results of Hasib (2004) [1] and Sabesan (2005) [9]. The results also indicated that the gene action is cross specific. However, as indicated by Venkatesan (2003) [13] the 'h' and 'l' signs took same signs in all the crosses thus, indicated the presence of complementary epistasis.

The additive effect 'd' was positive and significant for two crosses (1 and 4). The cross 3 showed positive and significant dominance effect('h') for the trait thousand grains weight. The additive x additive 'i' effect was positive and significant in cross 1 only. The cross 2 recorded significant and positive dominance x dominance effect 'l'. The 'h' and 'l' signs took opposite signs in all the four crosses which indicated the presence of duplicate epistasis. This is in accordance with the findings of Kavimani (2004) [3]. The 'h' and 'l' recorded opposite signs in all the crosses, thereby indicated the presence of dispersed alleles in the interacting loci. This is in accordance with the result of Nayak *et al*. (2007) [7].

For grain length, the additive 'd' and the dominance effect was positive and significant in two crosses (cross 2 and cross 3). This indicated that gene action is cross specific. The additive x additive 'i' effect was positive and significant in crosses 2, 3 and 4. This is the indication of that selection could be practiced in the immediate segregating generation. Whereas, the dominance x dominance effect 'l' was positive and significant in cross 1. This is in agreement of the findings of Ram *et al*. (1994) [8]. The 'h' and 'l' effects revealed unlike sign in three crosses thus indicated the presence of duplicate epistasis.

For grain breadth, the additive effect 'd' was positive and significant for two crosses (1 and 3). The cross 3 showed positive and significant dominance effect 'h' for this trait. The additive x additive 'i' effect was positive and significant in cross 3 only. The cross 1 recorded significant and positive dominance x dominance effect 'l'. The 'h' and 'l' signs took opposite signs in three crosses (crosses 2, 3 and 4) which indicated the presence of duplicate epistasis. This is in accordance with the findings of Lanzhi Li *et al*. (2008) [5]. The 'h' and 'l' recorded opposite signs in all the crosses, thereby indicated the presence of dispersed alleles in the interacting loci. This is in accordance with the result of Saleem *et al*. (2005) [10].

For grain L/B ratio, the additive effect 'd' was positive and significant in one cross (cross 2) while it was negative and significant in cross 1. The crosses 1, 3 and 4 showed negative and non significant dominance effect 'h' for this trait. The additive x additive 'i' effect was positive and significant in the cross 2, whereas the dominance x dominance effect 'l' was positive and significant in cross 3. The results indicated that gene action is cross specific. The 'h' and 'l' signs took opposite signs in all the four crosses thus indicated the presence of duplicate epistasis. This is in accordance with the findings of Hasib (2004) [1] and Sabesan (2005) [9].

Trait, grain yield per plant showed the additive effect 'd' was positive and significant in only one cross (cross 1). The 'h' effect was positive and significant in cross 3 only. The additive x additive 'i' effect was negative and significant in the crosses 2 and 4 whereas the dominance x dominance effect 'l' was positive in two crosses *i.e.,* crosses 1 and 4.The results also indicated that the gene action is cross specific. However, as indicated by Venkatesan (2003) [13] the 'h' and 'l' signs took opposite signs in three crosses thus, indicated the presence of duplicate epistasis. The 'h' and 'l' also recorded opposite signs in crosses 2, 3 and 4 thereby indicated the presence of dispersed alleles in the interacting loci. This is in accordance with the results of Kavimani (2004) [3].

Thus, it is understood and concluded as a whole additive, dominance and two types of interaction *i.e.,* additive x additive and dominance x dominance effects along with complementary and duplicate interactions were found to govern yield and all its component traits. However, predominance of unfixable and non-additive gene action was observed for all the traits. Therefore, improvement of these traits appeared to be difficult as simple pedigree breeding will not be able to fix the superior lines in the early segregating generations.

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