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Effect of gene actions on two lowland rice (*Oryza sativa L.*) accessions as influenced by submergence

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Abstract: The study on genetics of *Oryza sativa* L. lowland rice for submergence tolerance was carried out, using two most farmer-preferred commercial rice varieties in Nigeria. The experimental design was completely randomized design, having crossing blocks with three replications. Parameters estimated include; broad sense heritability (h2b), genotypic variance, phenotypic variance, additive variance, and narrow-sense heritability (h2n). Moderate to high narrow sense heritability in conjunction with moderate to high expected gain were observed in most of the traits, especially the yield component traits. The results of the generation mean analysis showed significance of at least one out of the four scales (A, B, C & D) for all the traits studied in the two crosses. The six parameters analysis revealed that besides the additive and dominance gene actions, epistatic interaction mechanisms have also contributed to the expressions of the traits studied. However, the relative magnitudes of these effects varied from character to character and cross to cross. The result showed a high magnitude of dominance gene effect with duplicate epistasis were observed for plant height, days to 50% flowering, numbers of panicle, panicle length and grain yield. Hence, the additive genes effect can also be considerable and significant for these traits.

Keywords: Epistatic, Additive, Variance, Dominance, Genetic

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1. Introduction

Rice (*Oryza sativa* L.) has become a commodity of strategic importance across most of Africa countries (Africa Rice, 2020). Driven by changing food preferences in both urban and rural areas and compounded by high population growth rates, rice consumption in the Saharan and sub-Saharan Africa (SSA) increased by 5.6% per annum between 2009 and 2012, a rate more than double the rate of population growth (Africa Rice, 2020). Projections by the Food and Agriculture Organization (FAO) suggested that rice consumption in West Africa will remain high with a continuous increase of about 4.5 % through the year 2014 and beyond (OECD/FAO, 2016). Its genetic improvement plays a crucial role in achieving higher yield. To establish a sound basis for any breeding program aimed at achieving higher yield, breeders must have genetic information on the nature of combining ability of the parents, their behaviour and performance in the hybrid combination (Liu et al., 2021). The knowledge of combining ability is essential for selection of suitable parents for hybridization and identification of promising hybrids for future exploitation in a breeding program (Fasahat et al., 2016). General combining ability (GCA) is the average performance of a line in hybrid combination and specific combining ability (SCA) is the deviation of crosses on the basis of average performance of the lines involved. General

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combining ability is associated with additive genetic effects while specific combining abilities associated with non-additive genetic effects (Begna, 2021; Gunasekaran et al., 2023).

Several studies on combining ability indicated that GCA is more important than SCA, although specific effects are of sufficient importance to merit attention in breeding program (Guo et al., 2018). The importance of the present study cannot be overemphasized in the face of the present rice production status in Nigeria and the lingering climate change. The study will generate useful segregating populations and provide genetic information on successful selection program to develop a flood-tolerant rice variety with characteristic features of the mega rice varieties in Nigeria. Therefore, objective of study is to determine the nature of gene action effects on some lowland rice accession as influenced by submergence.

2. Materials and Methods

The field work was carried out in 3 years (2019- 2022) at the National Cereals Research Institute (NCRI), Badeggi (Longitude N 09° 04.921' and Latitude E 006° 07.206') and the Rice Production and Research Field (N09° 04.238' and Latitude E 006° 06.638') of the National Cereals Research Institute (NCRI), Badeggi. NCRI averagely receives an annual rainfall of about 1184mm, with temperature ranging from 25.9 to 31.1°C and relative humidity of about 77 %.

2.1 Establishment of Crossing Block and Experimental Design

The experimental design was completely randomized design (CRD), having crossing blocks, with three replications. Two sets of crossing blocks were established at two weeks intervals to synchronize the flowering of the parents. Each of the crossing blocks was cleared and puddled with the dried weed incorporated into the soil. The blocks were levelled with help of a hand rake and then marked out. Each block consists of a 5m x 2 row plots for the donor parent and 5m x 3 row plot each for the susceptible parents. All the seeds were sown directly at a spacing of 20 cm x 20 cm. Fertilizer was applied as 15-15-15, N P K at the rate of 40 kg each of P2O5 and K2O/ha at planting, plus 40 kg N/ha as urea, three weeks after planting. Hand weeding was carried at 21 and 42 days after planting. The donor parent (Swarna Sub-1) was crossed to as many susceptible parents (FARO 44 and 57) plants as possible.

2.2 Sources of Experimental Materials

The seeds used for the research were obtained from the National Cereals Research Institute and the rice breeding unit of Africa Rice Center, Ibadan, Nigeria. The parent materials used for the study were three Oryza sativa lines, of which one is a donor parent line (Swarna Sub-1) already developed as being tolerant to submergence and the two others are susceptible parents to submergence (FARO 44 and 57). These two susceptible parents are commercially released and highly cultivated in Nigeria.

2.3 Estimation of Heritability

Heritability in broad sense (h2b) was calculated as the ratio of genotypic variance to the phenotypic variance (Salihu et al., 2018).

$$h_b^{\,2} = \sigma_g^{\,2} \Big/ \sigma_{p_h}^{\,2}$$

Where;

$h_b^{\,2}$ = broad sense heritability estimate

$\sigma^2{}_g$ = genotypic variance

$\sigma^2{}_{p_h}$ = phenotypic variance

Narrow-sense heritability ($h^2{}_n$) estimates were calculated as the ratio of additive genetic variance to total phenotypic variance.

$$h^2{}_n = {\sigma_a}^2 \Big/ {\sigma_{p_h}}^2$$

Where:

${\sigma_a}^2$ = Additive variance

${\sigma_{p_h}}^2$ = Phenotypic variance

2.4 Genetic Advance

Genetic advance in next generation in response to selection was determined as described by Salihu et al., (2018) as under:

$$GA = K \times \sigma p_h \times h^2$$

Where;

K = Selection intensity at 0.05 = 2.06

σp_h = Standard deviation of the phenotypic variance under selection

h^2 = Heritability in broad sense

GA = Genetic Advance

Genetic advance in term of percentage of mean = $GA/GM*100$

Where;

GM = Grand Mean (parents and hybrids)

The range of genetic advance in percentage of mean was classified as suggested by Johnson et al., (1995). Low = less than 10%, moderate = 10-20% and high = more than 20%**.**

2.5 Generation Mean Analysis

A package called "TNAUSTAT General breeding procedure" was used for the generation mean analysis. The three parameters model was estimated according to Jinks and Jones (1958), the six generation parameters was according to Hayman (1958), while the perfect fit model was calculated as described by Mather and Jinks (1982).

3. Results and Discussion

Table 1 shows the results of generation mean analysis for the studied traits in the two rice crosses. Simple additive-dominance model was observed to be inadequate to explain the inheritance of flag leaf length, flag leaf width, straw girth, and internode length in the two crosses according to the scaling test; however, the joint scaling test only supported the inadequacy of the model for the flag leaf width and internode length in the two crosses (Table 1). The Perfect Fit Model showed significant main effect (m), additive (a) and dominant gene effects (d) for the flag leaf length in the two crosses (Table 1). Significant gene effects of additive, dominant, additive-dominance and dominance-dominance with duplicate epistasis were observed for the flag leaf width in the two crosses. All the six parameters were significant for the internode length in the crosses (Table 1). A duplicate epistasis with high magnitude of dominant gene effect was observed for the internode length. Generation mean analysis provides information on the gene actions through the estimation of mean effect (m), additive effect (a), dominance effect (d) and their interactive effects (aa, ad & dd). The magnitudes of the six parameters and signs (- or +) of dominance effect (d) and dominance × dominance epistasis (dd) determine the traits inheritance (Salihu et al., 2018). Association and dispersion of alleles in parents is shown by positive and negative form of additive x additive (aa) interaction respectively. Negative sign of dominance (d) gene effect reflects reductive alleles involvement in dominant phenotype while when positive reflect increasing alleles involved in dominant phenotype. Negative sign of dominance x dominance (dd) interaction is an indication of ambi-directional dominance. The gene relation is measured to be complementary in nature when the (d) and (dd) estimations have the similar signs and considered to be duplicating in interaction when the signs are not similar Mather and Jinks (1982) and Abdelsatar et al. (2020).

Table 1. Gene Effects for Flag Leaf Length, Flag Leaf Width, Straw Girth and Internode Length of the Two Rice Crosses Evaluated

Models	Gene Effect	Flag Leaf Length (cm)		Flag Leaf Width (cm)		Stem Girth (cm)		Internode Length (cm)	
		Cross I	Cross II	Cross I	Cross II	Cross I	Cross II	Cross I	Cross II
Scaling test	A	-3.80*±1.25	2.72±1.44	-0.44±0.21	-0.24*±0.07	-0.08±0.29	-0.09*±0.01	-0.62±1.00	0.58±1.17
	B	5.58*±1.36	-4.84*±1.47	0.55*±0.16	0.90*±0.11	-0.01±0.33	-0.01±0.08	6.04**±0.70	17.09**±0.93
	C	2.57±1.82	-6.55*±2.16	-1.37**±0.16	0.47*±0.13	-1.46*±0.35	-0.02±0.13	20.19**±1.81	38.94**±1.83
	D	0.39±0.94	-2.21±1.08	-0.74*±0.13	-0.10±0.06	-0.69*±0.16	0.04±0.06	7.38**±0.86	10.64**±0.82
Joint Scaling Test	X^2	**0.44**	**1.40**	**21.63****	**42.81****	**3.77**	**0.03**	**52.39****	**17.56****
3 parameters	M	31.35**±1.94	36.89**±2.23	-0.27±0.27	1.43**±0.13	1.16*±0.35	2.07**±0.13	26.32**±1.75	32.67**±1.68
	A	2.17*±0.48	-1.81*±0.59	-0.15*±0.05	0.45**±0.05	0.03±0.13	0.05±0.03	0.54±0.29	0.53±0.37
	D	-0.46±5.16	5.53±5.79	3.77*±0.77	1.40*±0.33	2.30±1.03	-0.24±0.35	-23.81*±4.09	-23.50*±4.20
6 Parameters	M	30.87**±0.31	39.08**±0.38	1.22**±0.03	1.92**±0.02	1.99**±0.02	2.00**±0.02	16.75**±0.37	21.83**±0.32
	A	-2.52*±0.71	1.97±0.76	-0.64*±0.12	-0.13*±0.04	-0.01±0.15	0.01±0.05	-2.79**±0.44	-7.73**±0.52
	D	-1.45±2.00	3.22±2.29	2.18**±0.27	0.55*±0.13	1.02*±0.36	-0.06±0.14	-14.47**±1.80	-19.88**±1.77
	Aa	-0.79±1.88	4.43±2.15	1.48*±0.26	0.19±0.12	1.37*±0.32	-0.08±0.13	-14.77**±1.72	-21.28**±1.64
	Ad	-4.69**±0.86	3.78*±0.96	-0.50*±0.13	-0.57**±0.06	-0.04±0.20	-0.04±0.06	-3.33**±0.53	-8.26**±0.64
	Dd	-0.99±3.39	-2.31±3.74	-1.59*±0.51	-0.85*±0.22	-1.28±0.71	0.18*±0.03	9.35*±2.53	3.62*±0.77
Perfect fit	M	31.35**±1.94	36.89**±2.23	-0.27±0.27	1.43**±0.13	1.16*±0.35	2.07**±0.13	26.32**±1.75	32.67**±1.68
	A	2.17*±0.48	-1.81*±0.59	-0.15*±0.05	0.45**±0.05	0.03±0.13	0.05±0.03	0.54±0.29	0.53±0.37
	D	-0.46±5.16	5.53±5.79	3.77*±0.77	1.40*±0.33	2.30±1.03	-0.24±0.35	-23.81**±4.09	-23.50*±4.20
	Aa	-0.79±1.88	4.43±2.15	1.48*±0.26	0.19±0.12	1.37*±0.32	-0.08±0.13	-14.77**±1.72	-21.28**±1.64
	Ad	-4.69**±0.86	3.78*±0.95	-0.50*±0.13	-0.57**±0.06	-0.04±0.20	-0.04±0.06	-3.33**±0.53	-8.26**±0.64
	Dd	-0.99±3.39	-2.31±3.74	-1.59*±0.51	-0.85*±0.22	-1.28±0.71	0.18*±0.03	9.35*±2.53	3.62*±0.77
Type of epistasis		*NS*	*NS*	Duplicate	Duplicate	**NS**	**NS**	Duplicate	Duplicate

[m] = main effect; [a] = additive effect; [d] = dominance effect; [aa] = additive x additive gene interaction; [ad] = additive x dominance gene interaction; [dd] = dominance x dominance gene interaction, $\chi 2$ = Chi-square, A, B, C & D are scales

At least two out of the four scales (A, B, C & D) in the scaling test and the Chi-square of the joint scaling test were significant for the plant height, days to 50% flowering, number of tillers and number of panicles (Table 2). The perfect fit model revealed significant effects for all the six parameters for the plant height in the two crosses, except for the additive-additive interaction effect which was not significant in the Cross I. However, the results showed duplicate epistasis with high magnitude of dominant gene effects for the plant height in the two crosses. The perfect fit model for days to 50% flowering showed significant gene effects for all the six parameters in both crosses (Table 2). The gene effect with highest magnitude was dominant gene effects in both crosses and the type of epistasis revealed for the trait was duplicate epistasis in the two crosses. Significant positive main effect (m) and significant negative dominant effect and additive dominant interaction effects were revealed for number of tillers in Cross I, while in Cross II only dominant gene effect that was negative and significant out of the two aforementioned two gene effects (Table 2). The results revealed duplicate type of epistasis with high positive magnitude of dominant gene effect for the inheritance of the number of panicles in the two crosses evaluated (Table 2). The results revealed duplicate form of epistasis for the plant height, days to 50% flowering and number of panicles in the two crosses evaluated. There was dispersion of alleles in the parents for plant height and days to 50% flowering as indicated by negative form of additive x additive (aa) interaction. The positive form of additive × additive (aa) interaction indicated allele association for the number of panicles. All these findings coupled with the high magnitude and significant effects of the dominance genes suggest hybrid breeding and/or delay selections for the improvement of the traits. The result is in conformity with the report of Xie et al., (2019). Rao et al., (2017), in a study on six generations of a cross between HUR-105 × Swarna Sub1, also reported duplicate epistasis effect for plant height and panicle characters. The inheritance of the panicle length and seed weight was predominantly determined by the dominance gene effect with substantial dominance × dominance (dd) interaction in the two crosses. However, the contributions of the additive genes and additive × additive (aa) interaction were also significant indicating the possibility of exploiting the significant fixable genes in the selection program. To exploit the fixable genes, the selection may be exerted on nearly-homozygous generations to isolate superior individuals for the traits. In some earlier studies, non-additive gene actions have been implicated for the inheritance of the panicle characters (Saleem et al., 2010 and Kumar et al., 2016).

The simple additive-dominance model being not fitted for the survival scores after the submergence, the perfect fit model revealed significant effects of all the six parameters, except dominance × dominance (dd) interaction in Cross II. The positive values of the additive x additive interaction in the three crosses indicated that there were associations between the alleles of the two parents in each of the crosses for the trait. The predominance effect due to the dominant genes among the three main effects and the significance of the interactive effects of the genes proposed the adoption of hybrid breeding for development of superior submergence tolerant variety. Nevertheless, the significant effects of the additive genes also revealed the possibility of exploiting the fixable genes in the selection program for traits. This showed that both additive and non-additive are important for the expression of submergence ability of the crosses. Previous studies on understanding the genetic mechanism of submergence tolerance in rice revealed that the trait is controlled by both additive and non-additive gene effects (Oladosu et al., 2020).

Table 2. Gene Effects for Plant Height, Days 50% Flowering, Numbering of Tiller, and Number of Panicle of the Two Rice Crosses Evaluated.

Models	Gene Effect	Plant Height (cm)		Days 50% Flowering		Number of Tiller		Number of Panicle	
		Cross I	Cross II	Cross I	Cross II	Cross I	Cross II	Cross I	Cross II
Scaling test	A	-12.81*±2.78	-59.58**±4.06	1.40±2.30	-1.80±1.94	-1.15±2.67	0.70±1.72	-0.70±1.06	-8.80**±0.68
	B	4.13±2.91	-4.05±3.03	10.50*±2.53	4.80*±1.64	10.85**±1.39	-18.70*±5.11	0.30±0.80	5.10*±0.99
	C	-4.19*±1.07	42.49**±6.48	26.06**±4.24	28.08**±2.54	16.18*±4.15	-29.38*±5.24	-6.38*±1.18	-15.32**±0.96
	D	2.25±2.04	53.06**±3.32	7.08*±1.99	12.54**±1.26	3.24±2.76	-5.69±3.12	-2.99*±0.55	-5.81**±0.52
Joint Scaling Test	X^2	13.78*	186.59**	14.95*	19.30**	14.30*	32.66**	48.31**	15.16**
3 parameters	M	89.77**±4.22	211.06**±6.74	90.66**±4.03	111.38**±2.59	30.83*±5.73	28.32*±6.59	5.52*±1.16	0.43±1.07
	A	4.75*±1.11	28.81**±1.15	-10.80**±0.63	-4.60**±0.55	-2.05±1.51	-7.80*±2.14	-0.10±0.38	-0.05±0.28
	D	-22.96**±1.15	-295.32**±16.46	-22.92**±1.06	-46.96**±6.95	-6.26±6.46	-12.34*±4.56	9.36*±3.30	26.39**±3.10
6 Parameters	M	81.58**±0.68	105.83**±1.32	79.77**±0.76	93.42**±0.40	26.90*±0.56	23.81**±0.35	8.81**±0.13	11.65**±0.10
	A	-3.73±1.51	1.04±2.00	-15.35**±1.29	-7.90**±0.99	-8.05*±2.53	1.90±1.04	-0.60±0.48	-7.00**±0.48
	D	-9.79±4.35	-125.59**±6.90	-20.66*±4.24	-24.88**±2.72	-9.48±5.80	-5.72±3.72	3.78*±1.22	18.47**±1.12
	Aa	-4.49±4.08	-106.11**±6.64	-14.16*±3.98	-25.08**±2.53	-6.48±5.53	11.38±6.23	5.98*±1.10	11.62**±1.03
	Ad	-8.47*±1.88	-27.77**±2.31	-4.55*±1.43	-3.30*±1.13	-6.00±2.94	9.70*±3.71	-0.50±0.61	-6.95**±0.55
	Dd	13.17**±1.30	169.73**±10.31	2.26*±0.64	22.08*±4.69	-3.22±2.92	6.62±3.23	-5.58±2.26	-7.92*±2.13
Perfect fit	M	89.77**±4.22	211.06**±6.74	90.66**±4.03	111.38**±2.59	30.83*±5.73	28.32*±6.59	5.52*±1.16	0.43±1.07
	A	4.75*±1.11	28.81**±1.15	-10.80**±0.63	-4.60**±0.55	-2.05±1.51	-7.80*±2.14	-0.10±0.38	-0.05±0.28
	D	-22.96**±1.15	-295.32**±16.46	-22.92**±1.06	-46.96**±6.95	-6.26*±1.46	-12.34*±4.56	9.36*±3.30	26.39**±3.10
	Aa	-4.49±4.08	-106.11**±6.64	-14.16*±3.98	-25.08**±2.53	-6.48±5.53	11.38±6.23	5.98*±1.10	11.62**±1.03
	Ad	-8.47*±1.88	-27.77**±2.31	-4.55*±1.43	-3.30*±1.13	-6.00*±1.94	9.70*±3.71	-0.50±0.61	-6.95**±0.55
	Dd	13.17**±1.30	169.73**±10.31	2.26*±0.64	22.08*±4.69	-3.22±3.92	6.62±3.23	-5.58*±2.26	-7.92*±2.13
Type of epistasis		Duplicate	Duplicate	Duplicate	Duplicate	*NS*	*NS*	Duplicate	Duplicate

[m] = main effect; [a] =additive effect; [d] =dominance effect; [aa] = additive x additive gene interaction; [ad] = additive x dominance gene interaction; [dd] = dominance x dominance gene interaction, $\chi 2$ = Chi-square, A, B, C & D are scales

Inadequacy of simple additive-dominance model to depict the gene action for the inheritance of panicle length and 100 grain weight was revealed by both scaling and joint scaling tests carried out in the two crosses (Table 3). Only scaling test showed inadequacy of the simple three parameters model for the inheritance of the grain length and grain width in the two crosses (Table 3). The six parameters model revealed positive and significant additive gene effects for the panicle length, 100 grain weight and grain length (Table 3). The perfect fit model showed significant effects of all the six parameters with high magnitude of dominant gene effects and duplicate epistasis for the panicle length and 100 grain weight in the crosses. Only main effect (m) and additive gene effect were significant for grain length in Cross I, while main effect, additive gene effect and dominant effect were significant for the trait in Cross II (Table 3).

Grain weight inheritance was also reported to have been majorly governed by non-additive gene actions (Rao et al., 2017).

All the main gene effects (m, a & d) and the interaction effects were significant for the grain yield in the two crosses. The perfect-fit six parameter model revealed predominance of the dominance gene effects compared to others in the crosses. Evidence of dispersion of alleles in the parents, reduced dominant alleles in the hybrids and directional dominance were recorded for the yield in the crosses. All these revealed the effects of non-additive gene actions on the inheritance of the trait. However, the available and significant fixable genes observed could also be exploited if the selection is delay to the later generations when the manifestation of homozygous populations could be easily identified. Similar findings have been reported from earlier studies (Saleem et al., 2010; Rao et al., 2017; Xie et al., 2019).

The three parameters model was not adequate to explain the gene effects for the grain yield and comparative survival of the seedlings under submerged condition (Table 4). All the scales (A, B, C & D) and the Chi-square of the joint scaling test revealed statistical differences for the two traits in the two crosses. The perfect fit model revealed significant differences for all the six parameters for the grain yield and comparative survival scores (CSS), except for the dominance-dominance interaction for CSS in the Cross II. High magnitude of dominant main effects and dominance-dominance interactive effects with duplicate type of epistasis were observed for the grain yield in the two crosses (Table 4). Dominant main effect (d) and dominance-dominance epistasis interaction were showed to be more important for the CSS in Cross I; however, in Cross II, dominant effects and additive-additive gene effect showed higher magnitude for the CSS (Table 4).

Gyawali et al., (2019) reported dominant genes as major gene effects for submergence tolerance in rice. Involvement of one major gene for the inheritance of submergence tolerant in rice was reported by Akinwale et al., (2015). The findings reported here is in conformity with earlier reports by Suvi et al., (2021) and Kargbo et al., (2019). Dominant effects of Sub1 provided a substantial enhancement in the level of tolerance of all the sensitive mega varieties in Philippines (Kargbo et al., 2019). Rahman et al. (2022) also reported predominance GCA effects than SCA effects for all traits assessed.

Table 3: Gene Effects for Panicle Length, 100 Grain Weight, Grain Length and Grain Width of the Two Rice Crosses

Models	Gene Effect	Panicle Length (cm)		100 Grain Weight (g)		Grain Length (mm)		Grain Width (mm)	
		Cross I	Cross II	Cross I	Cross II	Cross I	Cross II	Cross I	Cross II
Scaling test	A	3.53±1.39	5.51*±1.35	0.04±0.06	-0.02±0.04	0.68±0.27	0.17±0.21	-0.27*±0.06	-0.13±0.06
	B	-0.61±1.08	-5.34*±0.92	-0.65*±0.20	-1.08**±0.13	0.71*±.22	0.66*±0.21	0.04±0.05	-0.06±0.08
	C	-11.43**±1.53	6.76*±1.30	0.89**±0.09	0.79**±0.06	1.87*±0.34	1.13*±0.29	-0.10±0.08	0.28**±0.04
	D	-7.18**±0.75	3.29*±0.71	0.75**±0.08	0.94**±0.17	0.25±0.11	0.16±0.11	0.07±0.04	0.24±0.22
Joint Scaling Test	X^2	15.26^{**}	641.15^{**}	18.67^{**}	30.22^{**}	0.16	0.06	0.09	0.43
3 parameters	M	11.47**±1.56	34.90**±1.47	3.91**±0.19	4.29**±0.13	9.18**±0.25	9.25**±0.24	2.43**±0.07	2.76**±0.44
	A	3.64**±0.43	-1.39*±0.38	0.46**±0.04	0.41**±0.02	0.59*±0.13	0.84**±0.09	0.05±0.03	-0.08*±0.03
	D	28.26**±4.45	-14.78*±4.24	-3.31*±0.58	-4.56**±0.38	1.01±0.72	0.51±0.68	-0.39±0.21	-1.02±0.91
6 Parameters	M	21.28**±0.17	29.11**±0.14	2.78**±0.01	2.75**±0.12	9.46**±0.67	9.38**±1.03	2.32**±0.01	2.41**±0.11
	A	5.70**±0.67	4.03**±0.65	0.80**±0.09	0.94**±0.06	0.57**±0.09	0.59**±0.09	-0.11*±0.03	-0.11*±0.04
	D	10.98**±1.65	-8.36*±1.54	-1.20**±0.19	-1.58**±0.13	0.12±0.27	0.01±0.26	-0.03±0.08	-0.36±0.44
	Aa	14.35**±1.50	-6.59*±1.42	-1.50**±0.17	-1.89**±0.12	-0.49±0.22	-0.31±0.22	-0.13±0.07	-0.47±0.42
	Ad	2.07*±0.79	5.42**±0.75	0.35*±0.10	0.53**±0.06	-0.02±0.16	-0.25±0.13	-0.16*±0.04	-0.04±0.05
	Dd	-17.27*±3.07	6.42**±0.91	2.11*±0.39	2.99**±0.25	-0.89±0.51	-0.51±0.48	0.36±0.14	0.66±0.47
Perfect fit	M	11.47**±1.56	34.90**±1.47	3.91**±0.19	4.29**±0.13	9.18**±0.25	9.25**±0.24	2.43**±0.07	2.76**±0.44
	A	3.64**±0.43	-1.39*±0.38	0.46**±0.04	0.41**±0.02	0.59*±0.13	0.84**±0.09	0.05±0.03	-0.08*±0.03
	D	28.26**±4.45	-14.78*±4.24	-3.31*±0.58	-4.56**±0.38	1.01±0.72	0.51**±0.07	-0.39±0.21	-1.02±0.91
	Aa	14.35**±1.50	-6.59*±1.42	-1.50**±0.20	-1.89**±0.12	-0.49±0.22	-0.31±0.22	-0.13±0.07	-0.47±0.44
	Ad	2.07*±0.79	5.42**±0.75	0.35*±0.10	0.53**±0.05	-0.02±0.16	-0.25±0.13	-0.16*±0.04	-0.04±0.05
	Dd	-17.27*±3.07	6.42**±0.91	2.11*±0.39	2.99**±0.22	-0.89±0.51	-0.51±0.48	0.36±0.14	0.66±0.47
Type of epistasis		Duplicate	Duplicate	Duplicate	Duplicate	NS	NS	NS	NS

[m] = main effect; [a] =additive effect; [d] =dominance effect; [aa] = additive x additive gene interaction; [ad] = additive x dominance gene interaction; [dd] = dominance x dominance gene interaction, $\chi 2$ = Chi-square, A, B, C & D are scales

In another investigation by Sadhana et al. (2022), total grain number per panicle, filled grain number per panicle, weight of 1000 grains, grain yield per plant, weight of panicle, head rice recovery, length of kernel after cooking, linear elongation ratio, length of kernel and kernel length/breadth ratio exhibited high heritability along with high genetic advance as percentage of mean. High heritability coupled with high genetic advance as per cent of mean was observed for flag leaf area, grains per panicle, panicle bearing tillers per plant, spikelet per panicle, and plant height which indicated that these traits were controlled by additive type of gene action (Singh & Verma, 2018). Tripathi et al., (2018) also reported high genetic advance in percent mean for flag leaf area, panicle bearing tillers per plant, spikelet per panicle, biological yield per plant in a Studies on Genetic Variability, Heritability and Genetic Advance in Rice (*Oryza sativa* L.) for yield and its components under salt affected soil.

Table 4. Gene Effects for Seed Yield and Comparative Survival Scores of the Two Rice Crosses Evaluated

		Seed Yield (g/plant)		**Comparative Survival Scores**	
Models	**Gene Effect**	**Cross I**	**Cross II**	**Cross I**	**Cross II**
Scaling test	A	-13.15**±1.41	-12.47**±0.99	-2.32**±0.02	-0.76**±0.04
	B	-19.75**±0.88	-15.54**±1.18	-2.08**±0.01	-1.20**±0.03
	C	20.08*±4.64	-14.50*±2.63	-4.42**±0.02	-3.79**±0.05
	D	26.49**±2.24	6.75**±1.14	-0.01*±0.00	-0.91**±0.02
Joint Scaling Test	X^2	24.47**	143.30**	12.64*	11.55*
3 parameters	*M*	72.03**±4.51	29.30**±2.30	1.24**±0.01	-0.56**±0.04
	A	-0.58**±0.02	-1.23*±0.25	0.12**±0.01	0.21**±0.01
	D	-120.23**±9.37	-39.03**±5.17	-4.47**±0.03	1.46**±0.11
6 parameters	*M*	33.39**±1.09	20.16**±0.52	0.11**±0.00	0.21**±0.01
	A	2.72*±0.49	0.30±0.48	0.00±0.00	0.43**±0.02
	D	-34.35**±4.54	2.48±2.42	-0.08**±0.01	1.61**±0.05
	Aa	-52.98**±4.48	-13.51**±2.28	0.01*±0.00	1.82**±0.04
	Ad	3.29*±0.71	1.53**±0.05	-0.12**±0.01	0.22**±0.02
	Dd	85.88**±5.04	41.51**±3.27	4.39**±0.02	0.14±0.08
Perfect fit	*M*	72.03**±4.51	29.30**±2.30	1.24**±0.01	-0.56**±0.04
	A	-0.58**±0.02	-1.23*±0.25	0.12**±0.01	0.21**±0.01
	D	-120.23**±9.37	-39.03**±5.17	-4.47**±0.03	1.46**±0.11
	Aa	-52.98**±4.48	-13.51**±2.28	0.01*±0.00	1.82**±0.04
	Ad	3.29*±0.71	1.53**±0.05	-0.12**±0.01	0.22**±0.092
	Dd	85.88**±5.04	41.51**±3.27	4.39**±0.02	0.14±0.08
Type of epistasis		Duplicate	Duplicate	Duplicate	NS

m = main effect; [a] =additive effect; [d] =dominance effect; [aa] = additive x additive gene interaction; [ad] = additive x dominance gene interaction; [dd] = dominance x dominance gene interaction, $\chi 2$ = Chi-square, A, B, C & D are scales

5. Conclusions

These findings showed that selection for the traits may be averted by presence of epistasis interaction; although this problem could be overcome through delaying selection to the later generations when the fixable portions of the genes could be easily harnessed. Therefore, high heritability coupled with high genetic advance as per cent of mean was observed for flag leaf area, grains per panicle, panicle bearing tillers per plant, spikelet per panicle, and plant height which indicated that these traits were controlled by additive type of gene action and in such crosses where non-additive gene effects played a dominant role in association with additive components, the recurrent and reciprocal recurrent selection could be used to exploit both components at the same time.

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