



Estimation of Generation Mean- Five Parameter Model for the Evaluation of Drought Tolerant Lines in Rice (*Oryza sativa* L.)

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Abstract

In order to study mode of gene action in rice for traits related to yield [spikelet per panicle, per cent filled grains, 1000-grain weight (g) and yield per plant] and drought tolerance (proline content and stomatal behavior), six varieties of rice (HUR 3022, Sarjoo 52, Nagina 22 and Birsa Gora) were investigated under two different conditions i.e. moisture stress (rain fed) and moisture non – stress (irrigated). Direct crosses were made between drought susceptible parents (HUR 3022 and Sarjoo 52) and drought tolerant parents (Nagina 22 and Birsa Gora). F1's were back crossed with the recipient parents i.e. drought susceptible parents at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi and off season at CRRRI, Cuttack, Odisha in 2009- 2010. In 2010, F1's been grown and were allowed to self for obtaining F2 seeds. In the next generation F2 seeds were planted to raise F3 population. Therefore, five different populations (generations) including P1, P2, F1, F2 and F3 were planted in a randomized complete block design with three replications. The additive × additive (i) model was significant for traits spikelet per panicle, 1000 – grain weight and yield per plant in both the environments where as dominance × dominance was found to be significant for per cent filled grains in both the environments. Simple scaling test indicated that the inheritance of traits related to yield was described by non-allelic interactions mainly additive × Additive and dominance × dominance and duplicate epistasis.

Introduction

Cereals have played a significant role in the evolution of human civilization. Rice (*Oryza sativa* L.) a member of cereals, belonging to the order Poales of the grass family Poaceae (Graminae) is the staple food of more than three billion people in the world, most of them living in Asia. In 2012- 13, the world

produced 730 million tons of rough rice (FAO, 2013), of this, Asian farmers produced around 600 million tons, which represents more than 90% of global rice. India and China together accounted for 341 million tons, with India producing 148 million tons. Rice is cultivated under diverse ecologies ranging from irrigated to rain fed upland to rain fed

lowland to deep water. Irrigated rice accounts for 55% of world area and about 75% of total rice production. Rain fed lowland represents about 25% of total rice area, accounting for 17% of world rice production. Upland rice covers 13% of the world rice area and accounts for 4% of global rice production. Deepwater rice, although it has less area, meets the need of around 100 million people. In India, the total area under irrigated, rain fed lowland and upland rice is 22.0, 14.4, and 6.3 million ha, respectively (Singh, 2009).

Studies on the plant response to water stress are becoming increasingly important, as most of climatic change scenarios suggest an increase in aridity in many areas of the globe (Petit et al., 1989). On a global basis, drought (assumed to be soil and/ or atmospheric water deficit) in conjunction with high temperature and radiation, possess the most important environmental constraints to plant survival and to crop productivity (Boyer, 1982). Drought itself is a very complex phenomenon and several parameters influencing it are found to be under genetic control. Thus genetic variations for quantitative characters in plant population are of prime concern to the breeders. The choice of breeding methods for genetic improvement of a crop depends upon the nature and magnitude of genetic variability present. It is usually not directly

measurable. One can measure only the phenotypic expression of genetic values as modified by the environment. Fisher (1918) and Wright (1921) partitioned hereditary variance for metric traits into three components viz., i) additive part resulting from average effect of the genes, ii) a dominance portion due to deviation arising from intra – allelic interaction and iii) an epistatic portion associated with inter – allelic interaction. This partitioning has provided a better knowledge for genetic analysis of quantitatively varying traits. The further partitioning of epistatic component into additive \times additive, additive \times dominance and dominance \times dominance was shown by Kempthorne (1954). Such partitioning of variability into various components needs variance estimates from a number of specifically related generations. Generations mean analysis as suggested by Hayman (1958) and Jinks and Jones (1958) provides all kinds of non – allelic interaction precisely in addition to the additive and dominance gene effects. This method is relatively more simple as compared to other mating designs (triallel, quadiallel, triple test cross analysis etc.) and estimates all kind of gene effects.

The magnitude of additive gene effect is particularly useful in the development of pureline varieties. Drought is predominantly

controlled by additive gene as have been reported by Solman et al., (2003). Likewise, the information concerning dominance and epistatic gene effects (non-additive components) are also valuable for development of hybrid varieties. Generation mean analysis is a relatively simple and statistically reliable tool suitable for preliminary estimation of various gene effects (Mather and Jinks, 1971). Estimation and interpretation of non-allelic interactions are more progressive with generation mean analysis as it utilizes the first order statistics which are less compounded with each other when compared with variance estimates. In present study, generation mean analysis for drought tolerance and quantitative traits in rice was undertaken to find out gene effects controlling drought tolerance in six crosses of rice.

Materials and Methods

The present investigation was conducted during three seasons i.e. 2010, 2011 and 2012 at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi and off season, 2010-2011 at CRRI, Cuttack, Odisha. HUR – 3022, derived from the cross IR – 36 × HR – 137 was selected as the recipient parent (High yielding variety). It is a semi dwarf variety, yields up to 50 – 55 q/ha, out yielded Saket –

4 and NDR – 80. It is lodging resistant having large panicles. The variety was notified in 2005 for Uttar Pradesh. Sarjoo – 52 is derived from T(N)1 × Kashi. It was notified in 1982 for general cultivation. It takes approximately 130-133 DAS. Sarjoo – 52 is an irrigated, semi dwarf (98 cm) and erect type. Grains are long, bold, AWP and white. It is moderately resistant to BLB. It is reported to yield 50-60 Q/ha. It is mainly grown in Uttar Pradesh. Nagina – 22 is a selection from Rajbhog. Nagina – 22 was notified in 1978. It takes around 85-102 days. Grains are short, bold and white. The variety is susceptible to blast, BLB and resistant to drought. It gives yield of about 20-25 Q/ha and grown well in Uttar Pradesh as upland crop. Birsa Gora was notified in 1993 as an upland rice variety. It takes about 95-100 days to mature. It is a tall type (165-180 cm) whose grains are medium bold and red. The variety is moderately resistant to major diseases and pests. Its average yield is 18-20 quintals/hectare. The variety is mostly grown in Bihar and Jharkhand. The variety is a selection from the germplasm collection of Gora. Five generations (P1, P2, F1, F2 and F3) for each of the four crosses (HUR 3022 × Nagina 22, HUR 3022 × Birsa Gora, Sarjoo 52 × Nagina 22 and Sarjoo 52 × Birsa Gora) were evaluated in this study (Table 1). The F1s were made at Agricultural Research Farm,

Institute of Agricultural Sciences, Banaras Hindu University, Varanasi (UP) during Kharif (summer), 2009. The subsequent generation - F2 required for the study was developed in off season 2009 - 10 at CRRI, Cuttack, Odisha. F3 was again planted in the main season, Kharif, 2010 at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi.

The experiment was laid in a randomized complete block design with three replications during Kharif (summer) 2009 crop season. The parental lines and F1s; F2s and F3s were planted in 1, 2 and 3 rows each of 3 m long at spacing of 30×15 cm, respectively. Data were recorded on 10 plants in case of parents and F1s, 30 plants of F2s and 75 plants in F3s per replication.

Adequacy of scale must satisfy two conditions namely, additivity of gene effects and independence of heritable components from non-heritable ones. The test of first condition provides information regarding absence or presence of gene interactions. The test of adequacy of scales is important because in most of the cases the estimation of additive and dominance components of variances is made assuming the absence of gene interaction. Mather (1949) and Hayman and Mather (1955) gave four tests for scale effects

but since, back cross is absent in the present study, I have considered only C & D scale.

It is computed as follows:

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

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

When the scale is adequate, the values of A, B, C and D should be zero within the limit of their respective Standard Errors.

Variances of above scales:

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

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

Standard errors of the above scale

$$SE_C = 2\sqrt{V_C}$$

$$SE_D = 2\sqrt{V_D}$$

Now, the 't' values are calculated as follows:

$$t_C = \frac{C}{SE_C}$$

$$t_D = \frac{D}{SE_D}$$

The calculated value of 't' are to be compared with tabulated value of 't' at 5% level of significance. In each test, the degree of freedom is sum of the degrees of freedom of

various generations (total number of observations - total number of replications) involved. However, in case of un-replicated data, the degrees of freedom will be number of observations

Hayman (1958) and Jinks and Jones (1958) devised the five parameter model for the estimation of various genetic components; these components were estimated according to Hayman (1958) as follows:

$$\text{Mean,} \quad m = \bar{F}_2$$

$$\text{Additive effect,} \quad d = 1/2 \bar{P}_1 - 1/2 \bar{P}_2$$

$$\text{Dominance effect,} \quad h = 1/6 (4\bar{F}_1 + 12\bar{F}_2 - 16\bar{F}_3)$$

$$\text{Dominance} \times \text{Dominance effect,} \quad l = 1/3 (16\bar{F}_3 - 24\bar{F}_2 + 8\bar{F}_1)$$

$$\text{Additive} \times \text{Additive effect,} \quad i = \bar{P}_1 - \bar{F}_2 + (1/2) (\bar{P}_1 - \bar{P}_2 + h) - 1/4l$$

Variances of above parameters are as follows:

$$V_m = \sqrt{F_2}$$

$$V_d = 1/4 (V\bar{P}_1 + V\bar{P}_2)$$

$$V_h = 1/36 (16V\bar{F}_1 + 144V\bar{F}_2 + 256V\bar{F}_3)$$

$$V_l = 1/9 (256V\bar{F}_3 + 576V\bar{F}_2 + 64V\bar{F}_1)$$

$$V_i = V\bar{P}_1 + V\bar{F}_2 + 1/4 (V\bar{P}_1 + V\bar{P}_2 + V_h)$$

Standard errors of the parameters:

$$\begin{aligned}
 \text{S.E.}_m &= \sqrt{V_m} & \text{S.E.}_d &= \sqrt{V_d} \\
 \text{S.E.}_h &= \sqrt{V_h} & \text{S.E.}_l &= \sqrt{V_l} \\
 \text{S.E.}_i &= \sqrt{V_i}
 \end{aligned}$$

Now, the 't' values are calculated as follows:

$$\begin{aligned}
 t_m &= \frac{m}{\text{S.E.}_m} & t_d &= \frac{m}{\text{S.E.}_d} \\
 t_h &= \frac{m}{\text{S.E.}_h} & t_l &= \frac{m}{\text{S.E.}_l} \\
 t_i &= \frac{m}{\text{S.E.}_i}
 \end{aligned}$$

The calculated value of 't' are to be compared with tabulated value of 't' at 5% level of significance. In each test, the degree of freedom is sum of the degrees of freedom of various generations (total number of observations - total number of replications) involved.

Results

The simple scaling test of Mather was applied

to determine the presence of gene interaction in four rice crosses. Perusal of results indicate that C and D were significant in each of the four crosses studied, suggesting the involvement of either one or both of the two epistatic components i and l. On the basis of simple scaling test for epistasis, the five parameter model was fitted to the observed components of mean in each of the four crosses (Table 2)

In the case of spikelet per panicle both the scale (C & D) were significant for all the crosses under both irrigated and rainfed conditions (Table 2). Dominance gene effects appeared to play an important role for the inheritance of spikelet's per panicle as it exhibited comparatively higher significant values in all the crosses. All the components of gene effects (m, d, h, i, l) were significant in four crosses, namely, HUR - 3022 × Nagina - 22, HUR - 3022 × Birsa Gora, Sarjoo - 52 × Nagina - 22 and Sarjoo - 52 × Birsa Gora in both irrigated and rainfed conditions. Preponderance of additive component under both the environments was recorded. Duplicate type of gene action was found to be predominant in both the environments (Table 3).

In case of per cent filled grains study revealed that three out of four crosses in both irrigated and rainfed conditions showed significant values for both the scales i.e. C & D, which led to the estimation of all the five type of gene effects (Table 2 cont.). Cross, Sarjoo - 52 × Nagina - 22 under irrigated and rainfed conditions showed insignificance for the scale C. All the components of gene effects were significant for two crosses (HUR - 3022 × Birsa Gora and Sarjoo - 52 × Birsa Gora) in irrigated condition, while three crosses, namely, HUR - 3022 × Nagina - 22, HUR -

3022 × Birsa Gora and Sarjoo - 52 × Birsa Gora under rainfed condition were found to be significant. The preponderance of dominance gene effects in irrigated and rainfed conditions was observed. Duplicate type of interaction was predominant in majority of the crosses under both irrigated and rainfed conditions. Cross, HUR - 3022 × Birsa Gora exhibited complimentary type of interaction under both irrigated and rainfed conditions (Table 3 cont).

Generation mean analysis for thousand grain weight revealed that all the four crosses showed significant result for both C & D scales (Table 2.1). Gene effects were significant for the cross, Sarjoo - 52 × Birsa Gora under irrigated condition and also for the crosses, HUR - 3022 × Nagina - 22, Sarjoo - 52 × Nagina - 22 and Sarjoo - 52 × Birsa Gora under rainfed condition for all the components. Additive x additive gene effect was found to be significant in all the nine crosses in both the conditions except in the cross HUR - 3022 × Birsa Gora in rainfed condition only. Component 'l' was found to be significant in all the crosses under rainfed condition. Most of the crosses exhibited duplicate type of epistasis in both irrigated and rainfed conditions. Crosses, HUR 3022 x Nagina - 22 and HUR 3022 x Birsa Gora under irrigated condition and HUR 3022 x

Nagina - 22 under rainfed condition exhibited complementary type of epistasis (Table 3.1)

In case of yield per plant all the four crosses in irrigated and rainfed conditions showed significant values for the estimates of scaling test C & D (Table 2 cont). Grain yield per plant too, gave the chance to estimate both allelic and non - allelic gene interactions which are unlike to many of the characters in the present study. All the five components of gene effect (m, d, h, i and l) were significant in all the crosses. Preponderance of additive gene effect was observed for two crosses namely, HUR - 3022 × Nagina - 22 and Sarjoo - 52 × Nagina - 22 in irrigated and rainfed conditions both. Among non-allelic interactions, both 'i' and 'l' were pronounced in irrigated and rainfed conditions, respectively. Duplicate type of gene action was observed in three out of four crosses under both irrigated and rainfed conditions. Cross, Sarjoo - 52 × Nagina - 22 exhibited complementary type of gene action (Table 3 cont)

For proline content, the estimates of scaling test revealed that all the four crosses showed significant differences for both the scales (C & D) under both irrigated and rain fed conditions (Table 2 cont.). The components of gene effects were also significant for all the four crosses in irrigated condition and two

crosses under rain fed condition. Significant additive gene effect was evident in both irrigated and rain fed conditions. Non - allelic gene action additive × additive (i) was predominant in both the environments. Similar to that of other traits, proline content in rice was observed to be governed by duplicate type of epistasis for most of the crosses in both irrigated and rain fed conditions. Crosses, HUR - 3022 × Nagina - 22, HUR - 3022 × Birsa Gora and Sarjoo - 52 × Birsa Gora exhibited complementary type of epistasis in irrigated condition whereas crosses, HUR - 3022 × Nagina - 22 and Sarjoo - 52 × Birsa Gora showed complementary type of epistasis in rain fed condition (Table 3 cont.)

The estimates of scaling test for stomatal behaviour revealed both the scales (C & D) were significant for seven crosses in irrigated and five crosses in rainfed conditions (Table 2 cont.). All the gene effects (allelic and non - allelic gene effects) were significant for all the crosses in both the conditions. Non - allelic gene effect 'i' was more pronounced as compared to 'l' under both irrigated and rainfed conditions. Only one cross namely, HUR - 3022 × Nagina - 22 exhibited duplicate type of epistasis, rest of the crosses showed complementary type of epistasis in both the conditions (Table 3 cont.).

Discussion

Grain yield is a complex polygenic trait resulting from interaction among number of inherent characters and environment. It can be improved more through indirect selection on the basis of yield components (Chandra et al. 2004). Favourable combinations of yield contributing characters may improve yielding capacity (Drezner, 1996). Sufficient understanding of the inheritance of quantitative traits and information about it is essential to develop breeding strategy. Generation mean analysis is a powerful technique in plant breeding for estimating main gene effects (additive and dominance) and their digenic (additive \times additive, additive \times dominance and dominance \times dominance) interaction responsible for inheritance of quantitative traits. It helps us in understanding the performance of the parents used in the crosses and potential of the crosses to be used either for heterosis exploitation or pedigree selection (Sharma et al, 2003). Therefore, the estimates of the relative magnitude of various gene effects including epistasis are of significance, when each cross combination is considered. Since linkage affects the epistatic term in generation mean (Hayman, 1958b) additive and dominant gene effects can not be precisely measured in the presence of epistasis (Hayman, 1960). Even with these limitations,

estimates of the several parameters provide indication of the relative importance of various types of gene effects influencing total genetic variation of an attribute (Gamble, 1962).

In the absence of backcross generation, Hayman (1958) and Jinks and Jones (1958) prescribed five parameter model for generation mean analysis which included F₃ as one of the generation in addition to P₁, P₂, F₁ and F₂. However, in the present investigation all the crosses for each trait were subjected to C and D scaling tests as suggested by Mather (1949) to examine whether epistatic gene effects exist in the materials under study, and if so what is the relative importance. Accordingly in interacting crosses all the five – parameters (m, d, h, i and l) were estimated. Presence of epistasis / gene interaction varied with crosses as well as traits, most of the crosses showed presence of epistasis. The generation mean for most of the characters showed the importance of both additive and dominant types of gene effects. However additive gene effects, in general were higher than dominance gene effects under both the conditions i.e. irrigated and rain fed. These findings are in agreement with Hasib et al. (2002) and Mahalingam and Nadarajan (2010). Snape (1987) pointed out that dominance could be small due to its ambi

directional nature. This might explain why additive genetic component⁵ of variance (VA) varied to a great extent.

In the presence of epistasis, predominance of duplicate type of gene interaction was observed. In such a situation intermating or biparental mating between selected plants from early segregating generations could help in improving this trait (Comstock et al., 1949). Few crosses showed complementary type, in such situation additive component is often relatively under estimated, while dominance effect tends to be overestimated (Pathak and Singh, 1970). Among the epistatic gene effects, additive x additive (i) gene effect was greater in magnitude than dominance x dominance (l) type. The sign of additive x additive gene effects was mostly negative for seedling height, plants height, proline content and stomatal behavior, indicating thereby that a diminishing effect due to this type of gene could occur for the traits considered.

The present studies have revealed that epistasis as a basic mechanism cannot be ignored. Thus, formulating breeding policies on the basis of only main gene effects i.e. additive and dominance could be misleading. Several workers have estimated gene effects in rice for different characters (Gnanamalar

and Vivekanandan, 2013). These workers also reported the importance of both, additive and dominance components in the control of various characters.

Conclusion

The generation mean for most of the characters showed the importance of both additive and dominance type of gene effects. However, additive effect, in general was higher than dominance gene effect under both the conditions. Among the epistatic gene effects, additive x additive gene effect was in greater magnitude than dominance x dominance type. In the presence of epistasis, almost all the crosses showed duplicate type of gene interaction.

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Table 1: Parental Genotypes, Pedigree and Drought Reaction of Parental Genotypes

S. No.	Cultivar	Pedigree	Drought Reaction	LR*	SG*	Characteristic Features
1.	HUR 3022	IR 36 × HR 137	S	9	5	Semi dwarf, 50-55 q/hq out yielded Saket4 & NDR 80, Lodging resistant, large (30-35 cm.) panicles, 105-110 Days maturity, high tillering (15-25)
2.	Sarjoo 52	T(N) 1 × kashi	S	9	5	Semi dwarf, yield 50- 60 quintal ha ⁻¹ 130-133 days maturity, moderately resistant to BLB
3.	Nagina 22	Selection from Rajbhog	R	1	1	Tall (115–120 cm), yield 20- 25 quintal ha ⁻¹ , 85-102 days maturity, presence of red awns, grains are short, bold and white
4.	Birsa Gora	Selection from germplasm collection of Gora	R	1	1	Tall (165- 180 cm), yield 18- 20 quintal ha ⁻¹ , 95-100 days maturity, tall and pubescent (120-140 cm), grain is medium sized, bold and red, moderately resistant to major diseases and pests

*LR = Leaf rolling (1–9 scale); SG = Stay green (1-5 scale).

Table 2: Scaling Test for Yield per Plant, Proline Content and Stomatal Behavior in Rice

Crosses	Simple Scaling Test of Spikelet per panicle			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	36.77**	60.43**	34.87**	57.23**
HUR 3022 × Birsa Gora	-22.07**	-40.7**	-20.97**	-37.87**
Sarjoo 52 × Nagina 22	-14.62**	-22.37**	-13.42**	-20.27**
Sarjoo 52 × Birsa Gora	1.73**	-4.33**	1.43**	-3.13**
	Simple Scaling Test of Percent filled grains			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	-13.58**	-2.34**	-10.51**	-2.05**
HUR 3022 × Birsa Gora	-50.62**	-27.39**	-49.62**	-24.19**
Sarjoo 52 × Nagina 22	0.07	-0.81**	0.07	-0.76**
Sarjoo 52 × Birsa Gora	1.71**	-7.17**	1.71**	-4.17**
	Simple Scaling Test of Thousand grain weight			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	2.20**	2**	1.08**	1.19**
HUR 3022 × Birsa Gora	1.91**	1.57**	0.79**	0.43**
Sarjoo 52 × Nagina 22	-0.92**	2.63**	-0.99**	2.05**
Sarjoo 52 × Birsa Gora	-1.33**	-3.54**	-1.17**	-2.86**

Table 2 cont. Scaling Test for Yield per Plant, Proline Content and Stomatal Behavior in Rice

Crosses	Simple Scaling Test of yield per plant			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	4.65**	19.76**	3.86**	16.27**
HUR 3022 × Birsa Gora	-0.43**	-33.26**	-0.41**	-30.26**
Sarjoo 52 × Nagina 22	-0.6**	6.60**	-0.6**	5.60**
Sarjoo 52 × Birsa Gora	12.5**	-8.3**	11.5**	-7.83**
	Simple Scaling Test of proline content			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	62.87**	48.47**	58.24**	46.81**
HUR 3022 × Birsa Gora	16.7**	15.39**	13.3**	11.29**
Sarjoo 52 × Nagina 22	18.75**	18.03**	16.75**	16.03**
Sarjoo 52 × Birsa Gora	21.47**	22.13**	19.42**	18.93**
	Simple Scaling Test of stomatal behaviour			
	Irrigated condition		Rain fed condition	
	C	D	C	D
HUR 3022 × Nagina -22	1**	1.67**	0.98**	0.97**
HUR 3022 × Birsa Gora	-13.67**	-3.67**	-10.47**	-2.37**
Sarjoo 52 × Nagina 22	-1**	2.33**	-1.35**	2.03**
Sarjoo 52 × Birsa Gora	-4.33**	-1**	-2.33**	-1**

Table 3 Estimates of Gene Effects from Generation Mean Analysis for Spikelet Per Panicle, Percent Filled Grains and Thousand Grain Weight in Rice Crosses

Cross	Condition	Components of generation mean (5 – parameter model)					Epistasis
		m	d	h	i	l	
Spikelet per panilce							
HUR 3022 × Nagina -22	I	122.77**	11.9**	33.71**	44.07**	-62.49**	D
	R	99.23**	31.05**	-36.91**	27.94**	31.56**	D
HUR 3022 × Birsa Gora	I	100.67**	11.43**	12.53**	46.43**	-25.07**	D
	R	97.67**	8.43**	10.53**	41.43**	-22.57**	D
Sarjoo 52 × Nagina 22	I	84.8**	8.98**	15.42**	30.44**	-10.33**	D
	R	81.8**	6.98**	13.42**	29.44**	-8.33**	D
Sarjoo 52 × Birsa Gora	I	91.37**	6.5**	6.11**	16.18**	-8.09**	D
	R	88.37**	5.65**	4.81**	13.18**	-6.39**	D
Percent filled grains							
HUR 3022 × Nagina -22	I	94.45**	1.01**	-0.69	1.33**	14.98**	D
	R	91.26**	0.99**	-0.67**	1.03**	12.18**	D
HUR 3022 × Birsa Gora	I	83.587	1.48**	7.28**	12.79**	30.97**	C
	R	80.29**	1.18**	5.65**	9.89**	28.91**	C
Sarjoo 52 × Nagina 22	I	97.24**	0.02	0.83	0.59**	-1.17**	D
	R	92.14**	0.02	0.83**	0.48**	-1.07**	D
Sarjoo 52 × Birsa Gora	I	97.30**	0.58**	4.65**	6.23**	-11.85**	D
	R	97.30**	0.58**	2.65**	5.23**	-9.85**	D
Thousand grain weight							
HUR 3022 × Nagina -22	I	21.41**	0.93**	-0.18	0.90**	-0.26**	C
	R	20.97**	0.43**	-0.10**	0.65**	-0.25**	C
HUR 3022 × Birsa Gora	I	21.70**	0.58**	-0.3	0.43**	-0.45**	C
	R	20.40**	0.12**	-0.28**	0.07	-0.42**	D
Sarjoo 52 × Nagina 22	I	21.14**	0.55**	-1.04	-0.81**	4.74**	D
	R	20.24**	0.45**	-0.94**	-0.77**	3.74**	D
Sarjoo 52 × Birsa Gora	I	20.68**	0.46**	1.69**	3.06**	-2.94**	D
	R	20.08**	0.21**	1.09**	1.95**	-2.04**	D

Table 3 cont. Estimates of Gene Effects from Generation Mean Analysis for Spikelet Per Panicle, Percent Filled Grains and Thousand Grain Weight In Rice Crosses

Cross	Condition	Components of generation mean (5 – parameter model)					Epistasis
		m	d	h	i	l	
Yield per plant							
HUR 3022 × Nagina -22	I	56.66**	5.46**	-4.3**	-1.47**	20.15**	D
	R	52.16**	3.77**	-3.1**	-1.17**	18.25**	D
HUR 3022 × Birsa Gora	I	44.64**	6.87**	13.73**	35.84**	-43.77**	D
	R	42.65**	5.87**	11.73**	33.84**	-40.77**	D
Sarjoo 52 × Nagina 22	I	44.9**	10.38**	2.92**	16.26**	9.6**	C
	R	41.89**	8.38**	2.62**	14.56**	8.6**	C
Sarjoo 52 × Birsa Gora	I	45.45**	4.66**	8.83**	16.95**	-27.73**	D
	R	42.15**	2.67**	7.83**	14.95**	-25.73**	D
Proline content							
HUR 3022 × Nagina -22	I	51.17**	-7**	-12**	-35.83**	-19.2**	C
	R	48.27**	-5.83**	-9.03**	-29.33**	-17.32**	C
HUR 3022 × Birsa Gora	I	38.43**	-6.55**	-0.73**	-20.58**	-1.74**	C
	R	48.27**	-5.83**	-9.03**	-29.33**	-17.32**	C
Sarjoo 52 × Nagina 22	I	43.57**	-7.62**	0.56**	-24.13**	-0.95**	D
	R	37.51**	-5.69**	0.56**	-23.13**	-0.95**	D
Sarjoo 52 × Birsa Gora	I	42.9**	-5.63**	0.22**	-22.44**	0.89**	C
	R	39.39**	-3.23**	0.19	-19.04**	0.78**	C
Stomatal behaviour							
HUR 3022 × Nagina -22	I	28.33**	-4.5**	-2.44**	-9.94**	0.89**	D
	R	25.73**	-3.75**	-2.04**	-7.34**	0.65	D
HUR 3022 × Birsa Gora	I	28.33**	-4.17**	3.33**	-8.17**	13.33**	C
	R	25.63**	-2.47**	2.13**	-6.77**	11.73**	C
Sarjoo 52 × Nagina 22	I	28.33**	-4.17**	3.33**	-8.17**	13.33**	C
	R	26.67**	-2.12**	1.07**	-4.72**	3.64**	C
Sarjoo 52 × Birsa Gora	I	28.33**	-4.17**	3.33**	-8.17**	13.33**	C
	R	26.67**	-3.86**	1.01**	-6.9**	3.24**	C