Received: 08 Dec 2023 | Revised: 23 Jan 2024 | Accepted: 28 Jan 2024

Electronic Journal of Plant Breeding

Research Article

Deciphering gene action for traits contributing to submergence tolerance and yield in rice (*Oryza sativa* L.)

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Abstract

Rice (*Oryza sativa* L.), a semi-aquatic crop cultivated in diverse environments from sea coasts to high altitudes, faces submergence issues impacting one-third of global cultivation. Effectively choosing superior offspring with a range of genetic traits is vital for improving yield stability, particularly in the development of submergence-tolerant varieties. This is accomplished by comprehending gene action through the generation mean analysis. This experimental material comprised six generations (P_1, P_2, F_1, F_2, B_1, and B_2) obtained from two rice crosses *viz*., ADT 45 x APD 19002 and CO 54 x APD 19002 involving three parents, examining twelve traits. In the cross ADT 45 x APD 19002, traits like days to fifty per cent flowering, plant height, number of productive tillers per plant, flag leaf width, total number of grains per panicle, number of filled grains per panicle, and single plant yield exhibited opposite signs of dominance (h) and dominance × dominance (l), indicating a prevalence of duplicate epistasis. Simultaneously, additive(d) and additive × additive(i) gene effects were displayed by days to fifty per cent flowering, total number of tillers per plant, panicle length, flag leaf width, total number of grains per panicle, and single plant yield. In cross CO 54 x APD 19002, traits such as days to fifty per cent flowering, plant height, flag leaf width, number of filled grains per panicle, spikelet fertility, and single plant yield suggested predominance of duplicate epistasis. Meanwhile, additive and additive × additive gene effects predominantly influenced the days to fifty per cent flowering, spikelet fertility, and single plant yield. These findings propose the potential for improvement through later-generation selection, emphasizing the integration of selection with screening for submergence tolerance to develop high-yielding submergence-tolerant varieties.

Keywords: generation mean analysis, scaling test, genetic effects, submergence tolerance

INTRODUCTION

Flooding poses a significant threat to rice ecosystems, intensifying over the past decades, and ranks as the third crucial constraint to high productivity, following heat and drought. This adversely affects crop production, resulting in substantial yield losses from both seasonal and unseasonal flooding (Ismail *et al.,* 2013). Approximately 30% (700 million) of people reside in flood-prone rice-cultivating regions. In India alone, 16.1 million hectares of rice-growing areas are periodically affected by floods (Oladosu *et al.,* 2020). Recent climate change projections indicate an increase in rainfall patterns, especially in flood-prone coastal regions. The rapid increase in flooding, coupled with the need to boost agricultural yield by 70% to feed a projected global population of over nine billion by 2050, presents an alarming challenge. Despite these challenges, rice remains a vital crop, serving as a staple food for over 3.5 billion people worldwide and ensuring food security for numerous countries in Africa and Asia (Bailey-Serres *et al.,* 2010).

https://doi.org/10.37992/2024.1501.007

Rice crop is semi-aquatic and its cultivation spans diverse environmental conditions from sea coasts to high altitudes. However, major rice-growing areas are significantly affected by flooding caused by river discharge, rainwater accumulation and tidal movements. Approximately one-third of globally cultivated rice areas are deep-water and rainfed lowland ecosystems, encompassing around 50 million hectares (Nayak *et al.,* 2022). Devastating hydrological conditions, especially in rice-cultivated areas, involve complete submergence up to several meters in depth. The range of flooding regimes in nature is notable, varying from soil waterlogging for a few days to prolonged complete submergence lasting for months (Voesenek and Bailey-Serres 2013). Flooding causes a potential grain yield loss of 20% to 40% or more in irrigated and rainfed lowland areas, respectively (Muthu *et al.,* 2020). Since yield is a complex polygenic trait, it is influenced by various quantitative traits. However, the selection of genetically inherited traits for submergence tolerance is crucial. Rice varieties with submergence tolerance exhibit varying levels of survival against deep conditions, making them crucial for areas prone to flooding (Ganapati *et al.,* 2020). Improving genetics involves efficiently selecting the best offspring with varied genetic traits. Understanding gene action, including the effects of additive and dominant genes and their interactions is crucial for determining the breeding values. Generation mean analysis (GMA), involving six populations or generations (P_1, P_2, F_1, F_2, B_1, and B_2), is a valuable tool for estimating gene actions and linkages. GMA has been successfully employed in various crops to study the gene effects of quantitative traits. Therefore, this study provides crucial insights into the gene actions of submergence tolerance traits in selected crosses and parents, guiding rice breeding programs, determining suitable breeding methods, and streamlining the selection process to develop climate-resilient crops capable of withstanding submergence.

MATERIALS AND METHODS

In an experimental context, two cross combinations, *viz.,* cross 1 (ADT 45 X APD 19002) and cross 2 (CO 54 X APD 19002), were examined across six generations, which included P_1, P_2, F_1, F_2, B_1, and B_2. A crossing block was raised during *rabi*, 2021 to generate hybrid seeds from the above crosses. A portion of hybrid seeds was planted during *summer*, 2022. The true F_1 plants were confirmed using molecular marker of their respective parents. They were subsequently backcrossed with P_1 and P_2 parental lines to develop a B_1 and B_2 generations. During the summer of 2023, seeds from all six generations of both Cross 1 and Cross 2 were sown. Initially, all generations were raised in plastic trays measuring 35 x 15 x 10 cm under normal growing conditions for a period of twenty-one days. Following this, the seedlings in the trays were subjected to submergence in a tank with a depth of 90 cm for a period of 10 days (**Table 1**). After de-submergence, the recovered plants were transplanted into the main field with the spacing of 20 x 20 cm at the Department of Rice, Tamil Nadu Agricultural University, Coimbatore. Furthermore, biometric traits were observed and recorded in all the available plants across the six generations. These observations aimed to provide a comprehensive understanding of the gene action controlling the expression of traits within these cross combinations and generations.

Statistical analysis: Generation mean analysis done by following the approaches of Hayman (1960) and Jinks and Jones (1958), proceeded in two stages. Initially, the study involved testing for epistasis to determine the presence of inter-allelic interaction. Subsequently, in the second stage, the analysis encompassed estimating gene effects, and variances after identifying the type of epistasis. A, B, C, and D scaling tests were applied, and the standard errors for A, B, C, and D were computed by taking the square root of respective variances. 't' values were then calculated by dividing A, B, C, and D values by their respective standard errors. The significance of any of these four scales indicated the presence of epistasis. All the statistical analyses were done using TNAUSTAT software (Manivannan 2014).

RESULTS AND DISCUSSION

Quantitative traits of considerable interest are influenced by a large number of genes exerting their effects and are additionally subject to modification by various environmental factors. Analyzing individual genes become impractical due to the large number involved in a comprehensive whole-genome analysis. In this study, the aim was to assess the nature and extent of allelic and non-allelic interactions in rice yield and yield-attributing traits under submergence stress conditions. The partitioning of genetic variability into broad components was a key focus. The scaling test results, whether considering both components or C and D alone, showed significant values, indicating that the additive dominance model was insufficient for all traits in this particular cross. The inadequacy of the additive-dominance model was primarily attributed to the presence of epistasis. To detect the non-allelic interaction component of the phenotypic distribution mean, generation mean analysis was employed. **Tables 2, 3 and 4** present the results of mean performance, scaling tests, and the estimation of genetic effects for the two analyzed crosses.

Mean performance for different generations: Mean performance with standard errors of different yield and yield attributing traits were presented in **Table 2**. An analysis of the means across various generations for the twelve studied characteristics of the two crosses revealed significant variation. This highlights the significance of assessing additive, dominance and epistatic interactions. Notably, significant differences were observed among the means of the six generations for characteristics such as days to fifty per cent flowering, plant height, number of productive tillers per plant, number of tillers per plant, panicle length, flag leaf length, flag leaf width, number

Table 1. Survival percentage across six generations following submergence imposition

Cross 1	**ADT 45 x APD 19002**					
Generations	**P_1**	**P_2**	**F_1**	**F_2**	**B_1**	**B_2**
Actual population	10	10	10	310	50	50
Resilient population post-submergence	2	7	6	102	13	19
Survival percentage	20.00	70.00	60.00	32.90	26.00	38.00
Cross 2	**CO 54 x APD 19002**					
Actual population	10	10	10	310	50	50
Resilient population post-submergence	3	8	7	105	12	17
Survival percentage	30.00	80.00	70.00	33.87	24.00	34.00

Table 2. Mean and standard errors for yield and yield related traits of rice

Generations	**P1**		**P2**		**F1**	
population	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**
DFF	85.5±1.5	92±1	98±0.8	103.14±1.45	92.25±1.03	94.2±0.37
PH	90.25±1.25	106.5±8.5	89.54±1.3	88.1±1.12	105.25±2.06	114±2.92
NPT	30±1	33±5	27±2.31	30±2.57	40.5±4.01	32.4±2.01
TNT	30.5±0.5	33.5±4.5	25.63±0.68	31.29±2.38	41.75±3.57	33.8±1.77
PL	20.1±0.4	25.95±1.65	24.35±0.56	23.8±0.59	22.95±0.32	23.78±1.57
FLL	20.3±1.1	27.45±1.05	28.23±1.02	26.23±1.11	27±5.04	28.88±1.99
FLW	1.5±0	1.6±0.1	1.61±0.1	1.5±0.04	1.75±0.12	1.62±0.07
TNGpP	177.5±4.5	184±8	165.88±4.14	166±6.48	231.5±9.32	230.2±14.78
NFGpP	149.5±1.5	161.5±9.5	146.5±5.35	152.71±6.24	221.75±10.77	216.6±13.73
SF	84.26±1.29	87.71±1.35	88.19±1.43	91.98±0.83	95.69±0.85	94.13±0.86
TGW	1.4±0.02	1.47±0.06	1.49±0.05	1.41±0.02	1.57±0.06	1.51±0.07
SPGY	22.85±1.45	25.2±0.7	29.86±0.52	30.46±0.98	39.66±0.99	39.64±4.41

Table 2. Continued..

Generations	**F2**		**B1**		**B2**	
population	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**
DFF	94.14±0.52	98.8±0.43	90.33±0.33	91.25±0.25	93.5±0.22	95.83±0.48
PH	98.97±0.93	101.82±0.68	88.67±8.69	114.75±2.43	87±2.67	108.5±2.91
NPT	33.78±0.79	25.09±0.58	27±3.61	25.75±2.02	25.67±2.38	27.5±2.38
TNT	34.1±0.73	25.94±0.57	28.67±2.4	25±1.47	29.5±3.33	27.83±2.27
PL	22.44±0.18	24.94±0.2	20.17±1.45	24.38±0.63	20.92±0.91	23.25±0.76
FLL	27.26±0.58	28.9±0.42	26±1.61	26.23±2.57	21.83±1.54	27.02±0.91
FLW	1.65±0.02	1.76±0.02	1.53±0.03	1.43±0.02	1.57±0.03	1.63±0.07
TNGpP	220.2±3.46	210.14±3.8	252±8.62	207.75±6.66	238.17±12.11	237.67±12.49
NFGpP	203.56±3.96	190.66±3.72	227.67±9.13	194.25±8.72	218±10.9	227±13.62
SF	91.69±0.85	90.9±0.75	90.35±1.86	93.4±1.51	91.59±0.99	95.31±0.96
TGW	1.62±0.02	1.46±0.02	1.55±0.09	1.4±0.04	1.58±0.07	1.47±0.08
SPGY	37.77±1.18	33.05±1.28	19.37±0.47	21.15±3.38	37.5±2.98	32.85±2.71

Cross 1- ADT 45 x APD 19002, Cross 2- CO 54 x APD 19002. DFF - Days to fifty per cent flowering, PH- Plant height, NPT- Number of productive tillers per plant, TNT- Total number of tillers per plant, PL-Panicle length, FLL- Flag leaf length, FLW-Flag leaf width, TNGpP- Total number of grains per panicle, NFGpP- Number of filled grains per panicle, SF- Spikelet fertility, TGW- Thousand-grain weight, SPY-Single plant yield of filled grains per panicle, total number of grains per panicle, spikelet fertility, thousand-grain weight and single plant yield in both the crosses (**Fig. 1**). Significant mean performance variations were found in earlier studies of Muthuvijayaragavan and Murugan (2019), Ganapati *et al.* (2020) and Ehirim, B. O *et al*. (2023).

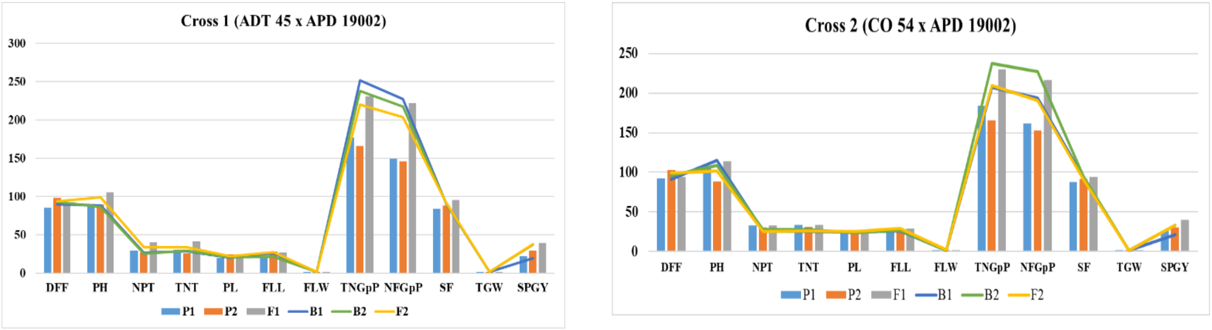

Fig. 1 Mean performance of yield and its related traits in different generations

Scaling test: The digenic non-allelic interaction model, characterized by six parameters (m, d, h, i, j, and l), demonstrated the suitability of the epistatic model in elucidating the gene action involved in the traits. The gene effect values clearly showed that there was a significant variation among the observed agro-morphological traits, as indicated in **Table 3**. In two crosses, at least one, two or three, or all of the A, B, C, and D scales were found to be significant, indicating the non-allelic interactions in the heritable traits. In Cross 1, all traits were significant on at least one scale, except spikelet fertility, whereas in Cross 2, except for flag leaf length and thousand-grain weight, all traits were significant. Almost all traits exhibited the non-allelic interactions in both crosses. The combined effects of additive × additive (i) and dominance × dominance (l) interactions generally exhibit a higher magnitude compared to the combined main effects of additive (d) and dominance (h) for all the traits in both crosses.

Genetic effects: The six-parameter model, encompassing additive, dominance and interactions was determined to be the best-fit model. It revealed significant non-allelic interactions for all traits, providing estimates for various genetic components in both crosses (**Table 4**). The additive genetic effect of Cross 1 was observed with positive significance for the traits *viz.,* total number of tillers per plant, whereas negative significance was observed in days to fifty per cent flowering, panicle length, flag leaf length and single plant grain yield. Likewise, traits such as days to fifty per cent flowering, plant height, panicle length, flag leaf width, spikelet fertility and single plant grain yield showed positive significance, while the total number of grains per panicle was observed with negative significance in Cross 2. The prevalence of additive gene action for days to fifty per cent flowering, plant height and number of productive tillers per plant was earlier reported

Table 3. Scaling test of genetic parameters for yield and yield contributing traits in rice

Scale	A		B		C		D	
Population	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**
DFF	2.92±1.94	-3.7±1.18*	-3.25±1.38*	-5.68±1.78**	8.57±3.39*	11.67±2.58**	4.45±1.12**	10.52±1.02**
PH	-18.17±17.53	9±10.21	-20.79±5.87**	14.9±6.6*	5.6±5.82	15.33±10.72	22.28±9.28*	19.62±4.03**
NPT	-16.5±8.31	-13.9±6.73	-16.17±6.63*	-7.4±5.77	-2.88±8.98	-27.45±7.3**	14.9±4.6**	-3.07±3.33
TNT	-14.92±6.01*	-17.3±5.66*	-8.38±7.6	-9.42±5.43	-3.24±7.76	-28.62±6.61**	10.02±4.36*	-0.95±2.94
PL	-2.72±2.95	-0.98±2.6	-5.47±1.92*	-1.08±2.26	-0.6±1.18	2.47±3.68	3.79±1.75*	2.26±1.06*
FLL	4.7±6.08	-3.88±5.61	-11.56±6	-1.08±2.92	6.53±10.46	4.15±4.57	6.69±2.52**	4.55±2.85
FLW	-0.18±0.14	-0.37±-0.13*	-0.23±0.17	0.15±0.16	-0.03±0.27	0.7±0.2**	0.19±0.06**	0.46±0.08**
TNGpP	95±20.11**	1.3±21.45	78.96±26.27**	79.13±29.73*	74.42±24.01**	30.15±34.79	-49.77±16.39**	25.14±16.06
NFGpP	84.08±21.26**	10.4±24.15	67.75±24.89*	84.69±31.14*	74.75±27.31**	15.21±33.24	-38.54±16.28*	-39.94±-17.81*
SF	0.74±4.04	4.97±3.43	-0.69±2.58	4.51±2.26	2.92±4.26	-4.34±-3.79	1.43±2.71	-6.91±-2.33**
TGW	0.14±0.18	-0.17±0.12	0.11±0.16	0.01±0.17	0.47±0.16**	-0.08±0.17	0.11±0.12	0.04±0.09
SPGY	-23.78±1.99**	-22.54±8.1*	5.48±6.07	-4.4±7.06	19.04±5.33**	-2.75±10.26	18.67±3.83**	12.09±5.03*

* & ** Significance at 0.05 and 0.01 probability levels, respectively; A- scale A; B- Scale-B; C- Scale C; D- Scale D

Table 4. Estimation of genetic parameters for yield and yield attributing traits in rice

	m		[D]		[h]	
Population	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**
DFF	100.65±2.39**	118.62±2.22**	-6.25±0.85**	-5.57±0.88**	-17.64±5.55**	-54.85±5.44**
PH	134.45±18.57**	58.07±9.12**	0.36±0.9	9.2±4.29	-112.71±55.13*	119.07±26.84**
NPT	58.29±9.28**	25.35±7.22**	1.5±1.26	1.5±2.81	-80.25±27.23**	-8.11±21.13
TNT	48.11±8.74**	30.49±6.4**	2.44±0.42**	1.11±2.54	-49.7±25.63	-21.51±18.6
PL	29.81±3.52**	29.4±2.29**	-2.13±0.34**	1.08±0.88	-22.62±10.43*	-12.21±6.84
FLL	37.65±5.09**	35.94±5.76**	-3.96±0.75**	0.61±0.76	-30.89±15.2*	-21.12±16.98
FLW	1.94±0.13**	2.46±0.17**	-0.06±0.05	0.05±0.05	-0.98±0.37**	-1.98±0.48**
TNGpP	72.15±32.93*	124.72±32.53**	5.81±3.06	9±5.15	432.85±94.28**	236.2±92.69*
NFGpP	70.91±32.67*	77.23±36.06*	1.5±2.78	4.39±5.68	379.76±92.02**	314.32±103.85**
SF	89.09±5.5**	76.02±4.73**	-1.96±0.96	-2.14±0.79*	3.79±14.68	41.4±12.56**
TGW	1.67±0.23**	1.52±0.19**	-0.05±0.02	0.03±0.03	-0.07±0.68	-0.26±0.55
SPGY	63.68±7.69**	52.01±10.08**	-3.5±0.77**	-2.63±0.6**	-79.65±20.56**	-63.49±28.35*
Epistasis (Cross 1)	duplicate	duplicate	duplicate	-	duplicate	-
Epistasis (Cross 2)	duplicate	duplicate	-	-	-	-

Table 4.Continued...

	[i]		[j]		[l]	
Population	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**	**Cross 1**	**Cross 2**
DFF	-8.9±2.24**	-21.05±2.04**	3.08±0.94**	0.99±1.03	9.24±3.75*	30.43±3.36**
PH	-44.56±18.55*	39.23±8.05**	1.31±9.13	-2.95±5.72	83.51±36.81*	-63.13±18.56**
NPT	-29.79±9.2**	6.15±6.65	-0.17±4.5	-3.25±4.2	62.46±19.47**	15.15±14.45
TNT	-20.05±8.73*	1.9±5.87	-3.27±4.13	-3.94±3.72	43.34±18.18*	24.82±12.69
PL	-7.58±3.5*	-4.53±2.12*	1.38±1.75	0.05±1.32	15.77±6.95*	6.59±5.39
FLL	-13.38±5.03**	-9.1±5.71	8.13±2.35**	-1.4±2.83	20.24±13.74	14.06±11.83
FLW	-0.38±0.12**	-0.91±0.16**	0.02±0.07	-0.26±0.09*	0.8±0.33*	1.13±0.35**
TNGpP	99.54±32.79**	50.28±32.12	8.02±15.17	-38.92±15.06*	-273.5±64.11**	-130.72±66.45
NFGpP	77.09±32.55*	79.87±35.61*	8.17±14.49	-37.14±17.15*	-228.92±63.09**	-174.96±72.74*
SF	-2.87±5.42	13.82±4.67**	0.72±2.32	0.23±1.96	2.81±9.45	-23.3±8.11**
TGW	-0.22±0.23	-0.09±0.19	0.01±0.11	-0.09±0.09	-0.03±0.46	0.25±0.38
SPGY	-37.33±7.65**	-24.18±10.06*	-14.63±3.11**	-9.07±4.38	55.62±13.2**	51.12±20.15*
Epistasis (Cross 1)	duplicate	duplicate	duplicate	-	-	duplicate
Epistasis (Cross 2)	duplicate	-	duplicate	duplicate	-	duplicate

* & ** Significance at 0.05 and 0.01 probability levels, respectively; m- Residual; [d]- Additive; [h]- Dominance; [i]- Additive × Additive; [l]- Dominance × Dominance; (-)- Absence of epistasis.

by Ganapati *et al.* (2020), Subbulakshmi *et al.* (2016), Solanke *et al.* (2019), Kumar *et al.* (2017). Simple pedigree selection can effectively exploit the additive component of variation. Meanwhile, mass selection for multiple early generations, aiming to enhance the heterozygous population by adjusting the frequencies of desirable genes through single-plant selection, represents an economical and efficient approach. However, the presence of non-fixable components (h, j and l) in conjunction with a duplicate type of epistasis might impede progress in trait improvement through early-generation selection. In such scenarios, the progeny selection process may be postponed to later generations.

The dominant genetic effect was observed to significantly influence traits such as days to fifty per cent flowering, plant height, number of productive tillers, panicle length, flag leaf length, and flag leaf width with negative significance and the number of grains per panicle, the total number of grains per panicle and single plant yield showed positive significance observed in Cross 1. Likewise, in Cross 2 days to fifty per cent flowering, flag leaf width and single plant grain yield showed negative significance, whereas plant height, number of grains per panicle, number of filled grains per panicle and spikelet fertility observed positive significance. These results align with earlier studies that reported dominance genetic effects on the number of productive tillers per plant and panicle length, as demonstrated by Das *et al.* (2022), Singh and Patel (2020), Solanke *et al.* (2019) and Ehirim, B. O *et al*. (2023).

Positive signs of the dominance x dominance (l) effect were observed in Cross 1 for traits such as days to fifty per cent flowering, plant height, number of productive tillers per plant, total number of tillers, panicle length, flag leaf width and single plant yield. In the case of Cross 2, days to fifty per cent flowering, flag leaf width and single plant yield showed positive significance. The negative signs of the dominance x dominance (l) effect in cross 1were observed in the number of grains per panicle and number of filled grains per panicle, while, plant height, number of filled grains and spikelet fertility were observed in Cross 2. The influence of non-fixable gene effects in the expression of these traits in the crosses suggest an opportunity for leveraging bi-parental mating through recurrent selection or adopting the population improvement concept as an alternative to traditional methods.The additive x additive effect (i) was positively significant with the number of grains per panicle, number of filled grains per panicle in Cross 1, and with plant height, number of filled grains and spikelet fertility in Cross 2. This suggests a more favorable response to selection pressure in the population for these traits. Employing a cyclic breeding method in these crosses could facilitate improvement, wherein desirable recombinants are selectively bred and intercrossed with favorable genes, ultimately synthesizing an elite population. Similar outcomes were reported by Muthuvijayaragavan and Murugan (2019), Das *et al.* (2022), Chamundeswari *et al.* (2013).

In the current study, significant additive and additive x additive epistasis were observed in Cross 1 for traits such as, days to fifty per cent flowering, total number of tillers, panicle length, flag leaf length, flag leaf width and single plant yield. In Cross 2, similar observations were made for days to fifty per cent flowering and single plant yield. These findings align with those reported by Ganapati *et al.*(2020), Das *et al.* (2022), Ehirim, B. O *et al.* (2023). Furthermore, duplicate epistasis was identified in most of the traits in both crosses, presenting a challenge in stabilizing genotypes with enhanced levels of trait expression. This challenge arises because the positive effect of one parameter tends to be nullified by the negative effect of another parameter.

The results from the six-parameter model revealed that, apart from the significance of mean (m), additive (d) and dominance (h) effects, all three digenic interactions such as additive x additive (i), additive x dominance (j) and dominance x dominance (l) were significant for the traits, days to fifty per cent flowering and single plant yield in both the crosses. Given the opposite signs of dominance (h) and dominance x dominance (l) for most traits in these two crosses, the nature of epistasis was identified as duplicate. The observed duplicate epistasis suggests a potential delay in single-plant selection. However, strategies like biparental mating or diallel selective mating could be implemented for incorporating desirable genes into a unified genetic background. These findings propose the potential for improvement through later-generation selection combined with screening for submergence tolerance to develop high-yielding submergence-tolerant varieties.

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https://doi.org/10.37992/2024.1501.007