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Estimation of genetic components for yield in rice using generation mean analysis

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ABSTRACT

The nature of gene interaction in the inheritance of ten yield related traits was studied deploying generation mean analysis following six parameter model for parents (P_1 and P_2), F_1, F_2, B_1 and B_2 generations of two crosses in rice during wetseason. The results of the scaling tests revealed that the additive-dominance model was inadequate for all of the characters evaluated in both of the crosses, suggested the existence of epistasis in the inheritance of these characters. Additive gene effect [d] had significant contributions in both of the crosses for the expression of days to 50 per cent flowering, plant height, effective tillers per hill, spikelet per panicle, kernel length, kernel breadth, kernel L/B ratio and 1000- grain weight where as dominance [h] genetic effects was significant for all of the characters in both of the crosses except panicle length, effective tillers per hill and kernel breadth in cross I and days to 50 per cent flowering and grain yield per plant in cross II. The nature of epistasis was identified as duplicate in both of the crosses for all of the yield related traits. The present study demonstrates the importance of additive, dominance and epistatic gene effects for the inheritance of almost all the characters studied.

Key words: *rice, scaling test, generation means, epistasis*

Rice is the world's largest food crop, providing the caloric needs of millions of people daily. It plays a pivotal role in Indian economy being the staple food for two third of the population. India stands second with 108.0 million tons as China occupies the first place with 144.0 million tons in the world's production table of 479.3 million tons (USDA, 2013). In the Indian scenario, it is estimated that rice demand by 2025 will be 140 million tonnes (Mishra, 2004). This projected demand can only be met by maintaining steady increase in production over the years. The knowledge of the nature of gene action in the inheritance of yield related traits would be useful to formulate a suitable breeding programme and develop better cultivars with higher yield. The major thrust area for genetic improvement would lie in identifying desirable parents for hybridization programme. This would depend to a large extent on the knowledge of gene actions controlling various characters. Scaling test and generation mean analysis are efficient biometrical tools for assessing the importance of epistasis and estimating the gene(s) effects. The reliability of the estimates and genetic gains of selection in segregating population largely depend upon the genetic divergence of the parents involved and the precision of testing. Keeping this in view, in the present study, an attempt has been made to estimate various kinds of gene effects through standard biometrical procedures and to know the relative importance of these gene effects in the control of grain yield and its component characters in rice. A number of studies have been carried out in the past to study the inheritance of quantitative traits in rice using the generation means analysis (Somrith *et al*., 1979; Kumar *et al*., 2007; Gnanamalar and Vivekanandan, 2013; Kiani *et al*., 2013; Yadav *et al*., 2013).

MATERIALS AND METHODS

The experimental material comprising two land races namely Karmi and Dhusari and two cultivated variety

Rajendra mahsuri and Sita with F_1, F_2 of two crosses namely Karmi × Rajendra mahsuri and Dhusari × Sita along with backcrosses (B1 and B2) were used for generation means analysis. The female parents Karmi and Dhusari were tall with submergence tolerant whereas, among the male parents Rajendra mahsuri was semi dwarf high yielding variety and Sita was semi dwarf medium yielder. Six generations namely P_1, P_2, F_1, F_2, B_1 and B_2 of the two crosses were raised in a randomized block design with three replications during *kharif* season 2013-14 at experimental field of Department of Plant Breeding and Genetics, RAU, Pusa, Samastipur, Bihar. In each replication the generations were transplanted with a single seedling per hill with a spacing of 20 x 15 cm row to row and plant to plant respectively. The recommended agronomic practices were followed to obtain a good harvest. For P_1, P_2, F_1, B_1 and B_2 observations were recorded on ten randomly selected plants where as for F_2 observations were recorded from 75 randomly selected plants in each entry in each replication for the characters days to 50 % flowering, plant height (cm), panicle length (cm), effective tillers/hill, spikelet per panicle, kernel length (mm), kernel breadth (mm), kernel L/B ratio, 1000 grain weight (g) and grain yield per plant (g). The individual scaling tests were applied to test the adequacy of additive dominance model as suggested by Mather (1949) and six parameter model (Jinks and Jones 1958). Weighted least square technique was used to estimate the components of different parameters viz., 'm', 'd', 'h', 'i', 'j', and 'l'. The joint scaling test as proposed by Cavalli (1952) was also applied to test the adequacy of additive-dominance model because the joint scaling test combines, very effectively, several scaling tests into one and offers a more general and informative approach.

RESULTS AND DISCUSSION

The analysis of variance of the six generations P_1, P_2, F_1, F_2, B_1 and B_2 revealed that the six generations differed significantly for all the ten quantitative traits in the two crosses. As compared to Karmi, Rajendra mahsuri was the better performer for five of the yield related traits viz., panicle length, effective tillers per hill, spikelet per panicle, kernel L/B ratio and grain yield per plant whereas, Karmi outperformed Rajendra mahsuri for rest of the five quantitative traits *viz*., days to 50 per cent flowering, plant height, kernel length, kernel breadth and 1000 grain weight as revealed by Table 1. Dhusari performed better than Sita in seven out of ten yield component traits viz. days to 50 per cent flowering, plant height, panicle length, spikelet per panicle, kernel length, kernel breadth and 1000 grain weight whereas, Sita outperformed Dhusari for rest of the quantitative traits namely effective tillers per hill, kernel L/B ratio and grain yield per plant.

The F_1 mean performance was midway between the parental values with inclination towards better parent in cross I for spikelet per panicle, kernel length and kernel breadth and in cross II for effective tillers per hill, kernel length, kernel breadth and kernel L/B ratio. This indicated that there may be preponderance of additive gene effects in expressing these traits. However, in case of days to 50 per cent flowering, plant height, panicle length, 1000-grain weight and grain yield per plant in cross I and days to 50 per cent flowering, plant height, panicle length, spikelet per panicle, 1000-grain weight and grain yield per plant in cross II the F_1 was superior to both of the parent which indicated that the preponderance of non additive gene effect in expressing these yield related traits (Table 1). The low mean performance of F_2's as compared to F_1's was observed for days to 50 per cent flowering, plant height, panicle length, effective tillers per hill, spikelet per panicle, kernel length, kernel L/B ratio, 1000 grain weight and grain yield per plant in cross I and for eight out of ten quantitative traits in cross II except plant height and kernel breadth indicating inbreeding depression of traits as reported by Sharma *et al*. (1986), Krishna Veni *et al*. (2005) and Roy and Senapati (2011). The mean value of B_1 was higher than B_2 in respect of all the characters studied, except for spikelet per panicle, kernel L/B ratio and grain yield per plant in cross I and spikelet per panicle and grain yield per plant in cross II indicating dispersion of genes among parents for these traits. However in case of cross II, the kernel breadth and kernel L/B ratio exhibited the same mean performance in B_1 and B_2.

The scale A is negatively significant for all of the characters studied except plant height, kernel breadth, 1000-grain weight and grain yield per plant in cross I and for plant height, panicle length and kernel breadth in cross II. However, A is non-significant for effective tillers per hill and kernel length in both of the

Table 1. Mean performance and standard error of different generations of two crosses for yield components in rice

Characters	Cross I (Karmi x Rajendra mahsuri)							Cross II (Dhusari x Sita)						
	P1	P2	F1	F2	B1	B2	Mean	P1	P2	F1	F2	B1	B2	Mean
Days to50 % flowering	133.3± 0.20	114.83± 0.18	139.20± 0.70	116.89± 0.42	128.50± 0.68	123.63± 0.64	121.30± 0.47	123.83± 0.17	105.00± 0.14	124.00± 0.43	114.60± 0.45	116.57± 0.63	112.47± 0.57	115.31± 0.37
Plant height (cm)	132.28± 0.75	116.66± 0.65	177.65± 1.01	169.36± 0.49	184.27± 1.17	162.88± 1.63	163.52± 1.00	145.62± 0.68	103.18± 0.23	175.50± 1.94	181.04± 0.43	187.25± 1.84	167.91± 1.91	170.98± 1.22
Panicle length (cm)	23.78± 0.28	24.39± 0.15	25.85± 0.22	23.93± 0.06	24.12± 0.23	23.42± 0.27	24.08± 0.06	24.90± 0.20	21.42± 0.12	25.39± 0.19	25.19± 0.08	26.24± 0.22	25.45± 0.27	24.98± 0.08
Effective tillers hill^{-1}	6.50± 0.35	9.03± 0.55	6.27± 0.28	5.93± 0.13	6.93± 0.31	5.83± 0.28	6.32± 0.11	4.70± 0.30	13.03± 0.29	5.23± 0.24	4.92± 0.09	5.30± 0.23	5.27± 0.26	5.64± 0.13
Spikelet panicle^{-1}	186.67± 3.06	239.13± 4.35	203.90± 2.56	142.60± 0.84	162.97± 1.88	203.33± 3.85	165.24± 1.82	186.87± 2.23	174.77± 3.75	203.83± 2.07	181.31± 0.76	173.83± 3.34	210.33± 4.10	184.76± 0.90
	7.17± 0.01	7.31± 0.02	6.49± 0.02	6.82± 0.02	6.54± 0.01	6.91± 0.04	6.70± 0.04	6.64± 0.01	7.39± 0.02	6.94± 0.02	7.21± 0.02		7.29± 0.03	7.19± 0.01
	2.63± 0.01	2.63± 0.02	2.21± 0.02	2.61± 0.02	2.74± 0.01	2.78± 0.04	2.57± 0.04	2.67± 0.01	2.63± 0.03	2.11± 0.01	2.52± 0.02		2.63± 0.02	2.58± 0.01
L/B ratio	2.63± 0.01	2.95± 0.02	2.61± 0.02	2.39± 0.01	2.49± 0.02	2.62± 0.03	2.50± 0.01	2.82± 0.03	3.29± 0.02	2.87± 0.02	2.72± 0.01	2.78± 0.02	2.78± 0.02	2.80± 0.01
1000 grain weight (g)	28.28± 0.13	21.78± 0.09	31.72± 0.09	31.64± 0.11	31.58± 0.22	30.43± 0.25	30.49± 0.16	32.35± 0.19	22.77± 0.16	33.75± 0.20	31.49± 0.10	32.03± 0.25	31.70± 0.22	31.10± 0.15
Grain yield/ plant (g)	30.08± 0.09	34.03± 0.10	38.47± 0.09	27.98± 0.21	34.69± 0.11	35.59± 0.12	30.62± 0.23	26.53± 0.12	26.97± 0.26	34.57± 0.16	28.92± 0.18	27.98± 0.17	29.59± 0.17	29.00± 0.15

crosses. Scale B is significant for all of the characters in both of the crosses except kernel length in cross I whereas, Scale C is significant for all of the characters in both of the crosses except kernel length in cross II. These results of the scaling tests as proposed by Mather (1949) revealed that the additive-dominance model was inadequate in all of the characters evaluated in both of the crosses, suggested the existence of epistasis in the inheritance of these characters (Table 2). These findings were further substantiated by the more robust "Joint Scaling Test" proposed by Cavalli (1952), in which the significant or non significant Chi-square values indicated the presence or absence of epistasis in the inheritance of the quantitative characters studied (Table 3). Similar observations have been reported by Chakraborty and Hazarika (1996) and Srivastava *et al*. (2012).

Studies on gene effects in generation mean analysis suggested by Jinks and Jones (1958) revealed that additive gene effect [d] had significant contributions in both of the crosses for the expression of days to 50 per cent flowering, plant height, effective tillers per hill, spikelet per panicle, kernel length, kernel breadth, kernel L/B ratio and 1000-grain weight where as dominance [h] genetic effects was significant for all of the characters in both of the crosses except panicle length, effective tillers per hill and kernel breadth in cross I and days to 50 per cent flowering and grain yield per plant in cross II (Table 4). The results indicated that there exist scopes for direct selection for yield contributing traits which showed significant additive effects. Results also indicated the presence of dominance effect too, in the inheritance of the traits of interest. For number of effective tillers per plant, additive effect was reported by Robin (1997) and dominance gene effect was earlier reported by Koodalingam (1994). Both gene effects, were reported by Roy and Panwar (1993) and Hasib *et al*. (2002) for plant height, panicle length, kernel length and grain yield per plant.

The additive gene effect [d] was more important than dominance [d] gene effect in the inheritance of effective tillers per hill [d = -1.27** / h = -0.40 and kernel breadth (d = 0.25** / h = 0.22) in cross I and days to 50 per cent flowering (d = 9.42** / h = -9.82) in cross II. The results indicated much scope for improvement of these traits in respective crosses through phenotypic selection. However, the progress of selection will depend on the nature and magnitude of different interaction effects in addition to dominance effect. Seven out of ten traits namely, days to 50 per cent flowering, plant height, spikelet per panicle, kernel length, kernel L/B ratio, 1000-grain weight and grain yield per plant for cross I and eight out of ten traits *viz.*, plant height, panicle length, effective tillers per hill, spikelet per panicle, kernel length, kernel breadth, kernel L/B ratio and 1000-grain weight for cross II exhibited high significant dominance gene effect. The findings are corroborated with Singh *et al*. (1996) and Mishra and Singh (1998). When the complexity of the inheritance of quantitative characters become more, the contribution of dominance gene effects to their inheritance becomes greater (Gamble, 1962). Conversely, the contribution of additive gene effects was greater for the characters which apparently had less complex inheritance.

Among the components of epistasis, additive × additive interaction was significant and important in both of the crosses for plant height, spikelet per panicle, kernel length, kernel L/B ratio and 1000-grain weight, additive × dominance interaction was found to be operative in both of the crosses for days to 50 per cent flowering, panicle length, effective tillers per hill, spikelet per panicle, kernel breadth, 1000-grain weight and grain yield per plant whereas, dominance × dominance interaction was significant in both of the crosses for days to 50 per cent flowering, plant height, panicle length, kernel length, 1000-grain weight and grain yield per plant. These results are in close agreement with earlier findings of Khaleque *et al*. (1978) and Manna *et al*. (2002). The higher magnitude of estimates of dominance × dominance interaction as compared to additive × additive and additive × dominance interactions for plant height, panicle length, kernel breadth and 1000-grain weight in cross I and for days to 50 per cent flowering, plant height, panicle length, effective tillers per hill, kernel length, kernel breadth, kernel L/B ratio, 1000-grain weight and grain yield per plant in cross II suggested the predominant role of dominance × dominance interaction for yield components which corroborated with the observations of Dikshit and Mani (1988) and Chauhan *et al*. (1993), who reported the importance of all the three types of interactions in the inheritance of different traits. Since, the sign of dominance (h) and dominance × dominance (l) for all of the yield related traits of both crosses was

Table 2. Scales for yield components in rice for two crosses

Characters	Cross I (Karmi x Rajendra mahsuri)				Cross II (Dhusari x Sita)			
	A	B	C	D	A	B	C	D
Days to50 % flowering	-15.57**± (1.54)	-6.77**± (1.46)	-59.04**± (2.20)	-18.36**± (1.26)	-14.70**± (1.34)	-4.07**± (1.22)	-18.45**± (2.00)	0.16± (1.23)
Plant height (cm)	58.62**± (2.66)	31.46**± (3.48)	73.23**± (2.98)	-8.43**± (2.24)	53.38**± (4.22)	57.13**± (4.29)	124.34**± (4.32)	6.92*± (2.79)
Panicle length (cm)	-1.39*± (0.58)	-3.41**± (0.61)	-4.16**± (0.60)	0.32± (0.37)	2.18**± (0.52)	4.09**± (0.58)	3.63**± (0.56)	-1.32**± (0.38)
Effective tillers hill^{-1}	1.10± (0.76)	-3.63**± (0.84)	-4.35**± (1.01)	-0.91± (0.49)	0.67± (0.59)	-7.73**± (0.64)	-8.50**± (0.74)	-0.72± (0.39)
Spikelet panicle^{-1}	-64.63**± (5.48)	-36.37**± (9.20)	-263.18**± (8.11)	-81.09**± (4.60)	-43.03**± (7.35)	42.07**± (9.26)	-44.07**± (6.73)	-21.55**± (5.51)
Kernel length (mm)	-0.09± (0.09)	0.09± (0.07)	-1.07**± (0.05)	-0.53**± (0.06)	0.01± (0.04)	0.43**± (0.06)	-0.09± (0.06)	-0.27**± (0.04)
Kernel breadth (mm)	0.25**± (0.08)	0.32**± (0.08)	0.83**± (0.06)	0.13*± (0.05)	0.11*± (0.04)	0.63**± (0.05)	0.76**± (0.05)	0.01± (0.03)
L/B ratio	-0.26**± (0.04)	-0.32**± (0.06)	-1.25**± (0.05)	-0.33**± (0.03)	-0.12*± (0.05)	-0.60**± (0.05)	-0.95**± (0.06)	-0.11**± (0.03)
1000 grain weight (g)	3.15**± (0.46)	7.35**± (0.52)	13.04**± (0.51)	1.27**± (0.40)	-2.04**± (0.57)	6.89**± (0.50)	3.33**± (0.60)	-0.76*± (0.38)
Grain yield/ plant (g)	0.82**± (0.26)	-1.32**± (0.27)	-29.15**± (0.86)	-14.33**± (0.44)	-5.13**± (0.39)	-2.35**± (0.45)	-6.95**± (0.84)	0.27± (0.43)

Table 4. Estimation of component of generation means for ten characters of two crosses for yield components in rice (Jinks and Jones)

Characters	Cross I (Karmi x Rajendra mahsuri)							Cross II (Dhusari x Sita)						
	m	d	h	l	i	j	E	m	d	h	l	i	j	E
Days to50 %	87.39**±	9.27**±	66.19** ±	-14.38**±	36.71**±	-4.40**±	D	114.73** ±	9.42** ±	-9.82±	19.08**±	-0.32 ±	-5.32**±	D
flowering	(2.52)	(0.13)	(6.59)	(4.33)	(2.52)	(0.94)		(2.47)	(0.11)	(6.25)	(3.94)	(2.47)	(0.85)	
Plant height	107.62**±	7.81** ±	176.96** ±	-106.93**±	16.85**±	13.58**±	D	138.23** ±	21.22** ±	133.95**±	-96.68** ±	-13.83*±	-1.88 ±	
(cm)	(4.50)	(0.50)	(12.80)	(8.57)	(4.47	(2.07)		(5.59)	(0.36)	(16.43)	(11.45)	(5.58)	(2.67)	D
Panicle														
length (cm)	24.73**	-0.31	-4.32	5.44**	-0.64	1.01*	D	20.52**	1.74**	13.80**	-8.92**	2.65**	-0.96*	D
	± (0.77)	± (0.16	± (2.25)	± (1.54)	± (0.75)	± (0.39)		± (0.78)	± (0.12)	± (2.21)	± (1.49)	± (0.77)	± (0.37)	
Effective	5.95**	-1.27**	-0.40 ±	0.72 ±	1.82 ±	2.37** ±	D	7.43**	-4.17**	-7.83**	5.63**	1.44	4.20**	D
tillers hill^{-1}	± (1.04)	± (0.33)	(2.89)	(1.95)	(0.98)	(0.53)		± (0.81)	± (0.21)	± (2.29)	± (1.56)	± (0.78)	± (0.40)	
Spikelet	50.72**	-26.23**	214.36**	-61.18**	162.18**	-14.13**	D	137.71**	6.05**	108.26**	-42.14**	43.11**	-42.55**	D
panicle^{-1}	± (9.57)	± (2.66)	± (27.84)	±(18.95)	± (9.19	± (5.04)		± (1.23)	± (2.18)	± (33.05)	± (22.22)	± (11.01)	± (5.73)	
Kernel length	5.72**	0.30**	2.16**	-1.07**	1.07** ±	-0.09 ±	D	6.64**	0.23**	1.55**	-0.98**	0.53**	-0.21**	D
(mm)	± (0.12)	± (0.01)	±(0.34)	±(0.23)	(0.12)	(0.06)		± (0.08)	± (0.01)	± (0.22)	± (0.14)	±(0.08)	± (0.03)	
Kernel breadth	(2.71) ±	0.25**	0.22 ±	-0.32 ±	-0.26*	-0.04**	D	2.39**	0.26**	0.84**	-0.72**	-0.02	-0.26**	D
(mm)	(0.11)	± (0.01)	(0.33)	(0.22)	± (0.11)	± (0.05)		±(0.06)	± (0.02)	± (0.18)	± (0.12)	± (0.06)	± (0.03)	
L/B ratio	2.13**	-0.16**	0.57**	-0.08	0.66**	0.03 ±	D	2.83**	-0.23**	-0.47**	0.50**	0.23**	0.24**	D
	± (0.07)	± (0.01)	± (0.21)	± (0.14)	± (0.07)	(0.03)		± (0.06)	± (0.02)	± (0.17)	± (0.11)	± (0.06)	± (0.03)	
1000 grain	27.57**	3.25**	12.13**	-7.97**	-2.54**	-2.10**	D	26.04**	4.79**	14.07**	-6.36**	1.52*	-4.47**	D
weight (g)	± (0.80)	± (0.08)	± (2.20)	± (1.42)	± (0.80)	± (0.34)		± (0.78)	± (0.13)	± (2.18)	± (1.46)	± (0.77)	± (0.36)	
Grain yield/	3.40**	-1.98**	63.23**	-28.16**	28.66**	1.07**	D	27.28**	-0.22±	-0.73 ±	8.02**	-0.54	-1.39**	D
plant (g)	± (0.89)	± (0.07)	± (1.92)	± (1.07)	±(0.89)	± (0.17)		± (0.87)	(0.14)	(2.08)	± (1.27)	± (0.86)	± (0.28)	

* and ** indicate significant at 5% and 1% level respectively. E = Epistasis, D = Duplicate.

Table 3. Chi-square test for means of different generations in two crosses for yield components in rice

Characters	Cross I (Karmi x Rajendra mahsuri)		Cross II (Dhusari x Sita)	
	Chi-square value	Epistasis	Chi-square value	Epistasis
Days to50 % flowering	740.07**	Present	179.33**	Present
Plant height (cm)	830.35**	Present	831.48**	Present
Panicle length (cm)	62.22**	Present	75.47**	Present
Effective tillers hill^{-1}	33.64**	Present	247.88**	Present
Spikelet panicle^{-1}	1222.17**	Present	113.49**	Present
Kernel length (mm)	479.79**	Present	72.07**	Present
Kernel breadth (mm)	195.50**	Present	335.78**	Present
L/B ratio	689.66**	Present	336.64**	Present
1000 grain weight (g)	807.30**	Present	223.71**	Present
Grain yield/plant (g)	1213.07**	Present	210.03**	Present

opposite, therefore, the nature of epistasis was identified as duplicate in both of the crosses for all of the yield related traits. Duplicate epistasis as observed may result in decreased variation in F2 and subsequent generations and may decrease heterosis and also hinder the pace of progress through selection (Singh *et al*., 2006). In other words, this type of epistasis tends to cancel or weaken the effect of each other in hybrid combination and hinders the progress made under selection and therefore, selection would have to be differed till later generations of segregation where dominance effects are dissipated (Perera *et al*. 1986).

The present study demonstrates the importance of additive, dominance and epistatic gene effects for the inheritance of almost all the characters studied. Under this situation breeders may opt for one of the two alternatives. On one hand the use of population improvement concept may become an amenable solution. Frey (1975) explained the use of this technique in highly autogamous crop. Biparental mating, recurrent selection and diallel selective mating system (Jensen, 1970) might be profitable in exploiting both additive and non additive gene action to obtain desirable recombinants. Another, perhaps more promising alternative is the exploitation of heterosis.

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