

Generation Mean Analysis in Physiomorphic Traits of Aerobic Rice

Abstract:

An experiment was carried out to study the genetic architecture of few physiomorphic quantitative traits of rice under aerobic condition. Generation mean analysis was carried out in three selected crosses viz. Banglami/Luit, Koimurali/Luit and Guni/Gopinath, involving six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2). The individual scaling tests were used to test the adequacy of additive dominance model. The gene effects were estimated using three parameter model (joint scaling test) suggested by Cavalli (1952) and six parameter model suggested by Haymen (1958). The analysis of variance among different generations of different crosses revealed significant variation for most of the characters indicating considerable variability in the material studied. All the characters except height growth rate in cross II, recorded significance for at least one of the four individual scaling tests in all the 3 crosses. Estimation of different gene effects and their interactions revealed significant positive additive effect for plant height and height growth rate in all the three crosses. Preponderance of dominance effect in the expression of height growth rate, spikelet fertility, grain yield, harvest index, root weight and root shoot ratio was evident from the significant positive dominance (h) effect in all the three crosses. With respect to interaction effects, all the characters except height growth rate in cross II, exhibited significant interaction effect for one or more epistatic interactions i.e. [i], [j] or [l] in all the three crosses studied. It is evident that for all the yield and other adaptive traits, additive, dominance and interaction effects were present indicating the complex inheritance of the traits under aerobic condition.

(Keywords: Aerobic rice, Generation mean analysis, Gene action, additive, dominance, duplicate epistasis, complementary epistasis)

Introduction:

Rice (*Oryza sativa* L.) is one of the world's most important food crops and a primary source of food for more than half of the world population. It provides 35-60% of the calories consumed in Asia, the main cultivation area of rice in the world. It is planted in about 163 million ha annually of the world's cultivated land (Degenkolbe *et al.*, 2013). It is the only crop in the world that is grown in most fragile ecosystem and hence a second green revolution is possible only if rice research is undertaken vigorously and persistently to address specific abiotic and biotic stress problems (Bouman, 2007).

Lowland rice occupies 55% of the world rice area producing 75% of world rice. But it is being threatened by growing water scarcity worldwide (Tuong and Bouman, 2003). In Asia half of the irrigated water is being consumed by rice alone. By 2025, an “economic water scarcity” is expected to hamper most of Asia’s 22 million ha of dry-season lowland rice (Tuong and Bouman, 2003). Therefore, researchers are looking for ways and means to reduce water use in rice production and increase the water use efficiency.

Aerobic rice- a term coined by the International Rice Research Institute (IRRI) is an emerging strategy in addressing the problems of water shortage in cultivation of rice. It describes a type of high-yielding input responsive rice capable of cultivating on unsaturated, puddle-free, non-flooded soil both in irrigated or rainfed ecosystem. Cultivation of aerobic rice is possible in areas with sufficient rainfall to bring the soil moisture content near to field capacity under rainfed condition; and in water deficit areas where irrigation is present but the water supply is insufficient for producing lowland rice. Availability of suitable cultivars is the determining factor in success in aerobic rice cultivation. The current ideotype of aerobic rice is that it should combine certain traits found in germplasm adapted to the irrigated environment with other traits found in upland germplasm (Okami *et al.*, 2012). To combine these traits, breeders have to overcome the potential antagonisms between them. Discovery of the genes, pathways and regulatory networks underlying the above traits would greatly aid the breeding programme (Lafitte and Bennett, 2002).

Knowledge of the gene action for the traits of interest is the prerequisite in any systematic plant breeding program. The success of aerobic rice breeding greatly depends on correct choice of parents for hybridization and the information on gene action involving different economic and drought tolerant traits. Generation mean analysis is one of the extensively used procedure describing detail account of gene effects and quality of the genes carried by the parents. It provides information on additive, dominance and three types of interaction, viz. additive x additive [i], additive x dominance [j] and dominance x dominance [l]. Such information can be effectively used to ascertain the genotypic value of individuals in a breeding programme. In order to obtain information on both main and interaction components, generation mean analysis helps to identify effective selection procedure. In comparison to lowland irrigated rice, genetic architecture study in aerobic rice is very meager. Present study envisaged to estimate the underlying gene effect and inheritance pattern on grain yield and few quantitative physiomorphic traits under aerobic condition in a few sets of selected crosses.

Materials and methods:

The experimental material for the present study was generated from three crosses involving five genotypes of rice selected based on their *per se* grain yield performance in a previous Line x Tester experiment under aerobic condition. The three crosses involved were Cross I (Banglami x Luit) , Cross II (Koimurali x Luit) and Cross III (Guni x Gopinath). Banglami, Koimurali and Guni are three direct seeded rice landrace with putative drought tolerance from Assam. Luit and Gopinath are two early maturing, photo insensitive HYV.

Fresh crosses were made to generate F_1 , BC_1 and BC_2 during *kharif*, 2017 at the experimental farm of SCS college of Agriculture, Assam Agricultural University, Dhubri, Assam, India. F_1 seeds from previous season Line x Tester experiment were advanced to obtain the F_2 generation. In the following season, i.e. February to June, 2018, all the six generations of the concerned crosses were raised in RBD with two replications under aerobic condition. All the parents, backcross and F_1 were grown in two rows each, while the F_2 populations were grown in five rows. Presoaked, sprouted seeds were sown directly in a 3 m row, maintaining a spacing of 30cm x 15 cm under aerobic condition. All the recommended package of practices was followed keeping the soil moisture content at field capacity till the grain filling stage. Observations were recorded from 5 randomly sampled plants on the following traits- Plant height, Number of productive tillers, Days to maturity, Harvest index, Spikelet fertility, Grain yield per plant, Panicle harvest index, 100 grain weight, Relative water content, Root dry weight, Shoot dry weight, Root shoot ratio, Root volume, Proline content, Chlorophyll content. Estimation of Relative water content, Proline content and Chlorophyll content were done following the procedure by Schonfeld *et al.* (1988), Bates *et al.* (1973) and Hiscox and Israelstam (1979), respectively.

The mean data of all the observations were subjected to ANOVA for estimating the variability present in the entries. Scaling tests following Mather (1949) and Joint Scaling test following Cavalli (1952) was done to validate the additive-dominance model and to detect non allelic interactions. Estimation of gene effects and their interactions were worked out following 6 parameter model of Hayman (1958). The calculated 't' values were compared to the tabulated 't' values at respective degree of freedom to test the significance of individual gene effects. All statistical analysis were carried out by OPSTAT.

Results and Discussion:

The analysis of variance revealed that significant difference existed among the six generations in all the crosses for most of the characters. The results of scaling tests clearly revealed the presence of gene interaction although the crosses and the characters varied as regards significance of the four scales (Table 2). All the characters recorded significance for

at least one of the four individual scaling tests A,B,C and D) across the three crosses. The individual scaling test of Mather (1949) calculates a scale by using only a few combinations of generations at a time. Joint scaling test (Cavelli, 1952) also failed to obtain a good fit for additive dominance model for all the traits except relative water content in Koimurali x Luit, indicated presence of digenic or higher order interactions or linkage influencing the inheritance of these characters (Table 2). Subhalakshmi *et al.* (2016) and Kumer *et al.* (2020) also reported inadequacy of simple additive dominance model for all the traits under study in rice.

Table1. Mean square for fifteen quantitative characters in three crosses in generation mean analysis

Characters	Cross-I			Cross-II			Cross-III		
	Replica tion	Progeny	Error	Replica tion	Progeny	Error	Replica tion	Progeny	Error
Days to maturity (in days)	0.04	5.89	1.65	9.01	9.75	3.33	0.00	54.71*	10.09
Plant height (cm)	8.79	121.48*	13.92	2.25	141.16*	12.46	3.7	61.09*	5.58
Number of productive tillers	0.19	9.89*	1.21	0.57	7.34*	1.02	0.37	6.62*	1.23
Panicle harvest index	0.000	0.0032*	0.0006	0.0004	0.0028*	0.0005	0.000	0.003	0.001
Spikelet fertility (%)	17.52	44.02	11.16	5.47	50.14*	5.90	2.90	57.40*	7.97
Grain yield per plant (gm)	0.84	6.14	1.37	1.45	4.88	1.00	0.14	6.93*	1.09
Harvest index	0.018	0.005	0.0007	0.0003	0.0013*	0.0003	0.0021	0.0041**	0.0005
100 grain weight (gm)	0.013*	0.007*	0.001	0.00	0.01**	0.00	0.01	0.017*	0.002
Relative water content	14.63*	11.02*	2.10	0.07	8.15	3.40	4.32	31.92*	4.64
Proline content (mg/ g Dry Weight)	15.64	107.78*	20.33	39.24	37.63	9.59	2.61	73.29*	11.54
Chlorophyll content (mg/g fresh wt.)	0.002	0.017	0.004	0.001	0.031	0.007	0.013	0.051	0.014
Root weight (gm)	1.88	5.78	2.60	0.45	5.68	1.23	17.52*	5.10	2.61
Shoot weight (gm)	17.02	51.47*	6.28	0.96	21.78	5.59	66.74**	14.52*	2.20
Root shoot ratio	0.0001	0.0022*	0.0004	0.0003	0.0013	0.0004	0.018*	0.003	0.00
Root volume (ml)	24.65	18.39	5.52	31.69	41.85	9.94	24.94	157.56	56.63

* $p < 0.5$; ** $p < 0.01$

Significance of scaling tests is an indication of the presence of gene interaction but for confirmation and estimation of components including different gene interactions further analysis is need. Hayman (1958) has developed methods for estimating additive, dominance and epistatic parameters based on components of means of different generations. Accordingly, estimates of different gene effects and their interaction were worked out for all the three selected crosses. With few exception, the estimates of m, d, h, i, j and l in six parameters model exhibited that epistatic interaction model was adequate to explain the gene action in all the characters under study across the 3 crosses.

Plant height recorded positive additive effect (d) in all the three crosses. Relative water content in cross I & II; shoot weight in cross I & III; root weight in cross I; 100 grain

weight and root volume in cross III also registered similar results. However, significant negative additive (d) effect was found for panicle harvest index, grain yield per plant and harvest index in all the three crosses, whereas number of productive tillers exhibited significant negative effect in cross I and cross III, spikelet fertility and days to maturity in cross II and Cross III, proline content and chlorophyll content in cross I, 100 grain weight and root volume in cross II, and root shoot ratio in cross III. Roy and Panwar (1993), Patel (2015), Senthilkumar (2011) and Roy and Senapati (2011) also reported importance of additive gene effects in inheritance of quantitative traits in rice. Thus improvement in yield could be brought through indirect selection of these characters in early generations.

In all the three crosses, significant and positive dominant (h) effect were recorded for spikelet fertility, grain yield, harvest index and root weight and root shoot ratio indicating preponderance of dominance in expression of these characters. On the contrary, number of productive tillers and days to maturity registered significant negative dominance effect in all the three crosses.

With respect to interaction effects, all the characters exhibited significant interaction effect for one or more epistatic interactions i.e. i , j or l in all the 3 crosses. Grain yield, harvest index and root shoot ratio recorded significant positive additive x additive (i) effect, whereas days to maturity recorded significant negative additive x additive interaction in all the 3 crosses. Roy and Senapati (2011) and Patel (2015) and Jondhale et al (2018) reported similar results for grain yield.

Relative water content, and root weight in cross I and cross II, chlorophyll content in cross II & III, proline content in cross II and shoot weight, root volume in cross III recored positive additive x dominance [j] effect. However, Plant height and harvest index were observed to be negatively significant in all the crosses.

Significant dominance x dominance [l] effect with positive estimate were recorded for the no of effectives tillers and negative estimate in harvest index and root shoot ratio in all the 3 crosses. Root shoot ratio and harvest index were found to be negatively significant for this interaction in all the three crosses.

The higher magnitude of estimates of dominance x dominance interaction as compared to additive x additive interaction for grain yield and their components which corroborated with the findings of Chauhan *et al.* (1993), Kumar *et al.* (2007) and Patel (2015) who reported the importance of all the two types interactions in the inheritance of different traits. Singh *et al.* (2015) also reported nature and magnitude of gene effects and epistatic interactions for a character exhibited considerable variation across the six crosses.

The dominance (h) and dominance x dominance (l) interaction effects were in opposite direction, suggesting the presence of duplicate epistasis for most of the characters in most of the crosses under study including grain yield. Highest number of characters were found to be under the influence of duplicate epistasis in cross I (12), followed by in cross III (8) and Cross II (4). Number of productive tillers, 100 grain weight, harvest index and root shoot ratio were found to be under this type of gene interaction in all the three crosses. Kumar *et al.* 2020 also reported duplicate epistasis in days to maturity, plant height, panicle length, chlorophyll content, harvest index in rice. Duplicate epistasis may result in decreased variation in F_2 and subsequent generations and may decrease heterosis and also hinder the pace of progress through selection (Singh *et al.*, 2006). 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 type of epistasis was determined as complementary when dominance (h) and dominance x dominance (l) gene effects have same sign. This epistasis suggests fixable nature of the character under selection in advanced generations. Spikelet fertility in cross II and harvest index in cross III recorded complementary type of epistasis.

The predominance of dominance effects over the corresponding additive effects indicated the importance of dominance or complete dominance effects in the inheritance of these traits. Epistatic components are known to constitute a sizeable part of variation in the character which show higher estimates of dominance effects (Gambel, 1962). Duplicate type of epistasis in majority of the cases further confirmed the prevalence of dominance effects in the inheritance of different characters under study. Similar results also reported by Hasib *et al.* (2002), Nayak *et al.* (2007), Savita and Ushakumari (2015) and Kumar *et al.* (2015). Lavanya (2000), have reported that the importance of non additive effects was high for traits such as yield and its components in rice.

In the present study, it was observed that additive, dominance and epistatic gene effects were found to play an important role or principally involved in the inheritance of majority of the characters indicating the complex inheritance of the traits. This implies that improvement of such characters cannot be attained easily by following a single approach. Heterosis breeding is not desirable in case of epistasis but it would be possible to isolate segregants as good as that of F_1 in the subsequent filial generations. More reliance should be placed on selection between families and lines for the traits with relatively high epistatic variance (Divya *et al.*, 2014). The characters predominantly under the control of additive gene action could be improved upon through selection in segregating generations. For non fixable

gene action breeding methods such as multiple crosses followed by intermating among desired segregants, or isolation of superior genotypes from the segregating population followed by biparental mating and selection are likely to result faster rate of genetic improvement. To improve upon the characters, where pronounced dominant effects are principally involved, selection of desired plants from segregating generations would help in effectively synthesizing desirable high yielding genotypes.

Conclusion:

The study generated some useful information regarding nature of gene action from the performance of the six generations viz. P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 of three rice crosses under aerobic condition. The inheritance of most of the adaptive traits exhibited complex nature involving additive, dominance and all the three types of non allelic interactions in all the crosses. It can be inferred that a single breeding approach is not adequate in bringing about desired improvement; rather, focus should be on improving individual characters separately based on the nature of gene action. Methods like diallel selective mating or reciprocal recurrent selection can also be adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages. Incorporation of desirable genes into a single genetic background following biparental mating with few cycles of crossing of promising segregants in F_2 and onwards could also be an attractive viable proposition.

Table 2 . Individual and Joint scaling test for six generations means of three crosses

Character	Scale				Joint scaling test			
	A	B	C	D	m	d	h	χ^2
CROSS I								
Days to maturity (in days)	2.9	1.800	14.5**	4.9*	102.99*	0.38	2.88*	13.03**
Plant height (cm)	1.250	11.185**	14.065**	0.815	109.36*	-8.64*	13.85*	27.23*
Number of productive tillers	-7.850**	-7.710**	-9.400**	3.080**	10.08*	1.81*	1.81*	123.12*
Panicle harvest index	-0.17**	-0.064**	-0.156**	0.041*	0.81*	0.01*	-0.02*	69.03*
Spikelet fertility (%)	-2.0	-7.1*	-35.9**	-13.4**	77.99*	2.56*	-5.88*	36.53*
Grain yield per plant (gm)	-2.25*	-0.71	-12.32**	-4.68**	12.75*	1.46*	-1.91*	36.72*
Harvest index	0.03	0.10*	-0.20*	-0.15**	0.51*	0.02*	-0.01	24.21*
100 grain weight (gm)	0.26**	0.20*	0.081	-0.19*	2.13*	0.02	0.10*	12.65*
Relative water content	0.65	-5.41**	-9.44	-2.34	78.39*	-3.13*	2.07*	10.14*
Proline (mg/ g Dry Weight)	-8.5	-13.0*	14.3	17.9**	53.81*	8.26*	1.15	9.84*
Chlorophyll (mg/g fresh wt.)	-0.3*	0.02	-0.55*	-0.13	1.20*	0.09*	-0.03	9.99*
Root weight (gm)	2.41	-5.16*	-11.78*	-4.515	23.37*	0.27	2.24*	11.12*
Shoot weight (gm)	-13.45**	-21.37**	-15.8	9.51*	67.60*	-3.49*	-2.05	42.75*
Root shoot ratio	0.114*	0.057	-0.085	-0.128*	0.35*	0.03*	0.02	10.10*
Root volume (ml)	7.5*	1.6	-12.9	-11.0**	63.06*	-0.87	-5.19*	9.69*
CROSS II								
Days to maturity (in days)	-1.50	6.90**	14.60**	4.60*	101.68*	1.47*	2.27*	24.74*
Plant height (cm)	-0.57	9.09**	10.09**	0.78	110.00*	-9.44*	12.56*	21.83**
Number of productive tillers	-8.50**	-6.13**	-9.54**	2.55	12.47*	-0.21	-0.33	84.39*
Panicle harvest index	-0.06	-0.06**	-0.23**	-0.06**	0.77*	0.04*	-0.06*	36.49*
Spikelet fertility (%)	-17.20**	-10.70**	-39.10**	-5.60*	75.78*	3.80*	-5.25*	104.54*
Grain yield per plant (gm)	-4.26**	0.00	-10.78**	-3.26*	15.65*	1.48*	-1.20	21.10*
Harvest index	0.028	0.068*	-0.142**	-0.090**	0.49*	0.05*	0.03*	12.83*
100 grain weight (gm)	0.11	0.27**	0.05	-0.17*	2.12*	0.11*	0.05	15.98*
Relative water content	-0.13	-7.95*	-7.34	0.37	79.54*	-1.27	-0.72	1.67
Proline (mg/ g Dry Weight)	4.40	-13.60*	13.20	11.20	55.38*	3.37*	-1.69	13.59*
Chlorophyll (mg/g fresh wt.)	-0.08	-0.39**	-0.71**	-0.12	1.34*	0.07*	-0.14*	17.95*
Root weight (gm)	1.45	-4.98*	-9.37*	-2.92	20.94*	0.97	2.26*	11.92*
Shoot weight (gm)	-10.53**	-15.07**	-6.12	9.74**	62.36*	1.38*	0.12	34.01*
Root shoot ratio	0.09*	0.01	-0.11	-0.10**	0.34*	0.01	0.02	13.40*
Root volume (ml)	-15.90**	-4.20	-41.20**	-10.55	63.89*	1.00	-1.74	20.41*
CROSS III								
Days to maturity (in days)	5.40	1.40	22.10**	7.65**	111.75*	6.75*	4.81*	22.97*
Plant height (cm)	4.44**	9.63**	25.25**	5.59**	122.44*	-6.00*	5.52*	62.25*
Number of productive tillers	-4.98**	-6.22**	-5.94*	2.63*	13.36*	1.30*	-1.49*	33.18*
Panicle harvest index	-0.14**	-0.06*	-0.13*	0.04	0.78*	0.00	-0.06*	29.59*
Spikelet fertility (%)	-18.70**	-7.30	-38.20**	-6.10	74.22*	4.66*	-2.51	35.83*
Grain yield per plant (gm)	2.55*	0.92	-6.41*	-4.94**	13.05*	2.24*	-0.64	16.87*
Harvest index	0.04	0.051	-0.08	-0.089*	0.49*	0.02*	0.004	8.59*
100 grain weight (gm)	-0.12	-0.17*	0.13	0.21*	2.09*	-0.12*	0.08*	7.92*
Relative water content	-13.30**	-14.70**	-16.40*	5.80	83.84*	2.77*	-5.03*	23.84*
Proline (mg/ g Dry Weight)	17.20*	10.20	-0.50	-13.95	40.92*	5.05*	12.78*	9.39*
Chlorophyll (mg/g fresh wt.)	0.04	-0.30**	-0.77**	-0.25*	1.41*	0.18*	0.07	18.77*
Root weight (gm)	1.35	2.49	-10.94*	-7.39**	16.30*	1.51*	-0.32	14.36*
Shoot weight (gm)	1.99	-5.34*	-9.73	-3.19	50.07*	-2.02*	3.86*	7.95*
Root shoot ratio	0.02	0.09*	-0.15	-0.13**	0.33*	0.05*	-0.04	8.93*
Root volume (ml)	-15.70*	-35.20**	-60.80**	-4.95	67.04*	-2.91*	-14.29*	28.65*

*p<0.5 ; **p<0.01

Table3. Estimate of gene effects in six parameter model in three crosses

Characters	m	d	h	i	j	l	Epitasis type
Cross-I							
Days to maturity (in days)	106.95**	-0.1	-8.05*	-9.8**	0.55	5.1	-
Plant height (cm)	118.11**	4.07**	10.09**	-1.63	-4.97**	-10.80*	Duplicate
Number of productive tillers	11.47**	-1.66**	-4.03*	-6.16**	-0.07	21.72**	Duplicate
Panicle harvest index	0.78**	-0.06**	-0.11**	-0.08*	-0.05**	0.32**	Duplicate
Spikelet fertility (%)	68.85**	-1.1	22.55**	26.80**	2.55	-17.70**	Duplicate
Grain yield per plant (gm)	11.68**	-2.12**	8.00**	9.36**	-0.77	-6.40*	Duplicate
Harvest index	0.27**	-0.09*	0.26**	0.30**	-0.05*	-0.41**	Duplicate
100 grain weight (gm)	2.13**	0.01	0.38*	0.38**	0.03	-0.84**	Duplicate
Relative water content	77.89**	5.12**	6.57	4.68	3.03**	0.08	-
Proline (mg/ g Dry Weight)	60.30**	-7.2*	-32.75*	-35.8*	2.25	57.3**	Duplicate
Chlorophyll (mg/g fresh wt.)	1.09**	-0.20**	0.22	0.26	-0.16*	0.02	-
Root weight (gm)	22.06**	2.85*	11.34**	9.03	3.79*	-6.28	Duplicate
Shoot weight (gm)	56.9**	6.95**	-16.57*	-19.02*	3.96	53.84**	Duplicate
Root shoot ratio	0.33**	0	0.28**	0.26*	0.03	-0.43**	Duplicate
Root volume (ml)	56.90**	3.3	16.55**	22.00**	2.95	-31.10**	Duplicate
Cross-II							
Days to maturity (in days)	105.6**	-4.70**	-7.9**	-9.2**	-4.20**	3.8	-
Plant height (cm)	117.71**	5.64**	10.11**	-1.57	-4.83**	-6.95	-
Number of productive tillers	11.67**	-0.66	-5.52**	-5.09	-1.19	19.72**	Duplicate
Panicle harvest index	0.71**	-0.03*	0.09*	-0.12**	0.004	0.002	-
Spikelet fertility (%)	68.35**	-5.30*	10.35*	11.20*	-3.25*	16.7*	Complementary
Grain yield per plant (gm)	13.37**	-2.91**	5.72*	6.52*	-2.13*	-2.26	-
Harvest index	0.21**	-0.05**	0.16*	0.18**	-0.05**	-0.22**	Duplicate
100 grain weight (gm)	2.09**	-0.14**	0.34*	0.33*	-0.08	-0.72**	Duplicate
Relative water content	78.35**	4.98**	-0.65	-0.74	3.91*	8.82	-
Proline (mg/ g Dry Weight)	58.65**	3.2	-23.1*	-22.4*	9.6*	31.6	-
Chlorophyll (mg/g fresh wt.)	1.18**	0.03	0.13	0.23	0.15*	0.24	-
Root weight (gm)	20.46**	1.34	8.08*	5.84	3.22*	-2.31	-
Shoot weight (gm)	63.65**	0.62	-16.73**	-19.48**	2.27	45.08**	duplicate
Root shoot ratio	0.32**	0.02	0.23**	0.21**	0.04	-0.31*	duplicate
Root volume (ml)	55.6**	-6.35*	22.7*	21.1	-5.85*	-0.1	-
Cross-III							
Days to maturity (in days)	118.2**	-4.45*	-10.85*	-15.30**	2	8.5	-
Plant height (cm)	129.0**	3.96**	-6.71*	-11.18**	-2.59*	-2.89	-
Number of productive tillers	12.97**	-1.14*	-5.4*	-5.26*	0.62	16.46**	Duplicate
Panicle harvest index	0.74**	-0.04*	-0.13*	0.07	-0.04*	0.27*	Duplicate
Spikelet fertility (%)	68.75**	-8.70**	16.40*	12.2	-5.70*	13.8	-
Grain yield per plant (gm)	10.98**	-1.58**	9.00**	9.88**	0.81	-13.35**	Duplicate
Harvest index	0.22**	-0.06**	0.14*	0.18*	0	0.27*	Complementary
100 grain weight (gm)	2.18**	0.13*	-0.35*	-0.42*	0.02	0.71*	Duplicate
Relative water content	81.40**	-1.6	-13.40**	-11.6	0.7	39.60**	Duplicate
Proline (mg/ g Dry Weight)	43.75**	-1.95	35.55*	27.9	3.5	-55.30**	Duplicate
Chlorophyll (mg/g fresh wt.)	1.32**	-0.05	0.61**	0.51*	0.17*	-0.25	-
Root weight (gm)	13.20**	-1.61	14.53**	14.78**	-0.57	-18.62**	Duplicate
Shoot weight (gm)	49.97**	5.32**	11.04	6.38	3.67*	-3.03	-
Root shoot ratio	0.27**	-0.07**	0.22**	0.25**	-0.04	-0.36**	Duplicate
Root volume (ml)	52.40**	10.95**	4.9	9.9	9.75*	41	-

*p<0.5 ; **p<0.01

references

1. Bates, L.S.; Waldre, R.P. and Teare, L.D. (1973). Rapid determination of free proline for water stress studies. *Plant and Soil* **39**: 205-207.
2. Bouman, B.A.M. (2007). The aerobic rice reality. *Rice Today* **6**: 38.
3. Cavalli, L. L. (1952). An analysis of linkage in quantitative inheritance. In: *Quantitative inheritance* (ed. E. C. R. Reeve and C. H. Waddington, pp. 135-141). HMSO, London, UK.
4. Chauhan, V.S.; Chauhan, J.S. and Tandon, J.P. (1993). Genetic analysis of grain number, grain weight and grain yield in rice (*Oryza sativa* L.). *Indian J. Genet.* **53** (3): 261-263.
5. Degenkolbe, T.; Phuc, T. D.; Kopka, J.; Zuther, E.; Hinch, D.K. and Kohl, I. (2013). Identification of Drought Tolerance Markers in a Diverse Population of Rice Cultivars by Expression and Metabolite Profiling. *PLOS One* **8** (5): 1-14.
6. Divya, B.; Biswas, A.; Robin, S.; Rabindran, R. and Joel, A.J. (2014). Gene interactions and genetics of blast resistance and yield attributes in rice (*Oryza sativa* L.). *J. Genet.* **93** (2): 415-424.
7. Gambel, E.E. (1962). Gene effects in corn (*Zea mays* L.) 1. Separation and relative importance of gene effects for yield. *Canad. J. Pl. Sci.* **42**: 339-348.
8. Hasib, K.M.; Ganguli, P.K. and Kole, P.C. (2002). Genetic analysis of some quantitative characters in aromatic rice involving induce mutants. *Trop. Agril. Res. Extn.* **5** (1&2): 1-6.
9. Hayman, B.I. (1958). The separation of epistatic from additive and dominance variation in generation means. *Heredity.* **12**: 371-390.
10. Hiscox, J.D. and Israelstam, G. F. (1979). A method for the extraction of chlorophyll from leaf tissue without maceration. *Can. J. Bot.* **57** (12): 1332-1334.
11. Jondhale A S, Bhawe S G , and Jogi S R. (2018) Genetic evaluation of quantitative traits of rice (*oryza sativa* l.) by generation mean analysis. *Journal of Pharmacognosy and Phytochemistry*; SP1: 2477-2480
12. Kumar A. , Kumar A., Singh N.K., Kumar R., Nilanjaya, Singh S K et al., (2020). Assessment of Gene Action for Grain Micronutrient Content, Yield and Yield Contributing Traits in Rice (*Oryza sativa* L.) . *Current Journal of Applied Science and Technology.* 39(21): 56-63
13. Kumar, A.; Singh, N.K.; Kumar, R.; Sharma, V.K.; Rai, B. and Dayaram (2015). Estimation of genetic components for yield in rice using generation mean Analysis. *Oryza* **52** (4): 284-291.
14. Kumar, T.; Narasimman, R.; Senthilkumar, N.; Eswaran, R. and Sampathkumar, C. (2007). Gene effects for grain yield and its component characters in rice (*Oryza sativa* L.). *Crop Improve.* **34** (1): 19-23.
15. Lafitte, H.R. and Bennett, J. (2002). Requirement for aerobic rice: Physiological and molecular considerations. In: *Water -Wise Rice Production*. Bouman, B.; Hensdijk, H.; Hardy, B.; Bindraban, P.; Tuong, T. and Ladha, J. (eds.). IRRI, Los Banos, Philippines, pp. 259-274.

16. Lavanya, C. (2000). Combining ability for yield and its components in hybrid rice. *Oryza* **37**: 11-14.
17. Mather, K. (1949). Biometrical genetics. *Dover Publication*, New York.
18. Nayak, A.R.; Chaudhury, D. and Reddy, J.N. (2007). Genetics of yield and yield components in scented rice. *Oryza* **4** (3): 227-230.
19. Okami, M.; Kato, Y. and Yamagishi, J. (2012). Allometric relationship between the size and number of shoots as a determinant of adaptations in rice to water-saving aerobic culture. *Field Crops Res.* **131**: 17–25.
20. Patel, S.K. (2015). Genetic analysis of yield and its components traits in rice (*Oryza sativa* L.). *Electron J. Plant Breed.* **6** (1): 19-25.
21. Perera, A.L.T.; Senadhira, D. and Lawrence, M.J. (1986). Genetic architecture of economically important characters and prediction of performance of recombinant inbred lines in rice. In: *Rice Genetics*. IRRI, Manila, Philippines, pp. 565-568.
22. Roy, A. and Panwar, D.V.S (1993). Nature of gene interaction in the inheritance of quantitative characters in rice. *Ann. Agric. Res.* **14** (1): 55-61.
23. Roy, S.K. and Senapati, B.K. (2011). Estimation of genetic components for grain yield and quality traits of rice. *Oryza* **48** (1): 22-30.
24. Savitha, P. and UshaKumari, R. (2015). Gene effects and genetic analysis of indigenous land races and improved cultivars for yield and yield components in rice (*Oryza sativa* L.). *IJAEB.* **8** (3): 489-499.
25. Schonfeld, M.A.; Johnson, R.C.; Carver, B.F. and Mornhinweg, D.W. (1988). Water relations in winter wheat as drought resistance indicator. *Crop Sci.* **28**: 526-531.
26. Senthilkumar, N. (2011). Genetics of grain yield and its component characters in rice. *Crop Improv.* **38** (1): 45-47.
27. Singh, A.K.; Mall, A.K.; Singh, P.K.; Singh, S.; Singh, A.K. and Verma, O.P. (2015). Genetic architecture, heterosis and Inbreeding depression for yield and yield Associated physiological traits in rice (*Oryza sativa* L.) under drought condition. *SAARC J. Agri.* **13** (1): 50-62.
28. Singh, I.; Gill, M.S. and Bains, T.S. (2006). Generation mean analysis for yield attributing traits in mungbean [*Vigna radiata* (L.) Wilczek]. *Indian J. Genet.* **66** (1): 47-48.
29. Subbulakshmi, K.; Shunmugavalli, N. and Muthuswamy, A. (2016). Generation mean analysis for yield and quality traits in F₂ and F₃ generation of rice (*Oryza sativa* L.): *Electron J. Plant Breed.* **7** (3): 491-495.
30. Subbulakshmi, K.; Shunmugavalli, N. and Muthuswamy, A. (2016). Generation mean analysis for yield and quality traits in F₂ and F₃ generation of rice (*Oryza sativa* L.): *Electron J. Plant Breed.* **7** (3): 491-495.
31. Tuong, T.P. and Bouman, B.A.M. (2003). Rice production in water-scarce environments, In: *Proc. Water Productivity Workshop*, 12–14 November 2001, Colombo, Sri Lanka. International Water Management Institute, Colombo, Sri Lanka.