

GENETIC ARCHITECTURE, HETEROSIS AND INBREEDING DEPRESSION FOR YIELD AND YIELD ASSOCIATED PHYSIOLOGICAL TRAITS IN RICE (*Oryza sativa* L.) UNDER DROUGHT CONDITION

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ABSTRACT

Simple and joint scaling tests led to similar inferences in respect of presence or absence of epistasis in majority of cases across the fourteen characters of six crosses in two conditions. The generation mean analysis revealed importance of additive (d) and/or dominance (h) gene effects as well as one or more of the epistatic gene interactions (i, j, l) for all the seven characters in most of the crosses under both the conditions. However, nature and magnitude of gene effects and epistatic interactions for a character exhibited considerable variation across the six crosses and two environmental conditions. Significance of dominance gene effects and epistatic interactions for most of the traits in six crosses under two conditions indicated that exploitation of heterosis through hybrid varieties appears to be a potential alternative. Only in drought condition, considerable number of crosses exhibited positive and significant estimates of standard heterosis across seven characters. Present study indicated apparent lack of desirable heterosis of requisite degree. It appears that extremely diverse nature of parents involved in six cross combinations may have resulted in incompatible gene combinations or genetic architecture in crosses resulting into poor performance and lack of heterosis for most of the characters. The positive and significant heterobeltiosis was noted for relative water content and membrane thermo stability in cross VI in irrigated condition.

Keywords: Rice, Drought, Physiological traits, Generation mean, Gene action, Heterosis, Inbreeding depression

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INTRODUCTION

Rice is the staple food for approximately 340 million people in South Asia and 140 million each in Southeast Asia and sub-Saharan Africa (IRRI, 2006). Progress has been slow in improving productivity, and drought is a major constraint affecting rice production, especially in rain-fed areas across Asia and sub-Saharan Africa. Pandey et al. (2007) estimated that at least 23 million ha of rain-fed rice area (20% of the total rice area) in Asia are drought-prone. Drought is a particularly important production constraint in eastern India, with more than 10 M ha of drought prone, where yield losses due to drought are reported to cost an average of US \$250 million annually (Bernier et al., 2008). In recent years, crop physiology and genomics have led to new insights in drought tolerance providing breeders with new knowledge and tools for plant improvement (Tuberosa and Salvi, 2006). Drought resistance is improved either if the crop is able to access more water or if it can use available water more efficiently (higher transpiration efficiency) (Passioura, 2006). Several secondary traits are known to contribute in drought resistance in rice. Most of the secondary traits (leaf water potential, epicuticular osmotic adjustment etc) have moderate to high heritabilities under stress indicating the possibility of incorporating them into breeding program (Kumar et al, 2008). Certain secondary traits such as leaf water potential (LWP) had good correlation ($r = 0.69$) with yield under stress as well in rice (Jongdee et al., 2006).

New varieties tolerant to drought are needed to evolve that can grow well under moisture stress. Research is needed to reduce the risk of crop failure by understanding an action of drought related traits to develop drought resistant cultivars. Data on agronomic, morphological and physiological plant traits are generally used to characterize the varieties, however such data may not provide an accurate picture because, environment influence upon the expression of observed traits are difficult in scoring due to the presence of multiple allele or gene. The inheritance of the characteristics chosen has a major influence on the strategy employed for cultivar development. Though the goals of rice breeding programs vary considerably depending on the intended use, yet some traits considered important in most breeding program such as yield where genetic improvement for yield and its components are most difficult to achieve due to the complex nature of their inheritance and influence of numerous environmental factors. The ability of the parents to combine well depends on the complex interactions among the genes adaptation which cannot be judged by mere yield performance and adaptation of the parents. Moreover, in a breeding program an objective judgment about a particular cross combination likely to produce transgressive segregants in self pollinating crops like rice would mainly depend upon the precise estimates of various components of genetic variances. An experimental method known as generation mean analysis (Jinks and Jones, 1958; Hayman, 1958) provides the opportunity to detect the presence or absence of epistasis and quantify them appropriately. In view of limited reports on estimation and comparison of estimates of gene effects and heterosis in irrigated and drought conditions, such experiments were conducted.

MATERIALS AND METHODS

Plant materials, experimental design and site

In the present study, six generations (P_1 , P_2 , F_1 , F_2 , B_1 , B_2) of six crosses viz., Sarjoo-52 x P0 359, P0 359 x Sonam, NDR-359 x P0 1564, P0 1564 x Sarjoo-52, IR 74409 x Saita, DSL-63-8 x NDR-359 were evaluated in Compact Family Block Design with three replications under irrigated (E_1) and reproductive stage drought conditions (E_2). The two evaluation trials were conducted during 2011 and 2012 in wet season at Student's Instructional Farm of Narendra Deva University of Agriculture and Technology, Kumarganj, Faizabad (U.P.). The rows of 3 m length were used for making subplots of two rows for P_1 , P_2 and F_1 generations, 4 rows for B_1 and B_2 generations and 6 rows for F_2 generations of each cross. Inter and intra-row spacing was kept 20 cm and 15 cm, respectively.

Management of water stress

Irrigated control (E_1): The experimental field was left uncovered to receive natural rainfall. In addition to this, experimental plots were irrigated using well laid channels for supplying tube well water, as and when required, to maintain appropriate moisture levels as recommended for irrigated rice.

Reproductive stage drought stress (E_2): The experiment field was covered by constructing temporary shelter at a height of 10-12 fetes using polythene sheets to exclude any possibility of natural rainfall falling in the experimental plots. Care was taken to check the inflow or seepage of water from the adjoining areas by making adequate bunds around the experiment in drought condition. The flowering stage drought was created by withholding the irrigation on week before panicle exertion. Plants were exposed for two weeks drought at flowering stage (60-80 KPa). Drought was released by irrigation. Recovery was measured at 10th days after released of drought.

Observations

The characters studied in the two experiments were relative water content (RWC), membrane thermo stability (MTS), apparent translocation rate (ATR) and apparent contribution rate (ACR), harvest-index (HI), biological yield plant⁻¹ (BY/P) and grain yield plant⁻¹ (GY/P).

Biometrical analyses

The data on seven characters of 36 genotypes (treatments) were subjected to analysis of variance for Compact Family Block Design and whole set of treatments following Singh and Singh, (1994). Heterosis expressed as per cent increase or decreases of hybrids (F_1) over better-parent (heterobeltiosis) and standard variety (standard heterosis) were calculated according to the method suggested by Hayes et al., (1955). To find out the presence of gene interaction scaling test and joint scaling test were computed following Singh and Chaudhury (1985). The three-parameter

model of Jinks and Jones, (1958) was used to test the adequacy of the additive dominance model in the absence of non-allelic gene interaction and the six-parameter model of Hayman, (1958) and Jinks and Jones, (1958) were used to estimate various gene effects including the non-allelic interaction.

RESULTS AND DISCUSSION

Analysis of variance:

The analysis of variance for Compact Family Block Design revealed that six cross families differed significantly for all the seven characters in irrigated as well as drought condition except for ATR in E_2 . The analysis of variance for differences between progenies (generations) within families (crosses) showed significant differences among the progenies of the six crosses for all the characters in both conditions except for HI in crosses III and V in E_1 and HI in cross VI in E_2 . The significance of mean squares due to progenies (generations) within families (crosses) in majority of cases, indicated existence of significant and substantial variation in the experimental material of the present study validated further statistical and genetical analysis.

Simple and joint scaling tests:

Simple as well as joint scaling tests revealed that role of epistasis had greater impact in E_2 as compared to E_1 for all characters across the six crosses. Significant chi-square value indicated the presence of epistasis and significance of digenic interactions along with inadequacy of additive-dominance model or three-parameter model (Table 1). Besides, non significant chi-square value showed the absence of epistasis and adequacy of additive-dominance model. For HI, presence of epistasis was revealed by simple as well as joint scaling tests in both the conditions except lack of epistasis noted in cross I and II from simple scaling tests, cross V from joint scaling test and cross III from both types of tests in E_1 and in cross VI from both type of tests in E_2 . Furthermore, GY/P and BY/P and physiological traits, namely, RWC, MTS, ATR and ACR, the simple as well as joint scaling tests detected presence of epistasis in all the six crosses in both conditions except absence of epistasis for physiological traits recorded in cross IV from simple scaling tests in E_1 .

The consistent absence of epistasis in both conditions by the two type of scaling tests was recorded only for HI in cross III and HI in cross VI in E_2 . Thus, highly important role of epistasis in the inheritance of seven characters under study was evident in both environments. Importance of epistasis in inheritance of GY/P and its components in rice has also been reported earlier (Saravanan et al., 2006 and Singh et al., 2007).

Gene effects:

The present study, was undertaken to use P_1 , P_2 , F_1 , F_2 , B_1 and B_2 generations of each of the six crosses of rice in order to obtain information about epistasis

(additive \times additive, additive \times dominance, dominance \times dominance epistatic components) in addition to additive and dominance gene effects for grain yield, yield components and some physiological traits.

Cross I (Sarjoo-52 \times P0 359)

In E_1 , the significance of additive (d) and dominance (h) gene effects along with (i), (j) and (l) type of gene interaction effects were recorded for RWC, MTS and ATR except for non-significant of (j) for ATR. The additive (d) gene effects were found to be significant along with (j) and (l) type gene interactions for ACR. The additive (d) and dominance (h) gene effects were predominant for GY/P and BY/P which also had significant (j) type of gene interaction effects. None of the gene effects or gene interaction effects was significant for HI. In E_2 , additive (d) and dominance (h) gene effects along with (i), (j) and (l) type of gene interaction effects were recorded for RWC and ATR. The additive (d) and dominance (h) gene effects with absence of three types of non-allelic interactions were noted for HI while, additive (d) and dominance (h) gene effects and additive \times additive (i) interactions were important for GY/P. The significance of only three epistatic components (i, j, l) was noted for MTS.

Cross II (P0 359 \times Sonam)

In E_1 , all the five gene effects (d, h, i, j, l) were found significant for ATR only. Four types of gene effects were recorded for BY/P and ACR (except for l). The significance of both additive (d) and dominance (h) gene effects without any epistasis interaction was recorded for GY/P. Only (j) and (l) type of epistatic interactions were significant RWC and MTS. Significance of only additive gene effect was found to be present for HI. With regards to gene effects for drought condition in cross II, only ACR was found to have significant estimates for all the five (d, h, i, j, l) gene effects. Both additive (d) and dominance (h) gene effects along with (i) and (l) type the epistatic interactions effects were noted for GY/P, BY/P and ATR, while MTS were found to have significance for all the three epistasis gene interactions (i, j and l) along with dominance (h) gene effect. Only additive \times dominance (j) gene interaction effects were significant for RWC.

Cross III (NDR-359 \times P0 1564)

The additive (d) gene effects with additive \times dominance (j) non allelic interactions were per dominant for MTS, ATR and ACR. The significance of three effects each were recorded for BY/P (h, i and j) while two parameters each were important for GY/P (h and j). Only additive \times dominance (j) interactions were important for RWC in E_1 . With regards to E_2 , all the five estimates of gene effects were found to be significant for ACR. Four gene effects were found to be significant for MTS, HI, GY/P (h, i, j and l), BY/P (d, h, i and l) and ATR (d, h, i and j).

Cross IV (P0 1564 \times Sarjoo-52)

The results revealed that RWC (h, i, j and l), ATR and ACR (d, h, i and l) had the significant estimates for four effects. The additive (d) gene effects were important along with dominance \times dominance (l) effects for GY/P and BY/P. In case of E₂, all the seven characters investigated under present study had significant gene effect for at least one gene effect, there by suggesting the role of different gene actions in the inheritance of all the traits. However, none of the traits had recorded significance for all the five gene effects. The significance of additive (d) as well as dominance (h) gene effects was recorded with importance of (h) gene effects was recorded with importance of (i) and (j) interaction effect for ATR and (j) and (l) type of interaction effects for GY/P and ACR, BY/P and MTS showed existence of additive \times dominance (j) and dominance \times dominance (l) type of non-allelic interactions. Only additive \times dominance (j) gene interactions were significant for RWC.

Cross V (IR-74409-730-08 \times Saita)

The results suggested that both additive (d) and dominance (h) gene effects were significant along with the significant (i) type epistasis for RWC and with (i) and (j) type epistasis for ATR. Whereas, significance of additive (d) gene effects along with (j) type of gene interactions was observed for MTS, while significant (l) type epistasis along with significant additive (d) gene effect was found to be responsible in the inheritance of GY/P and BY/P. Beside this, none of the gene effects was found to be present for harvest index. For apparent contribution rate significance of (d), (i) and (j) effects was found.

The gene effects in cross V under drought condition revealed that both additive (d) and dominance (h) gene effects along with all the three types epistasis (i, j and l) were significant for BY/P. The significance of all the five gene effects except for (j) type epistasis was observed for HI. Presence of dominance (h) gene effects in addition to presence of all the three type epistatic interactions was noted for GY/P. While, ATR which had additive as well as additive \times additive and additive \times dominance gene effects to be significant. The trait which was governed by additive (d) gene effects and additive \times dominance (j) epistasis was ACR. The significance only additive (d) gene effect for MTS and additive \times dominance (j) for RWC was noted.

Cross VI (DSL-63-8 \times NDR-359)

Apparent translocation rates the dominance (h) gene effects in combination with all the three types of non allelic interactions (I, j and l) were important. The dominance (h) gene effects in combination with additive \times additive (i) type gene interactions were present for GY/P and BY/P. None of the five estimates of gene effects were important for HI while, significance of only (j) type epistasis of RWC and (l) type epistasis for ACR was found. Membrane thermo stability had significant estimates for additive (d) gene effects with all the three types of epistatic interactions

(I, j and l) in E_1 . In drought condition, among all the five estimates of gene effects, three effects each were found to be significant for GY/P (d, i and l), BY/P (i, j and l) and MTS (h, i and j), while only two estimates of gene effects were observed for ACR (d and j). The significance of only additive (d) gene effect was observed for HI and ATR while only additive \underline{x} dominance (j) gene interaction effects assumed importance for RWC.

Heterosis and inbreeding depression

The estimates of heterosis over better-parent in E_1 and E_2 are presented in Table 2. The estimates of standard heterosis were calculated by taking NDR-359 as standard parent in irrigated condition and P0-1564 as standard parent in drought condition (Table 3). The heterobeltiosis for GY/P ranged from -4.42% (cross VI) to 4.24% (cross IV) in E_1 and from -17.65% (cross III) to 7.11% (cross II) in E_2 . Standard heterosis for GY/P varied from -15.24% in cross IV to 3.29% in cross I in E_1 and from -49.56% in cross VI to 8.30% in cross I in E_2 . Besides GY/P, very low and non-significant heterobeltiosis of positive nature or non-significant and significant heterobeltiosis of negative nature was observed in most of the crosses for most of the characters in both environments except few exceptions. Similarly majority of the estimates of standard heterosis across fourteen characters of six crosses were either non-significant in negative or positive direction or significant in negative direction in irrigated condition. Only in drought condition, considerable number of crosses exhibited positive and significant estimates of standard heterosis across seven characters.

Results indicated that extremely diverse nature of parents involved in six cross combinations may have resulted in incompatible gene combinations or genetic architecture in crosses resulting into poor performance and lack of heterosis for most of the characters. In earlier reports in rice have reported existence of wide range of heterosis in negative and positive directions for grain yield and most of the yield contributing characters (Yadav et al., 2004; Eradasappa et al., 2007; Singh et al., 2007; Rashid et al., 2007 and Salem et al., 2008). It was interesting to note all the four physiological traits were found mostly to have negative estimates of non-significant or significant nature in all the six crosses with some exceptions. The notable exceptions were the positive and significant heterobeltiosis recorded for RWC and MTS in cross VI in E_1 and for RWC in cross II in E_2 . In case of standard heterosis, the positive and significant estimates were obtained for MTS in all the crosses and for ACR in cross I, II, V and VI in E_2 only. This showed that the six crosses did not show high heterosis in desirable direction for physiological traits in most of the cases and higher standard heterosis for MTS and ACR in E_2 may be attributed perhaps to low mean performance for these traits by standard parent, P0-1564.

The in-breeding depression was also estimated for seven characters of six crosses in E_1 and E_2 (Table 4). All the six crosses emerged with highly significant

inbreeding depression in irrigated condition for GY/P, BY/P, ATR and ACR except non-significant values recorded cross I for ATR and cross I, II and VI for ACR in E₁. Similarly, five crosses showed significant inbreeding depression for GY/P and HI (except cross VI) and ACR (except cross III) in E₂. Significant inbreeding depression was also noticed for BY/P (cross II, III and V) and ATR (cross I) in some of the six crosses in E₂.

CONCLUSION

Like the gene effects and non-allelic interactions, the estimates of heterosis and inbreeding depression showed considerable variation across the two conditions. This indicated that genotype \times environment interactions played significant role in altering the estimates of various genetic parameters under study. Thus, in order to get precise understanding of gene actions, heterosis, inbreeding depression and direct and indirect selection parameters for a specific condition or environment, the studies should be carried out in the condition or environment in question. More precise study should be undertaken to make conclusive recommendation.

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Table 1. Chi-square estimates for joint scaling test for seven metric traits under irrigated and drought conditions

Characters	Chi-square estimates											
	Irrigated Condition						Drought Condition					
	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
RWC	47.24**	104.94**	45.54**	38.86**	28.83**	31.88**	109.34**	76.55**	104.90**	42.40**	97.78**	95.13**
MTS	177.48**	27.42**	50.27**	18.45**	19.39**	52.23**	373.74**	328.26**	217.23**	203.56**	397.26**	431.93**
ATR	601.47**	67.15**	640.62**	578.83**	314.98**	152.60**	31.03**	64.92**	255.42**	220.95**	41.66**	28.04**
ACR	61.60**	40.56**	317.72**	229.35**	41.18**	55.81**	283.82**	222.89**	206.93**	713.56**	152.62**	202.21**
HI	7.39**	10.04**	3.81	8.81*	5.96	15.17**	14.28*	28.65**	214.28**	83.68**	159.48**	6.13
BY/P	25.03**	68.29**	89.15**	102.09**	129.45**	102.14**	91.59**	70.99**	427.21**	469.08**	193.45**	59.12**
GY/P	27.55**	64.54**	27.69**	74.27**	75.99**	108.59**	89.65**	19.23**	1020.13**	204.03**	308.58**	15.98*

*, ** Significant at 5% and 1% level of probability, respectively.

Legend: RWC: relative water content; MTS: membrane thermo stability; ATR: apparent translocation rate and ACR: apparent contribution rate; HI: harvest-index; BY/P: biological yield plant⁻¹ and GY/P: grain yield plant⁻¹

Table 2. Heterosis over better parent for seven metric traits under irrigated and drought conditions

Characters	Heterobeltiosis											
	Irrigated Condition						Drought Condition					
	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
RWC	-6.93	-4.41	-1.39	-3.11	-4.92*	9.00**	-13.56**	10.47**	-9.31**	-8.96**	-13.39**	-9.21**
MTS	-14.89**	-7.08*	-8.43**	-3.21	-3.83	10.12**	-19.18**	-17.80**	-15.46**	-15.18**	-17.59**	-19.33**
ATR	-24.66**	4.93	-8.77*	-15.70**	-10.73*	-9.62*	-10.10*	-3.93	-10.41**	-14.39**	-6.45*	-2.57
ACR	-12.32*	-10.93*	-17.23**	-16.45**	-12.32*	-5.46	-17.32**	-15.05**	-11.74*	-13.42**	-16.39**	-13.53*
HI	0.23	-0.47	0.05	0.50	-0.08	1.27	2.18	-5.43	-13.34*	8.10	-2.00	-5.72
BY/P	-1.84	-3.56	-1.79	3.62	-3.08	4.02	-6.48*	13.64*	-5.02	-28.57**	-7.52	10.23*
GY/P	-1.88	-4.16	-1.89	4.24	-3.43	-4.42	-4.30	7.11**	-17.65**	-17.60**	-9.39	3.61

*, ** Significant at 5% and 1% level of probability, respectively.

Legend: RWC: relative water content; MTS: membrane thermo stability; ATR: apparent translocation rate and ACR: apparent contribution rate; HI: harvest-index; BY/P: biological yield plant⁻¹ and GY/P: grain yield plant⁻¹

Table 3. Heterosis over standard variety for seven metric traits under irrigated and drought conditions

Characters	Standard Heterosis											
	Irrigated Condition						Drought Condition					
	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
RWC	6.89	7.34	2.95	1.75	3.12	6.17	-12.94**	-10.44**	-8.21**	-10.04**	-12.94**	-9.06**
MTS	-1.68	-1.32	-3.00	-6.33	-6.40	-8.11	22.55**	23.45**	26.29**	23.00**	23.80**	24.67**
ATR	-10.64*	-10.64*	-10.64*	-10.64*	-16.49*	-22.34**	-14.32**	-7.98*	-11.57**	-13.22**	-14.60**	-16.52**
ACR	-48.55**	-47.11**	-50.00**	-51.45**	-52.89**	-52.89**	101.35**	104.72**	-12.16**	-12.83**	96.62**	94.59**
HI	0.57	-1.28	-1.33	-1.80	-1.60	-0.80	6.07**	-0.30	-8.66	9.29*	-11.09	-4.05
BY/P	2.85	0.38	-5.07	-13.75*	-12.10*	-10.05*	2.02	-36.74	-4.79	-28.73**	-23.01**	-47.26**
GY/P	3.29	-0.94	-6.51	-15.24*	-13.45*	-10.55*	8.30	-37.11**	-13.00*	-22.26**	-29.44**	-49.56**

*, ** Significant at 5% and 1% level of probability, respectively.

Legend: RWC: relative water content; MTS: membrane thermo stability; ATR: apparent translocation rate and ACR: apparent contribution rate; HI: harvest-index; BY/P: biological yield plant⁻¹ and GY/P: grain yield plant⁻¹

Table 4. Inbreeding depression (%) in F₂ over F₁ for seven metric traits under irrigated and drought conditions

Characters	Inbreeding Depression											
	Irrigated Condition						Drought Condition					
	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
RWC	4.81	5.36	0.59	3.13	1.14	0.52	0.70	0.58	1.10	0.49	0.87	1.05
MTS	4.73	1.73	1.69	2.12	2.75	1.89	1.93	2.09	1.25	2.68	2.50	3.35
ATR	0.00	28.64**	14.42**	24.47**	9.62*	19.15**	8.67*	4.29	6.54	6.13	4.20	4.40
ACR	5.62	0.00	10.41*	13.80**	8.43*	5.78	8.62*	8.91*	4.09	10.59*	8.26*	12.63*
HI	2.36	1.76	2.53	2.17	1.59	2.51	10.41*	9.26*	12.36*	16.35**	17.53**	-5.45
BY/P	16.14**	13.13**	15.99**	16.22**	12.85*	17.63**	5.81	14.64**	7.77*	7.06	15.24**	4.64
GY/P	17.94**	14.60**	17.97**	18.09**	14.18**	19.55**	15.92**	22.92**	19.23**	22.05**	30.34**	-0.79

*, ** Significant at 5% and 1% level of probability, respectively.

Legend: RWC: relative water content; MTS: membrane thermo stability; ATR: apparent translocation rate and ACR: apparent contribution rate; HI: harvest-index; BY/P: biological yield plant⁻¹ and GY/P: grain yield plant⁻¹