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Genetic Architecture, Heterosis and Inbreeding Depression for Metric Traits in Rice (*Oryza sativa* L.) under Drought Condition

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Analysis of variance of Compact Family Block Design revealed significant differences among the six cross families for twelve characters in E_1 and E_2 except for spikelet fertility in E_1. Simple and joint scaling tests indicated presence of epistatic gene interactions and fitness of digenic interaction model for all the twelve characters in most of the six crosses in both conditions. Significance of epistasis was detected by either one or both type of scaling tests in irrigated and/or drought condition for all the characters across six crosses. In several instances, results indicated role of genotype x environment interactions in conditioning the epistasis for various characters in crosses. Across the six crosses, role of epistasis was comparatively more pronounced in drought condition as compared to irrigated condition, especially for DFF, PH, SF and HI. The nature and magnitude of gene effects and epistatic interactions for a character exhibited considerable variation across the six crosses and two environmental conditions. The considerable crosses exhibited positive and significant estimates of standard heterosis across sixteen characters in E_2. However, heterosis was comparatively higher for G/P in both conditions, for S/P in E_1 and for PH and EBT in E_2. The 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.

Kew words: Rice, Drought, Metric traits, Gene action, Heterosis, Inbreeding depression

Rainfed rice-growing areas are highly prone to abiotic stresses such as drought or submergence depending upon the amount and distribution of rainfall and topo-sequence of the region. Drought is a perennial and recurring feature in many parts of India. According to Government of India reports, about 68 per cent of the country is prone to drought in varying degrees. Drought leads to large-scale migration in search of alternative livelihoods, loss of human life due to stress, suicide, starvation or unhygienic conditions, and increased social conflict. Multidimensional effect of drought on rice cultivation in Asia is a recurring climatic event and climatically induced phenomenon. India accounts for the largest share (13.57 m ha) of the total drought prone rice area in Asia (Pandey *et al*., 2007). Drought has direct effect on India's economic growth as agriculture contributes about one-fourth of gross domestic product (GDP). In three states of eastern India Chhattisgarh, Jharkhand and Orissa where, rainfed rice is grown widely. The average production loss of rice during drought years is estimated to be 5.4 million tons over 30 per cent of the annual production in non drought years (Pandey and Bhandari, 2006).

Grain yield is a complex polygenic trait resulting from interaction among a number of inherent characters and environment. Because of these complex interactions it is difficult to improve yield through breeding (especially in the early generations) if yield is the only factor recorded, suggesting that component traits should also be used as selection criteria for yield improvement. This is the reason why it is necessary to know the genetic architecture of yield components. The developments in statistical genetics have made possible to study the various facts of the operation of quantitative genes and to use this information in formulating appropriate breeding strategy to effect genetic improvement of traits. The estimation of gene effects involved in the inheritance of yield contributing or quantitative characters are helpful in planning breeding programme. Generation mean analyses provides information on the relative importance of average effects of the genes (additive effects), dominance deviations, and effects due to non allelic interactions, in determining genotypic values of the individuals and, consequently, mean genotypic values of families and generations (Jinks and Jones, 1958). Generation mean analysis is a simple, but useful technique for estimating gene effects for a polygenic trait, its greatest merit lying in the ability to estimate epistatic gene effects such as additive x additive, dominance x dominance and additive x dominance effects (Singh *et al*., 2007). However, studies on the

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genetics of drought tolerance in rice have been limited, inhibiting the realization of breeder's goal. Considering these facts, the present study was taken to estimate genetic effects and heterosis for twelve important quantitative traits (grain yield components) in order to improve breeding efficiency in six rice crosses.

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 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

The experiments were conducted with well defined protocol for water management under natural field conditions during wet season. 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. Thus no stress condition was maintained.

Reproductive stage drought stress (RSS)

The experiment field was covered by constructing temporary rainout shelter at a height of 10-12 feet using polythene sheets to exclude any possibility of natural rainfall falling in the experimental plots with proper drainage channel. Care was taken to check the inflow or seepage of water from the adjoining areas by making adequate bunds around the experiment and covered with polythene in drought condition. The heading stage drought was created by withholding the irrigation for 15 days up to 80 K Pa at 0-15 cm soil profile and 60 K Pa at 30 cm soil depth. Plants were exposed for two weeks (60-80 KPa.). Soil moisture content (SMC) during stress period was monitored through periodical soil sampling at 0-15, 15-30 cm soil depth. Drought was released by irrigation. Recovery was measured at 10th days after released of drought. Genotypes were scored for leaf rolling and leaf drying at the peak stress period using the IRRI Standard Evaluation System (IRRI, 1996).

Observations

The characters studied in the two experiments were days to 50 per cent flowering (DFF), size of flag leaf excluding sheath (FL), plant height (PH), ear bearing tillers plant^{-1} (EBT), panicle length (PL), grains panicle^{-1} (G/P), spikelets panicle^{-1} (S/P), spikelet fertility (S/F), test weight (TW), biological yield plant^{-1} (BY/P), harvest-index (HI) 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 performed following the method of Mather and Jinks, (1982) and Cavalli, (1952), respectively. 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

The analysis of variance for Compact Family Block Design revealed that families or crosses evaluated under present investigation possessed wide spectrum of variation for almost all the characters in both conditions except a few exceptions. 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 SF and HI in all the six crosses in E_1 and SF in cross III and VI and HI in cross I, II, IV, V and VI in E_2.

Gene effects

Days to 50 per cent flowering (DFF)

In E_1, the additive gene effect was significant in Cross I, III and IV, while dominance gene effect was significant in cross I and VI. Among the epistatic interactions, significance of (i) in cross I and VI; (j) in cross II and V and (l) in cross I, II and cross VI was observed. Duplicate epistasis was noted for cross I and VI. In drought condition, significant estimates of all the five gene effects (d, h, i, j, l) with duplicate epistasis were observed for DFF in cross IV, V and VI except non-significance of (d) in cross IV and VI. The significance (i) was recorded in cross I, II and III along with significance of (j) in cross III and (l) in cross I and III. Sanghera and Hussain (2012)

Table 1. Chi-square estimates for joint scaling test for nine metric traits under irrigated (E_1) and drought conditions (E_2)

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
DFF	24.41**	9.37**	51.18**	24.26**	3.98	10.47*	0.34	2.63	3.37	29.54**	152.57**	55.10**
SFL	137.75**	61.50**	133.00**	66.35**	58.40**	29.16**	4.48	7.71*	9.15*	165.64**	46.22**	158.63**
PH	73.61**	66.80**	3.16	19.46**	0.10	27.55**	10.70**	-13.41**	3.35	49.16**	43.45**	42.49**
EBT	17.58**	9.38*	27.75**	75.58**	41.22**	24.22**	-2.86	1.49	3.73	113.14**	236.84**	110.12**
PL	102.94**	11.91**	43.59**	102.88**	54.63**	215.09**	7.82*	8.44*	8.66*	54.29**	197.85**	31.42**
G/P	30.46**	41.18**	292.95**	18.15**	54.68**	0.95	6.64*	5.05	7.91*	12.93*	116.00**	16.42*
S/P	3.17	37.39**	171.84**	61.65**	86.15**	3.01	4.28	2.69	6.34	73.39**	528.67**	119.57**
SF	21.28**	138.78**	5.04	1.84	9.15*	9.13**	2.42	2.30	2.00	150.05**	24.69**	58.74**
TW	2.70	39.58**	29.68**	11.96*	24.73**	136.80**	35.60**	129.70**	136.25**	56.07**	186.95**	77.30**
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**	17.94**	14.60**	17.97**	204.03**	308.58**	15.98*

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

DFF: days to 50 per cent flowering; SFL: size of flag leaf excluding sheath; PH: plant height; EBT: ear bearing tillers plant^{-1}; PL: panicle length; G/P: grains panicle^{-1}; S/P: spikelets panicle^{-1}; SF: spikelet fertility; TW: Test weight; HI: harvest index; BY/P: biological yield plant^{-1} and GY/P: grain yield plant^{-1}

observed significant role of non-additive gene effects for DFF while, Roy and Mandal (2001) noticed importance of additive gene effects for this trait. Mazumdar *et al*. (1990) reported role of additive as well as non-additive gene action for DFF.

Size of flag leaf excluding sheath (FL)

In E_1, cross II, III and VI showed significance of additive (d) and dominance (h) gene effects and (i) interactions along with (l) and duplicate epistasis in cross II and VI. Thus, improvement of size of flag leaf in cross II, III and VI would require handling of further generations by breeding methods meant for exploiting additive and/or non-additive gene actions. In E_2, the additive gene effects along with (i), (j) and (l) interactions were significant in cross I and II with exception of non-significant (j) in cross II. In case of cross III, IV, V and VI, the significance of (h), (i), (l) and duplicate epistasis along with (j) interactions in cross III and IV hinted that these four crosses should be subjected to breeding methods aimed at exploitation of non-fixable non-additive gene actions.

Plant height (PH)

In E_1, the (d) and (h) gene effects were significant in cross I, II, IV and VI along with significant estimates of (i) and (j) in cross I, (i), (j) and (l) in cross IV and (i) and (l) in cross VI which suggested that exploitation of fixable additive as well as non-fixable non-additive gene actions may be recommended for changing the plant structure in their advance generations. However, presence of duplicate epistasis in cross IV and VI would render progress through selection slower. In E_2, the (d) and (h) gene effects were significant in cross I, III and VI along with significance of (i) in cross I and VI, (j) in cross III and VI and (l)) in cross III. The significance of only non-fixable non-additive components of genetic variance in cross II (j), cross IV (j, l) and cross V (h, j) indicated that these crosses should be recommended for exploitation by methods meant for utilizing non-additive gene action for bringing changes in plant stature. Importance both effects in inheritance of plant height were reported by Gosh (1993) while preponderance of non-additive gene action was observed by Sharma *et al*. (1996).

Panicle bearing tillers plant^{-1} (EBT)

In E_1, cross I and IV showed significant (d) gene effect in addition to significant (j) interaction. Cross III exhibited non-significant estimates of all the five gene effects (d, h, i, j, l) which revealed that cross III

Table 2. Heterosis over better parent nine metric traits under irrigated (E_1) and drought conditions (E_2)

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
DFF	11.03**	15.59**	14.67**	11.11*	12.30**	12.12**	8.60*	14.65**	10.36**	8.24*	14.57**	7.07
SFL	-7.21	-6.47	-11.14	-5.59	-10.87*	-12.02*	5.72	-8.97	-0.66	-5.87	4.38	-3.64
PH	-2.61	-1.25	16.87*	15.27**	23.42**	14.90	6.13	9.70**	10.78**	10.66**	14.25**	10.26*
EBT	-14.23*	-8.21	2.67	-4.96	-9.43	1.08	-5.54	9.08*	-7.98*	-10.08**	-14.29**	6.47*
PL	-8.41	1.51	-6.39	2.05	-1.25	0.23	-0.61	-5.09	-4.93	-3.63	-12.82*	-8.17
G/P	5.22	-6.48	19.11*	11.23*	13.23	13.13	2.78	9.71*	9.17*	8.98*	12.78*	10.39*
S/P	7.44	4.15	24.95**	12.23*	12.31*	11.74	1.45	-3.58	6.89	4.19	-2.68	1.55
SF	-2.11	-10.08*	-4.45	-0.99	-0.81	-2.58	1.35	-0.70	2.14	3.50	0.64	5.93
TW	-7.21	-3.42	-0.33	11.44*	-8.87**	-4.07	-6.11	-7.14	-2.40	-4.79	-14.03**	-6.96
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.

DFF: days to 50 per cent flowering; SFL: size of flag leaf excluding sheath; PH: plant height; EBT: ear bearing tillers plant^{-1}; PL: panicle length; G/P: grains panicle^{-1}; S/P: spikelets panicle^{-1}; SF: spikelet fertility; TW: Test weight; HI: harvest index; BY/P: biological yield plant^{-1} and GY/P: grain yield plant^{-1}

holds little promise for significant improvement of EBT due to lack of requisite genetic variation. For panicle bearing tillers per plant in E_2, all the five estimates of gene effects (d, h, i, j, l) along with duplicate type of epistasis were observed in cross VI. This indicated importance of additive, dominance and epistatic gene effects in inheritance of panicle bearing tillers per plant in cross VI. The significance of (d) and (h) gene effects in cross I suggested possibility of attaining improvement for this trait in later generations of this cross by exploiting additive as well as non-additive gene actions. Sharma *et al.* (1987) and Banumathi and Prasad (1991) reported importance of additive and non-additive gene action with preponderance of additive gene action in expression of EBT. Singh and Srivastava (1982) observed that EBT was conditioned by additive gene action.

Panicle length (PL)

In irrigated condition, the additive and dominance gene effects with additive x additive interactions were significant for panicle length in cross II and VI while additive gene effects with dominance x dominance interactions were importance in cross IV. The presence of duplicate epistasis in cross I and III would be cause further hindrance in success of selection producers.

In E_2, only additive gene effect was significant in cross III for panicle length which suggested that this cross should be handled in further generations by selection procedures meant for exploiting additive gene actions. The significance of (d), (h), (i) and (l) with duplicate epistasis in cross II, suggested application of breeding methods meant for utilizing additive and/or non-additive gene actions. Ghosh (1993) recorded importance of additive as well as non-additive gene effects with predominance of additive gene effects for panicle length. Perraju and Sarma (1999) reported that panicle length was under control of non-additive gene effects.

Grains panicle^{-1} (G/P)

In E_1, estimates of all the five gene effects (d, h, i, j, l) along with duplicate epistasis were found to be important for G/P in cross II and III, while significance of (d) and (j) in cross IV and (d) and (h) in cross VI was observed. The presence of duplicate epistasis in cross II, III and V is likely to reduce the effectiveness of selection procedures, if applied, in improving G/P in E_1. In E_2, the importance of (d), (h), (j) and (l) gene effects along with complementary epistasis was recorded for G/P in cross I and III while importance of (d) and (h) in cross VI and (d), (h) and (j) in cross IV was also noted. Thus, the later generations of cross I, III, VI and IV may be subjected to breeding procedures meant for utilization of additive and/or non-additive gene actions found important in their cases for grains per panicle. Perraju and Sarma (1999) observed predominance of non-additive gene action, whereas preponderance of additive gene action was found by Mohanty and Mohapatra (1973) for G/P.

Table 3. Heterosis over standard variety for nine metric traits under irrigated (E_1) and drought conditions (E_2)

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
DFF	-2.99	1.00	-1.33	-3.65	-8.97	-1.66	8.41**	11.99**	10.56**	8.06*	4.12	8.41**
SFL	-24.90**	-24.48*	-25.41**	-28.26**	-27.70**	-33.38**	-0.21	-7.80	7.58	-1.12	9.62*	1.50
PH	-2.70	-4.00	-5.37	-13.11*	-11.92*	-7.60	-19.52**	-20.09**	-5.61*	-5.31*	-21.84**	-10.36**
EBT	-17.86**	-16.94*	-15.19*	-15.50*	-13.79*	-16.22*	21.13**	8.86**	7.35*	16.79**	1.13**	24.33**
PL	-16.28**	-14.54*	-15.34*	-22.83**	-26.22**	-33.40**	12.00**	1.35	6.50*	5.65	11.55*	13.20*
G/P	41.28**	43.62**	36.89**	31.90**	29.99**	32.04**	24.42**	-13.30**	9.97*	8.19*	-13.19**	9.12*
S/P	44.42**	47.79**	43.51**	38.24**	36.05**	35.28**	26.47**	-1.88	9.34	6.53	-1.68	4.54
SF	-2.23	-2.87	-4.73	-4.60	-4.47	-2.40	-1.66	-11.71	8.91*	1.52	-11.65**	4.49
TW	-4.50	-0.99	-1.51	-2.75	-3.59	-1.32	5.34	-5.65*	9.09*	10.41*	-11.47**	8.83*
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.

DFF: days to 50 per cent flowering; SFL: size of flag leaf excluding sheath; PH: plant height; EBT: ear bearing tillers plant^{-1}; PL: panicle length; G/P: grains panicle^{-1}; S/P: spikelets panicle^{-1}; SF: spikelet fertility; TW: Test weight; HI: harvest index; BY/P: biological yield plant^{-1} and GY/P: grain yield plant^{-1}

Spikelets panicle^{-1} (S/P)

In E_1, all the five estimates of gene effects (d, h, i, j, l) along with duplicate epistasis were found important in cross II and III while additive (d) and dominance (h) gene effects, assumed importance in cross VI for spikelets per panicle. In case of E_2, the (d), (h), (i) and (j) components of genetic variance were significant for spikelets per panicle in cross III, IV and V while dominance x dominance (l) and duplicate epistasis were also important in cross V. Thus, cross III, IV and V can be handled in further generations by breeding methods based on utilization of additive and/or non-additive gene actions which emerged important in them for S/P.

Test-weight (TW)

For TW in E_1, the (d), (h), (i), and (j) gene effects were significant in cross IV, V and VI with exception of non-significant (j) component in case of cross V while only additive (d) and dominance (h) gene effects were significant in cross II. However, existence of duplicate epistasis in cross V would render the exploitation of additive gene actions difficult. In E_2, additive (d) gene effect was found non-significant in all the six crosses for test-weight. Cross II, III, IV, V and VI had significant estimates of (h), (i) and (j) parameters except non-significant (j) noted for cross III. The significance of dominance x dominance (l) component was also observed in cross IV and V while only additive x dominance (j) interactions assumed importance in case of cross I. Importance of additive as well as non-additive gene effects with greater role of additive component in inheritance of TW was recorded by Manjappa *and* Hittalmani (2014), while Patile *et al*. (2003) reported greater role of non-additive gene effects.

Grain yield plant^{-1} (GY/P)

For GY/P in E_1, additive (d) and dominance (h) gene effects were significant in cross I and II while additive (d) gene effect with dominance x dominance interactions was significant in cross IV and V. This indicated that the later generations of cross I, II, IV and V may be subjected to breeding methods based on utilization of fixable additive and/or non-fixable non-additive gene actions for isolating genotypes with higher grain yield potential in their advance generations. The significance of only non-additive components of genetic variances in cross III (h, j) and cross VI (h, i), suggested exclusive role of breeding methods utilizing non-additive gene actions in improving grain yield per plant in later generations of these crosses in irrigated condition. In E_2, additive (d) and dominance (h) gene effects were significant along with (i) in cross I, (i) and (l) in cross II and (j) and (l) in cross IV. In case of cross VI, additive (d) gene effect with additive x additive (i) and dominance x dominance (l) interactions assumed importance. The significance of additive as well as non-additive genetic variance component in cross I, II, IV and V suggested that exploitation of these crosses would be possible through breeding methods meant for utilizing additive and/or non-additive gene actions. Haque *et al.* (1981) reported that GY was conditioned by additive gene effects while Singh and Srivastava (1982) and Perraju and Sarma (1999) found GY under control of non-additive gene effects. Importance of additive as well as non-additive gene effects with predominance of non-additive gene effects was observed for grain yield by Chakraborty *et al.* (1994) and Sharma *et al.* (1996).

Biological yield plant^{-1} (BY/P)

For BY/P in E_1, the significance of parameters (d), (h), (i) and (j) in cross II, (d), (h) and (j) in cross I and (d) and (l) in cross IV and V was recorded. This indicated that additive as well as non-additive components of genetic variance were important in cross I, II, IV and V. The significance of parameters (h), (i) and (j) in cross III and (h) and (i) in cross VI, revealed main role of breeding procedures based on utilization of non-additive gene actions for enhancing BY in later generations of these crosses for irrigated conditions though some improvement through selection procedures exploiting partially fixable additive x additive interactions component may also be possible. In drought condition for biological yield per plant, all the five parameters (d, h,i, j, l) were significant in cross II, III and V except non-significant (j) in case of cross II and III. In case of cross I, additive (d) gene effects with dominance x dominance (l) interactions were significant. The significance of parameters, (j) and (l) in cross IV and (i), (j) and (l) in cross VI, representing mainly non-additive components of genetic variance, indicates usefulness mainly of breeding procedures exploiting non-additive gene action for enhancement of biological yield in advance generations of these crosses though some improvement may also be achieved by utilizing partially fixable additive x additive interactions.

Table 4. Inbreeding depression (%) in F_2 over F_1 for nine metric traits under irrigated (E_1) and drought conditions (E_2)

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
DFF	0.34	2.63	3.37	4.83	2.92	4.39	2.31	2.88	4.84	0.99	11.68*	4.29
SFL	4.48	7.71*	9.15*	6.30	4.45	5.05	6.50*	2.80	14.22**	5.22	14.97**	11.95*
PH	10.70**	-13.41**	3.35	6.38	8.54*	17.03**	3.44	4.38	4.62	3.70	9.62*	8.71*
EBT	-2.86	1.49	3.73	10.91*	4.55	4.09	0.00	8.38*	11.60*	1.72	3.30	8.60*
PL	7.82*	8.44*	8.66*	23.09**	16.81**	14.90**	0.37	8.86*	4.57	10.55*	8.58*	0.80
G/P	6.64*	5.05	7.91*	7.05*	16.33**	8.42*	10.10*	14.29**	11.64*	7.17*	-0.28	9.88*
S/P	4.28	2.69	6.34	6.62*	11.50*	6.67*	7.85*	0.91	12.27*	10.34*	-4.62	12.92*
SF	2.42	2.30	2.00	0.53	5.91	1.88	2.36	13.54*	-0.82	-3.46	4.11	-3.39
TW	-1.83	6.14	-3.36	3.04	1.44	8.84*	1.69	5.46	11.94*	-4.35	10.83*	7.40*
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.

DFF: days to 50 per cent flowering; SFL: size of flag leaf excluding sheath; PH: plant height; EBT: ear bearing tillers plant^{-1}; PL: panicle length; G/P: grains panicle^{-1}; S/P: spikelets panicle^{-1}; SF: spikelet fertility; TW: Test weight; HI: harvest index; BY/P: biological yield plant^{-1} and GY/P: grain yield plant^{-1}

Harvest-index (HI)

For HI in irrigated condition, only additive (d) gene effect was significant in cross II and IV indicating thereby exclusive role of breeding methods utilizing additive gene action in later generations of these crosses for enhancing the better partitioning of photo-synthates. The non-significance of all the five parameters in cross I, III, V and VI indicated apparent lack of variation for this trait, perhaps due to absence of requisite genetic diversity among their parents. In E_2, the significance of parameters (d), (h), (i) and (l) in cross V and (d) and (h) in cross I indicated that the later generations of these crosses can be handled through breeding methods meant for utilizing additive and/or not additive gene actions for deriving desirable segregants for harvest-index. Only additive (d) gene effect was significant in cross II and VI which showed exclusive role of breeding methods meant for exploiting additive gene action for enhancing harvest-index.

Simple and joint scaling tests

Scaling tests were devised for the purpose of testing the presence or absence of epistasis in inheritance of characters in crosses. In the present study, simple as well as joint scaling tests (Table 1) were used to detect the presence of epistasis for sixteen characters in six cross families in irrigated and drought conditions.

For days to 50% flowering simple as well as joint scaling tests detected presence of epistasis in all the six crosses in both conditions except in cross III, IV and joint scaling test in cross V in irrigated condition and both type of tests in cross II in drought condition. In case of size of FL and PH, the presence of epistasis was revealed by both type of tests in all the six crosses in E_1 and E_2 except absence epistasis observed for cross II and III in simple scaling tests and cross III and V in joint scaling test in E_1 for PH. For EBT, both tests showed presence of epistasis except absence of epistasis recorded from simple scaling tests in cross IV in E_1. In case of PL and G/P, both tests detected existence of epistasis in crosses and both conditions except lack of epistasis recorded for cross VI by both tests in E_1. The presence of epistasis was also revealed for S/P by in both conditions except absence of epistasis denoted by both type of tests in cross I and VI in E_1. For SF, presence of epistasis was noted from both tests in E_1 and E_2 for all the crosses except absence of epistasis in cross II and V by simple scaling tests and cross III and IV by joint scaling tests in E_1 and in cross I by simple scaling tests in E_2. In case of TW, GY/P and BY/P, simple as well as joint scaling tests detected presence of epistasis in all the crosses in E_1 and E_2 except absence of epistasis found in cross I by both type of tests for TW in E_1. For HI, presence of epistasis was revealed by both 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.

The results of simple and joint scaling tests discussed above, emphatically underlined the highly important role of epistatic interactions in expression of these traits. The consistent absence of epistasis in both conditions by the two types of scaling tests was recorded only for PH in cross III, G/P in cross VI, TW in cross I, HI in cross III and S/P in cross I and VI in E_1 and DFF in cross II and HI in cross VI in E_2. Thus, highly important role of epistasis in the in heritance of 12 characters under study was evident in both environments. Importance of epistasis in inheritance of grain yield and its components in rice has also been reported earlier (Saravanan *et al.,* 2006 and Singh *et al*., 2007). There were several instances in which a cross exhibiting presence of epistasis for a character in one condition showed absence in other condition for the same trait by the same scaling test. This suggested that existence of epistasis for a character in a cross was, often, affected by its interaction with the environment in question. Therefore, it may be concluded that genotype x environment interactions played considerable role in conditioning the impact of epistasis in expression of different characters of a cross. Simple as well as joint scaling tests revealed that role of epistasis had greater impact in drought condition as compared to irrigated condition for all the 12 characters across the six crosses. In general epistasis was more pronounced across the six crosses in E_2 than E_1 especially for DFF, PH, SF and HI according to both types of tests.

Heterosis

The six crosses exhibited either very low and non-significant or negative and significant estimates of heterobeltiosis and standard heterosis for GY/P under both the conditions. The heterobeltiosis for GY/P ranged from -4.42 (cross VI) to 4.24 per cent (cross IV) in E_1 and from -17.65 (cross III) to 7.11 per cent (cross II) in E_2. Standard heterosis for GY/P varied from -15.24 in cross IV to 3.29 per cent in cross I in E_1 and from -49.56 in cross VI to 8.30 per cent 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 (Table 2). Similarly majority of the estimates of standard heterosis across sixteen characters of six crosses were either non-significant in negative or positive direction or significant in negative direction in irrigated condition (Table 3). Only in drought condition, considerable number of crosses exhibited positive and significant estimates of standard heterosis across twelve characters.

However, degree of both types of heterosis was comparatively higher for G/P in both conditions, for S/P in E_1 and for PH and EBT in E_2. The low order positive or negative to high order negative estimates of heterobeltiosis and standard heterosis observed for majority of characters in six crosses indicated apparent lack of desirable heterosis of requisite degree. However, existence of excessive and incompatible diversity among parents of the six crosses under present study may be perhaps attributed to lack of heterosis observed for different characters. Since the six crosses resulted by involving one parent suitable to irrigated condition having drought susceptible nature with other parent suitable to drought condition having drought tolerance, the diversity in parental gene combinations may have led to non-synergistic gene combinations. Hence, the estimates of heterosis over better-parent and standard parent for twelve characters of six crosses in E_1 and E_2 are mostly contrary to the results of earlier studies in rice. (Yadav *et al*., 2004; Eradasappa *et al*., 2007; Singh *et al.,* 2007; Rasid *et al*., 2007 and Salem *et al.*, 2008).

In spite of lack of high heterosis in desirable direction recorded for GY/P, very high positive and significant heterobeltiosis and standard heterosis were observed in cross III, IV and V in E_1 for G/P and S/P, while cross I, II and VI had high order positive and significant standard heterosis for these two traits in E_1. The positive and significant heterobeltiosis was noted for PH in cross III, IV and V E_1. Similarly, high order positive and significant estimates of heterobeltiosis and standard heterosis were found for EBT in cross II and VI and for G/P in cross III and VI in E_2. The crosses mentioned above may merit exploitation for isolating desirable segregants for characters for which high heterosis was possessed by them in either irrigated or drought condition. The high heterosis observed in some crosses for above characters is in accordance with reports of earlier workers (Joshi, *et al*., 2004; Yadav *et al*., 2004; Eradasappa *et al*., 2007; Singh *et al*., 2007).

Inbreeding depression

The in breeding depression was also estimated for 12 characters of six crosses in E_1 and E_2 (Table 4). All the six crosses emerged with highly significant inbreeding depression in E_1 for GY/P, BY/P, G/P and PL except non-significant values was recorded in cross II for G/P. Significant inbreeding depression was also noted for some other characters in some crosses in E_1, *viz*. SFL (cross II and III), PH (cross I, II and III) and S/P (cross IV, V and VI). Similarly, four to six crosses showed significant inbreeding depression for SFL excluding sheath (except cross II and IV), G/P (except cross V), S/P (except cross II and IV), GY/P and HI (except cross VI) in E_2. Significant inbreeding depression was also noticed for DFF (cross V), PH (cross V and VI), EBT (cross II, III and VI), PL (cross II, IV and VI), SF (cross II), BY/P (cross II, III and V) in some of the six crosses in E_2.

Conclusion

The significance of additive gene effects for most of the sixteen characters in the six crosses under two conditions suggested substantial improvement in yield status can still be achieved in rice by using breeding procedures exploiting fixable components of genetic variance leading to development of pureline varieties in rice for irrigated and drought condition. 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. The non-additive gene effects may also be utilized for facilitating development of pureline cultivars by involving population improvement methods.

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