Generation Mean Analysis in Physio-morphic Traits of Aerobic Rice in Assam India

Abstract:

An experiment was carried out to study the genetic architecture of few physio-morphic 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) at the experimental farm of SCS college of Agriculture, Assam Agricultural University, Dhubri, Assam, India during 2017 and 2018. The individual scaling tests were used to test the adequacy of additive dominance model. The gene effects were estimated using three parameter models (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 were done in OPSTAT software. Significant positive additive effects were recorded for plant height and height growth rate for 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. Hence, focus should be on improving individual characters separately based on the nature of gene action.

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 worlds 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 under taken 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. In 2025 approximately 20% out of 75 million hectares of irrigated rice cropping areas in Asia will be affected by water scarcity (Abdullah *et al*., 2021). Therefore, researchers are looking for ways and means to reduce water use in rice production and increase the water use efficiency.

The term "Aerobic rice" was 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 procedures 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 underling 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 materials consisted of P1, P2, F1, F2, BC1 and BC2 genotypes of rice. These materials were generated from three crosses involving five rice genotypes which were selected based on their *per se* grain yield performance in a previous Line x Tester experiment under aerobic condition. In this design broad based testers “t” were crossed to each one of the “l” lines. It is widely used in deciding the relative ability of female and male lines to produce desirable hybrid combinations. 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.

The 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 selfed to obtain the F_2 generation.

In the following season, i.e. February to June, 2018, all the six generations were grown in *boro* season in two replication following RBD design. All the parents, backcrosses and F_1 were grown in two rows, while the F_2 populations were grown in five rows. Presoaked, sprouted seeds were sown directly in a 3 m row length, 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 fifteen 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 and 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 was carried out by the OPSTAT statistical package.

Results and Discussion

Scaling test: 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 (Table2). 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. Estimation of Mean sum of square in three crosses

Characters	Cross-I			Cross-II			Cross-III		
	Replication	**Progeny**	**Error**	**Replication**	**Progeny**	**Error**	**Replication**	**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. However 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 three crosses.

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***	$\chi2$
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	-8.50**	-6.13**	-9.54**	2.55	12.47*	-0.21	-0.33	84.39*

Character	**Scale**				**Joint scaling test**			
	A	**B**	**C**	**D**	***m***	***d***	***h***	**$\chi 2$**
tillers								
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*

$^{*}p<0.5$; $^{**}p<0.01$

Additive gene effects: Plant height recorded positive additive effect (d) in all the three crosses. Relative water content in cross I and II; shoot weight in cross I and 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.

Dominant gene effects: In all the three crosses, a significant and positive dominant (h) effect was 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.

Epistatic gene effects: 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 and III, proline content in cross II and shoot weight, root volume in cross III recorded 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 was recorded for the number of effective 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. Finding corroborated with the reports of Hassan *et al.* (2023)

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 gene 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). Abd-El-Aty *et al*. (2023) also reported preponderance of dominance genetic variance over additive genetic variance in rice for several physio-morphic traits under normal as well as water deficit condition.

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	-

Characters	**m**	**d**	**h**	**i**	**j**	**l**	**Epitasis type**
Cross-I							
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	-

$^{*}p<0.5$; $^{**}p<0.01$

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.

Disclaimer (Artificial intelligence)

Option 1:

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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