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Estimation of Gene Action and Interaction for Some Quantitative Characters in Rice (*Oryza sativa* L.) by Generation Mean Analysis

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Abstract

The present investigation was conducted to understand the genetic action for controlling the inheritance of some quantitative characters. The experimental materials consisted of three rice varieties, i.e., Mahsuri, Bhutmuri, IR36 and F_1, F_2, and F_3 populations of Mahsuri×Bhutmuri (Cross I) and IR36×Bhutmuri (Cross II). To conduct the generation mean analysis, the parents and their F_1, F_2, and F_3 populations were evaluated during June to October month of *Kharif* 2016 and *Kharif* 2017. Generation mean analysis was done for eighteen quantitative characters following the five parameter model. The Analysis of Variance revealed significant differences among the five generations for all the characters studied. The results of the scaling tests and joint scaling test revealed that the Simple additive-dominance model was inadequate for days to 50% flowering, days to maturity, number of panicles plant^{-1}, number of primary branches panicle^{-1}, number of secondary branches panicle^{-1} in Cross I, while it was for plant height, number of tillers plant^{-1}, number of panicles plant^{-1}, number of grains panicle^{-1}, number of filled grains panicle^{-1} and fertility % in Cross II. Hence, the present studies have revealed that epistasis as a basic mechanism that cannot be ignored. Thus, formulating breeding policies on only main gene effects i.e. additive and dominance could be misleading.

Keywords: Rice, gene action, GMA, joint scaling test

1. Introduction

Rice (*Oryza sativa* L.) is one of the major cereal food crops of the world, contributing nearly 73% of the total calorie intake of the population. It covers around a 20% of the total land area covered under cereals as reported by Gaballah et al., 2020. It is the most important cereal crop and primary energy source for two thirds of world's population (Khan et al., 2015). Twenty one percent of global human per capita energy and 15% of per capita protein is provided by rice. Asia cultivates and consumes around 90% of the world's rice is cultivated and around a half of the population depends on rice for food reported by Tenorio et al., 2013. Self-sufficiency in rice production was made possible by the development of high yielding varieties. Grain yield is a complex polygenic trait in rice that is affected by the large numbers of its component traits (Liu et al., 2011). These components traits are dependent on their expression on several morphological and developmental traits, which are interrelated with each other. So, the selection and genetic improvement of these characters is the principal way of enhancing yield. In order to make the

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genetic improvement of rice, the breeding method adopted mainly depends on the nature of gene action involved in the expression of the polygenic trait. Gene action is nothing but additive and dominant effects and their interactions which are reported to be associated with a breeding value (Falconer, 1989). In such manner, generation mean analysis is an extremely valuable strategy used to estimate gene action for a polygenic trait (Kearsey and Pooni, 2004). It is a simple yet useful technique used to estimate gene effects for a polygenic trait (Kearsey and Pooni, 2004). Its greatest positive is its ability to estimate epistatic gene effects, such as additive×additive, dominance×dominance and additive× dominance effects (Kearsey and Pooni, 2004; Viana, 2008). Using this, the gene effects of quantitative traits has been studied for various crops like in rice (Rao, 2017), Wheat (Said, (2014) pearl millet (Gaoh et al., 2020), safflower (Golkar, 2018), corn (Azizi et al., 2006), cotton (Srinivas et al., 2015, Giri et al., 2020 and Naghera et al., 2021), castor (Patel et al., 2021) and peanut (Ajay et al., 2018). Genetic analysis using generation mean analysis (GMA) has been utilized to evaluate the gene actions controlling the quantitative traits, and it gives the information on additive, dominance, and epistatic effects. Mather's individual scaling tests (Scale A, B, C, and D) and Cavalli's joint scaling test were used to detect the presence or absence of the epistatic gene interactions i.e. non–allelic gene interactions. Therefore the present investigation was carried out to estimates the gene actions, i.e., additive, dominance and epistatic effects, that control quantitative traits in rice by using five parameter model (generation mean analysis) i.e, parent 1 (P_1), parent 2 (P_2), first filial (F_1), second filial (F_2) and third filial (F_3) generations in two rice crosses.

2. Materials and Methods

2.1. Experimental material and procedure

The experiment was carried out at the Instructional Farm, Bidhan Chandra Krishi Viswavidyalaya, Jaguli, Nadia West Bengal, India located at 22.9452° N Latitude and 88.5336° E Longitude at an altitude of 9.5 m above mean sea level during June to October month of *Kharif* 2016 and *kharif* 2017. The experimental materials consisted of three rice varieties, i.e., Mahsuri, Bhutmuri, IR36 and F_1, F_2, and F_3 populations of Mahsuri×Bhutmuri (Cross I) and IR36×Bhutmuri (Cross II). The five populations i.e., P_1, P_2, P_3, F_1 and F_2 of the two crosses were grown in two separate experiments in a randomized complete blocks design with two replicates for each one. Plants were grown in 1, 2, and 3 rows each of 3 m length at a spacing of 30×15 cm^2 respectively. Observations were recorded on 10 randomly selected plants in case of parents and F_1, 30 plants of F_2 and 60 plants in F_3 per replication against 18 quantitative different characters such as days to 50% flowering, days to maturity, plant height (cm), number of tillers $plant^{-1}$, number of panicles $plant^{-1}$ (cm), panicle length, number of primary branches $panicle^{-1}$, number of secondary branches $panicle^{-1}$, number of grains $panicle^{-1}$, number of filled grains $panicle^{-1}$, fertility percentage (%), 1000 grain weight (g), grain length (mm), grain breadth (mm), grain L/B ratio, straw weight (g), harvest index (%) and grain yield $plant^{-1}$ (g).

2.2. Statistical analysis

The analysis of variance was worked out to test the differences among genotypes by F-test. It was done by the technique of Randomized Block Design for each character according to approach upheld by Panse and Sukhatme (1967). The Scaling test was done as described by Mather (1949) and Hayman and Mather (1955) The joint scaling test as proposed by Cavalli (1952) was also applied to test the adequacy of the additive-dominance model .The different components of generation mean m, d, h, i, and l were calculated following Hayman (1958) and their test of significance were calculated following the appropriate t-test.

3. Results and Discussion

3.1. ANOVA

Analysis of variance revealed significant differences among the parents, F_1 hybrids and F_2 generation against all characters studied (Table 1 and Table 2). Among the yield component in cross I, the number of secondary branches per panicle exhibited the highest significant difference. Among the yield component in cross II, the number of grains $panicle^{-1}$ exhibited the highest significant difference and grain length/ breadth (L/B) exhibited the lowest significant difference in both cross I and II. It shows the presence of variation among rice genotypes used in this study.

3.2. Scaling test, Joint scaling test and gene effects

Generation mean analysis is a very useful technique for estimating gene effects for a polygenic character (Hayman, 1958) and determines the presence and absence of non-allelic gene interactions. Generation mean analysis can be use for the estimation of epistatic gene effects namely additive×additive (i), additive×dominance (j), and dominance×dominance (l). The variation among the means of different generations in all the eighteen characters studied suggesting the usefulness of the estimation of additive, dominance and epistatic interaction. The C and D scaling test for all the characters in the two crosses showed that at least one or both were found significant indicating the presence of non-allelic interaction. Both the crosses exhibiting non-allelic interaction for the inheritance of almost all the traits studied. However, the characters like number of grains $panicle^{-1}$ and harvest index (%) in cross I and 1000 grains weight (g) in cross II showed non-significant values for both C and D scales (from table 2) indicating the non-interacting mode of inheritance. Similar finding were reported by Yadav et al. (2013) for number of grains per panicle and Jondhale et al. (2018) for harvest index (%). The present study shows that significant additive and epistatic effects exist in this population. Although their presence may vary from the Cross to Cross, the estimated values of joint scaling test and the five-parameter model are presented in Table 3.

Table 1 : Analysis of variance for different characters in Cross I (Mahsuri×Bhutmuri)

Sl. No.	Characters	Mean sum of square			SEm±	CD (p=0.05)
		Replication (d.f. 3)	Generation (d.f. 4)	Error (d.f. 12)		
1.	Days to 50% flowering	5.12	537.58***	12	2.39	5.20
2.	Days to maturity	3.0	473.33***	4.13	1.44	3.13
3.	Plant height(cm)	3.23	118.11***	4.84	1.56	3.39
4.	No. of tillers plant^{-1}	0.15	74.89***	1.29	0.8	1.75
5.	No. of panicles plant^{-1}	3.0	115.36***	1.66	0.91	1.99
6.	Panicle length(cm)	2.15	29.13**	4.90	1.57	3.41
7.	No. of primary branches panicle^{-1}	0.48	37.66***	1.09	0.74	1.61
8.	No. of secondary braches panicle^{-1}	5.90	1301.27***	10.83	2.33	5.07
9.	No. of grains panicle^{-1}	20.01	847.44***	66.30	5.76	12.55
10.	No. of filled grains panicle^{-1}	18.75	910.18***	18.14	3.01	6.56
11.	Fertility percentage (%)	5.32	48.56*	7.61	1.95	4.25
12.	1000 grain weight (g)	1.79	22.07**	3.87	1.39	3.03
13.	Grain length (mm)	0.05	0.89*	0.18	0.30	0.66
14.	Grain breadth (mm)	0.08	0.67***	0.03	0.12	0.27
15.	Grain length/breadth (L/B) ratio	0.13	0.40*	0.08	0.20	0.45
16.	Straw weight (g)	2.06	62.06***	5.59	1.67	3.64
17.	Harvest index (%)	23.18*	37.89***	2.96	1.22	2.65
18.	Grain yield plant^{-1} (g)	19.73	141.15***	6.56	1.81	3.94

*Significant at (p=0.05); **(p=0.01), **(p=0.001), SEm: Standard Error of mean; CD: Critical Difference

Table 2: Analysis of variance for different characters in Cross II (IR36×Bhutmuri)

Characters	Mean sum of square			SEm±	CD (p=0.05)
	Replication (d.f. 3)	Generation (d.f. 4)	Error (d.f. 12)		
Days to 50% flowering	25.73	305.30***	27.73	3.72	8.11
Days to maturity	28.18	415.88***	16.64	2.88	6.28
Plant height(cm)	3.61	1073.75***	8.39	2.05	4.46
No. of tillers plant^{-1}	1.25	488.16***	0.80	0.63	1.38
No. of panicles plant^{-1}	1.93	126.40***	4.62	1.52	3.31
Panicle length(cm)	6.68*	10.70**	1.56	0.88	1.92
No. of primary branches panicle^{-1}	1.99	9.21**	1.60	0.90	1.95
No. of secondary braches panicle^{-1}	6.41	51.73**	8.72	2.09	4.55
No. of grains panicle^{-1}	8.25	4936.73***	12.01	2.45	5.34
No. of filled grains panicle^{-1}	1.95	3921.83***	14.72	2.71	5.91
Fertility percentage (%)	2.36	121.66***	3.24	1.27	2.77
1000 grain weight (g)	7.30*	7.66*	1.67	0.91	1.99
Grain length (mm)	0.05	0.55***	0.05	0.15	0.33
Grain breadth (mm)	0.07	0.39*	0.06	0.18	0.39
Grain length/breadth (L/B) ratio	0.09	0.37*	0.31	0.39	0.81

Figure 2: Continie...

Characters	Mean sum of square			SEm±	CD (p=0.05)
	Replication (d.f. 3)	Generation (d.f. 4)	Error (d.f. 12)		
Straw weight (g)	2.95	24.52***	1.94	0.98	2.14
Harvest index (%)	14.02	29.93*	9.06	2.13	4.64
Grain yield plant^{-1} (g)	8.31	41.61*	8.46	2.06	4.48

*Significant at (p=0.05); **(p=0.01), **(p=0.001), SEm: Standard Error of mean; CD: Critical Difference

Table 3: Different scales for yield components and component of generation means for different characters in cross I and cross II as suggested by Hayman (1958)

C*	Scaling test		Three parameter mode			Joint scaling test	Five parameter model					Epistasis
	C	D	m	d	h	(χ^2)	m	d	h	i	l	
Days to 50% flowering												
I	1.25	11.75***	_	_	_	8.82*	117*** ± 0.43	15.63*** ±0.25	0.50± 1.36	23.63*** ± 1.53	14** ± 4.93	C
II	-9	-14**	79.18*** ±1.17	-12± 0.79	6.5± 1.81	0.45	_	_	_	_	_	_
Days to maturity												
I	-4*	15.00***	_	_	_	55.68***	147.5***± 0.34	14.75** ± 0.37	-3.67*** ± 0.83	18.83*** ± 1.16	25.33*** ± 1.16	D
II	-1.25	-4.75	116.25*** ±0.52	-13.89 ± 0.87	10.73*** ± 0.70	2.42	_	_	_	_	_	_
Plant height (cm)												
I	-27.25***	-25.50***	126.56*** ±0.32	2.88** ± 0.41	17.96*** ± 0.547	1.04	_	_	_	_	_	_
II	28.01***	-17.49***	_	_	_	125.62***	130.75*** ± 0.23	-20.63*** ± 0.55	30.83*** ±0.85	-24.93*** ±1.25	-60.67*** ±2.52	D
Number of tillers Plant^{-1}												
I	-10.37***	-1.13	19.88*** ±0.25	-2.19 ± 0.20	0.88± 1.21	3.63	_	_	_	_	_	_
II	-21.88***	14.38***	_	_	_	91.81***	24.37*** ± 0.21	-5.43***± 0.14	12.08*** ± 0.69	-24.10*** ±0.68	48.33*** ± 1.99	C
Number of panicles plant^{-1}												
I	27.90***	15.40***	_	_	_	13.59***	29.88*** ± 0.21	-2.80*** ±0.13	1.33 ± 1.33	-11.21*** ±1.10	-16.66*** ± 3.07	D
II	-0.6	8.9**	_	_	_	0.08**	25.63*** ± 0.22	-2.80*** ± 0.18	6.67***± 1.89	-11.63*** ±1.46	12.67** ± 4.18	C
Panicle length (cm)												
I	-11.25***	-11.50***	21.80*** ±0.44	2.13*** ± 0.13	3.33± 0.66	0.01	_	_	_			
	_	_	_									
II	1.5	-5.75***	22.52*** ±0.39	-1.88± 0.24	2.64± 0.54	8.8	_	_	_	_	_	_

C*: Crosses

Table 3: Continue...

C*	Scaling test		Three parameter mode			Joint scaling test	Five parameter model					Epis-tasis
	C	D	m	d	h	(χ^2)	m	d	h	i	l	
Number of primary branches panicle^{-1}												
I	7.13***	-6.12***	_	_	_	21.76***	17.25*** ± 0.19	1.06*** ± 0.11	11.58*** ± 0.90	7.39*** ± 0.79	-17.67*** ± 2.26	D
II	-8.40***	-7.79***	6.88*** ±0.144	-0.38 ±0.22	2.96* ±1.81	3.14	_	_	_	_	_	_
Number of secondary braches panicle^{-1}												
I	-8.13*	79.13***	_	_	_	308.58***	39.13*** ± 0.61	7.81*** ± 0.24	-15.41*** ± 1.77	-38.47*** ±1.93	116.3*** ± 6.06	D
II	-11.13*	-24.13***	27.47*** ±0.45	2.063* ±0.27	10.66*** ±0.48	3.74	_	_	_	_	_	_
Number of grains panicle^{-1}												
I	4.88	7.88	95.17*** ±0.56	18.61*** ±0.59	15.23* ±1.75	3.42	_	_	_	_	_	_
II	16***	-143***	_	_	_	1109.33***	34.87*** ±1.09	2.06*** ± 0.27	15.17*** ± 2.38	18.35*** ± 2.80	-17.33 ± 8.96	D
Number of filled grains panicle^{-1}												
I	-4.13	17.88**	61.17*** ±0.41	14.41*** ±0.43	26.76*** ±0.60	0.15	_	_	_	_	_	_
II	-4.88	-120.38***	_	_	_	496.34***	133.50*** ± 0.74	40.63*** ± 0.56	123.50*** ±1.78	179.25*** ± 2.14	-212*** ±6.36	D
Number of panicles plant^{-1}												
I	27.90***	15.40***	_	_	_	13.59***	29.88*** ± 0.21	-2.80*** ±0.13	1.33 ± 1.33	-11.21*** ±1.10	-16.66*** ± 3.07	D
II	-0.6	8.9**	_	_	_	0.08**	25.63*** ± 0.22	-2.80*** ± 0.18	6.67*** ± 1.89	-11.63*** ±1.46	12.67** ± 4.18	C
Fertility percent (%)												
I	9.52***	15.48***	66.62*** ±0.49	-0.89 ±0.45	-0.13 ±0.71	6.69	_	_	_	_	_	_
II	4.74***	-11.57***	-	-	-	99.06***	67.60*** ± 0.22	7.29*** ± 0.36	4.32*** ± 0.62	23.09*** ± 0.99	-21.75*** ±1.98	D
1000 Grain weight (g)												
I	-6.97***	1.75	19.77*** ±0.23	-3.04 ±0.233	-7.89± 1.54	1.28	_	_	_	_	_	_
II	-1.93	-0.27	18.74*** ±0.22	-1.52 ±0.28	-1.47± 0.34	2.49	_	_	_	_	_	_

C*: Crosses

Table 3: Continue...

Crosses	Scaling test		Three parameter mode			Joint scaling test	Five parameter model					Epistasis
	C	D	m	d	h	(χ2)	m	d	h	i	l	
Grain length (mm)												
I	-1.57***	-1.46***	7.28***±0.09	-0.46±0.04	0.26±0.18	2.27	__	__	__	__	__	__
II	-1.38***	-1.53***	7.18***±0.05	-0.04±0.03	0.09±0.71	3.54	__	__	__	__	__	__
Grain breadth (mm)												
I	-1.65***	-1.60***	2.01***±0.05	-0.4±0.03	0.64**±0.05	0.027	__	__	__	__	__	__
II	-0.73*	-1.23***	2.35***±0.07	0.34**±0.03	0.23±0.07	1.17	__	__	__	__	__	__
Grain length/ breadth (L/B) ratio												
I	1.21***	1.20***	3.57***±0.06	0.32*±0.045	-0.72±0.07	0	__	__	__	__	__	__
II	0.57	1.03***	3.24***±0.08	-0.36±0.03	-0.62±0.14	0.97	__	__	__	__	__	__
Straw weight (g)												
I	12.23***	10.92***	47.29***±0.45	3.84**±0.38	-10.57±0.72	0.3	__	__	__	__	__	__
II	4.32***	2.59	37.25***±0.16	3.31***±0.06	-0.84±3.14	0.071	__	__	__	__	__	__
Harvest index percent (%)												
I	-3.82	0.96	40.65***±0.34	3.39**±0.39	4.79±0.62	2.93	__	__	__	__	__	__
II	-1.18	7.89*	40.34***±0.33	0.86±0.51	-6.64±5.56	4.32	__	__	__	__	__	__
Grain yield plant^{-1} (g)												
I	8.01**	10.17***	32.28***±0.75	7.86***±0.43	-1.32±1.23	1.44	__	__	__	__	__	__
II	0.75	9.67**	27.72***±1.34	2.94*±0.48	-8.15±4.54	3.22	__	__	__	__	__	__

*: indicate significant at (p=0.05) level, **: indicate significance at (p=0.01) level, **: Indicates significant at (p=0.001) level, D: Duplicate gene effect, C: Complementary gene effects

In Cross I all gene effects (mean, additive, dominance, additive×additive and dominance×dominance) for days to maturity, number of primary branches panicle^{-1} and number of secondary branches panicle^{-1} were significant except dominance gene effect in days to 50% flowering and number of panicles plant^{-1}. Roy and Senapati (2011) also reported that the dominance effect was not significant for the days to 50% flowering. In the case of the adequacy of the Simple additive-dominance model, only additive gene effects were significant in panicle length, grain L/B ratio, straw weight (g) and grain yield plant^{-1} (g). Similarly, only the dominance gene effect was significant in grain breadth (mm). In plant height (cm), number of grains panicle^{-1}, number of filled grains panicle^{-1} and harvest index (%) both additive and dominance gene effects were significant. An additive effect for panicle length and grain length/breadth ratio was reported by Roy and Senapati (2012). Also the importance of additive gene effects were reported by Roy and Senapati (2011), Kacharabhai (2014) and Sultana, et al. (2016). In Cross II all gene effects(mean, additive, dominance, additive x additive and dominance×dominance) for plant height, number of tillers plant^{-1}, number of panicles plant^{-1}, number of filled grains panicle^{-1} and fertility percentage were significant except dominance x dominance gene effect in the number of grains panicle^{-1}. Similar dominance results were earlier reported for the number of panicles plant^{-1} (Denary et al., 2012), number of tillers plant^{-1} (Kumar et al., 2007) and L/B ratio (Rani et al., 2015). Chaturvedi et al. (2010 and Rao et al., 2017 reported that days to 50% flowering, 50% flowering to maturity, plant height, panicle length, grain filling percentage and length–breadth ratio were controlled by both additive and dominance gene action. In the case of the adequacy of the simple additive dominance model, only additive gene effect was significant in grain breadth (mm), straw weight (g) and grain yield plant^{-1} (g). Similarly, only dominance gene effect was significant in, days to maturity and number of primary branches panicle^{-1}. In a number of secondary branches panicle^{-1}, both dominance and additive gene effects were significant. Mather and Jinks (1971) showed that the classification of interactions on the basis of the related magnitudes and signs of the estimates of the five parameters largely depends on the magnitude and signs of the estimates of h and l. The opposite sign of dominance (h) and dominance×dominance (l) sign indicated a prevalence of duplicate epistasis whereas complementary epistasis is indicated when signs are the same. In Cross I, days to maturity, number of primary branches panicle^{-1} and number of secondary branches panicle^{-1} showed the duplicate

type of epistasis whereas, in Cross II plant height, number of filled grains panicle^{-1}, number of grains panicle^{-1} and fertility % showed the duplicate type of epistasis. The duplicate effect of these traits would tend to hinder progress at an increased level of manifestation. Similar results were reported for a number of spikelet panicle^{-1} (Liu and Hong, 2005), for a number of filled grains panicle^{-1} (Kumar et al., 2007), for all the yield and quality related traits like plant height (Roy and Senapati, 2011) and a number of grains panicle^{-1} (Subbulakshmi et al., 2016). In cross 1 the traits like Days to 50% flowering and number of panicles plant^{-1} showed the presence of a complementary type of epistasis whereas in cross II the complementary type of epistasis was recorded for the number of tillers plant^{-1} and number of panicles plant^{-1}. Subbulakshmi et al*.,* 2016 reported the presence of a complementary type of epistasis for days to 50% flowering. The complementary effect of these traits will produce new recombinants capable of improving yield.

4. Conclusion

An additive, dominance, additive×additive and dominance×dominance interaction effects were present along with either duplicate dominant epistasis or complementary recessive epistasis for most of its contributing traits in Cross I and Cross II. Hence, selection in the early segregating generations might not give desirable recombinants. Pureline selection, heterosis breeding, and reciprocal recurrent selection might be profitable in exploiting additive, dominance, both additive and non-additive gene action to obtain desirable recombinants.

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