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# Gene action of yield and yield contributing traits of submergence tolerant rice (*Oryza sativa* L.) in Bangladesh



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# **Abstract**

**Background:** Trait selection for rice production under submergence stress and its effective investigation are important for sustainable improvement. Gene action is a principle, measures allelic interactions for traits that express the nature of phenotypic behavior, and leads to perfect selection of traits.

**Aim:** This study was aimed to measure the allelic interactions of genes responsible for different quantitative traits which have strong association with yield of submergence tolerant rice.

**Results:** In this study, generation mean analysis has been performed for yield-contributing traits and found that plant height, no. of primary branches panicle<sup>-1</sup>, no. of secondary branches panicle<sup>-1</sup>, no. of filled grain panicle<sup>-1</sup>, no. of grain panicle<sup>-1</sup> and dominant effects for yield hill<sup>-1</sup>, yield tiller<sup>-1</sup>, and 1000 grain weight have association to yield, governed by additive gene effect. In respect of epistatic effect, duplicate epistasis was predominant for all the traits except panicle length. From a heritability view, plant height, no. of primary branches panicle<sup>-1</sup>, and no. of grain panicle<sup>-1</sup> showed high heritability and plant height, panicle length, no. of filled grain panicle<sup>-1</sup>, and 1000 seed weight which found high genetic advance.

**Conclusion:** It could be concluded that days to heading is an important trait that needs to be investigated in every generation and days to maturity and panicle length that needs to be selected in early segregating generation.

Key words: Generation mean analysis, Rice, Genetic advance, Epistasis, Gene action

# Introduction

Rice (*Oriza sativa* L.) is the staple food for nearly two thirds of the world's population. In 2010, China, India, Indonesia, Bangladesh, Vietnam, and Myanmar alone provided more than 75% of the world's total rice production (Elke and Emanuele 2014). In South Asia, 80% of rice is produced by marginal farmers. They suffered a wide range of biotic and abiotic stresses. Among them, submergence is the most widespread abiotic stress for growth and development of rice plant (Soumya et al. 2017). Rice varieties having submergence tolerance showed low to high survival capability against deep condition, for

example 10 or more days particularly in shallow water up to 40 cm depth in India and up to 50 cm depth in International Rice Research Institute, respectively (Mohanty et al. 2000). Flash floods are highly unpredictable and may occur at any growth stage of the rice crop, which may result in yield loss up to 100% depending on different climatic and agronomic factors (Setter et al. 1997). Yield is a complex and polygenic trait which is a final product affected by the large numbers of its component traits (Renukadevi and Subbalakshmi 2006). So, selection of genetically inherited traits for submergence is very important.

The genetic improvement primarily depends on the effectiveness of selection among progenies that differ in genetic value. The additive and dominant effects and their interactions are known as gene actions and are reported to be associated with breeding value (Falconer

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1989). Genetic analysis using generation mean analysis (GMA) has been used to estimate the gene actions controlling the quantitative traits, and knowledge of additive, dominance, and epistatic effects would benefit breeders in designing the most appropriate breeding approaches for developing a new variety. GMA consists of six population/generations, i.e., parent 1 (P1), parent 2 (P2), first filial (F1), second filial generation (F2), first filial of the backcross with recurrent parent 1 (BC1), and first filial of the backcross with recurrent parent 2 (BC2), for estimating gene actions and linkages. GMA has been used to study the gene effects of quantitative traits, for example in chickpea (Deb and Khaleque 2009), cotton (Abd-El-Haleem et al. 2010), barley (Eshgi and Akhundova 2009), and corn (Azizi et al. 2006). As for rice, it was exploited for cooking characteristics which is controlled by additive and dominance gene actions for the selected crosses involving aromatic rice (Nikita et al. 2019). Additive and dominance gene actions were reported as important for other morplant heightological and agronomic traits such as plant height, days to flowering, panicle number per hill, panicle length, and grain yield per plant. In context of submergence tolerance of Indica rice, GMA was not yet used to estimate the gene action of quantitative traits (Nikita et al. 2019). Therefore, this study aimed to understand the gene actions of submergence tolerance traits in selected crosses and parents with different characteristics and utilize the information of gene actions that facilitate rice breeding programs in terms of illustrating the appropriate breeding methods and selection process for submergence tolerance.

# Materials and methods

# Plant materials, approach, and experimental designs

The study was carried out at the Department of Genetics and Plant Breeding research field of Bangabandhu Sheikh Mujibur Rahman Agricultural University, Bangladesh, during the three consecutive growing seasons of 2016, 2017, and 2018, respectively. The crossing was accomplished in 2016 between a submergence tolerance FR 13A as a recurrent parent and local variety Chamara as donor parent. In the 2017 growing season,  $F_1$  seeds (FR 13A  $\times$ Chamara) were planted, and crosses were accomplished with both parents to obtain BC<sub>1</sub> and BC<sub>2</sub> generations. Therefore, the six populations, P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub>, and BC<sub>2</sub>, were planted in the 2018 growing season. The experiment was arranged in a randomized complete block design (RCBD) with three replications. Seventy-five plants from each P<sub>1</sub>, P<sub>2</sub>, and F<sub>1</sub>; and 100 plants from each BC<sub>1</sub> and BC2; and 200 plants from the F2 population per replication were taken at random for subsequent measurements of the following traits: days to heading, days to maturity, plant height, internode length, no. of tillers hill<sup>-1</sup>, panicle length, no. of primary branches panicle<sup>-1</sup>, no. of secondary branches panicle<sup>-1</sup>, no. of grain panicle<sup>-1</sup>, no. of unfilled grain panicle<sup>-1</sup>, yield hill<sup>-1</sup>, yield tiller<sup>-1</sup>, and 1000 grain weight.

# Statistical analysis

The analysis of variance (ANOVA) was carried out through Statistics10. To confirm the data adequacy, Mather's (1949) scaling test (A, B, C, and D) was performed for confirmation of additive-dominance model reported by Singh and Chaudhary (2012).

$$\begin{split} A &= P_1 + F_1 - 2BC_1 = 1/2([i] - [j] + [l]). \quad C &= P_1 + P_2 + 2F_1 - 4F_2 = 2[i] + [l] \\ B &= P_2 + F_1 - 2BC_2 = 1/2([i] + [i] + [l]). \quad D &= 2F_2 - BC_1 - BC_2 \end{split}$$

Estimates of various gene effects, allelic interaction, and their test of significance were computed by a six-parameter model of Hayman (1958) and Jinks and Jones (1958) by the following equations:

$$\begin{split} m &= Mean = F_2 \\ d &= \text{Additive effect} = \text{BC}_1 \text{-BC2} \\ h &= \text{Dominance effect} = 2\text{BC}_1 + 2\text{BC}_2 \\ &\quad + \text{F}_1 \text{-4F}_2 \text{-} (1/2) \text{P}_1 \text{-} (1/2) \text{P}_2 \\ i &= \text{Additive} \times \text{Additive genetic interaction} \\ &= 2\text{BC}_1 + 2\text{BC}_2 \text{-4F}_2 \\ j &= \text{Additive} \times \text{Dominance genetic interaction} \\ &= 2\text{BC}_1 \text{-P}_1 \text{-2BC}_2 + \text{P}_2 \\ l &= \text{Dominance} \times \text{Dominance genetic interaction} \\ &= \text{P}_1 + \text{P}_2 + 2\text{F}_1 + 4\text{F}_2 \text{-4BC}_1 \text{-4BC}_2 \end{split}$$

# Results

# Mean analysis of different generations

Mean of different generations along with standard errors of different traits are shown in Table 1 which indicated that all traits except for days to heading, days to maturity, panicle length, primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, no. of filled grains panicle<sup>-1</sup>, no. of unfilled grain panicle<sup>-1</sup>, and yield tiller<sup>-1</sup> were partially dominant over lower parents. A similar result was also found by Rao et al. (2017), Singh and Singh (1974), Malik and Singh (1986), Bhadra and Dey (1985), and Malhotra (1983).

# Estimation of heterosis and inbreeding depression

From the progenies of FR13A  $\times$  Chamara, heterosis and inbreeding depression were calculated for 14 traits. The cross showed significant positive heterosis for all traits except primary branches, inter-node elongation, and unfilled grain panicle<sup>-1</sup>. Days to maturity showed significant but negative heterosis, while dominant (h) and

Table 1 Mean performance and standard error of yield-contributing traits in six populations of submergence rice

Traits	P <sub>1</sub>	P <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>
DTH	87.67 ± 0.15	78.83 ± 0.20	76.17 ± 0.08	75.83 ± 0.08	75.50 ± 0.13	78.50 ± 0.13
DTM	$113.80 \pm 0.05$	$106.77 \pm 0.07$	113.67 ± 0.15	95.33 ± 0.15	$88.43 \pm 0.13$	$88.83 \pm 0.20$
PH	127.10 ± 0.48	122.77 ± 0.23	139.74 ± 0.13	$151.00 \pm 0.09$	$142.13 \pm 0.11$	135.63 ± 0.25
INL	26.07 ± 0.11	$25.93 \pm 0.04$	26.87 ± 0.11	25.73 ± 0.09	21.60 ± 0.29	$24.83 \pm 0.15$
TH	$6.27 \pm 0.29$	$6.67 \pm 0.17$	$9.87 \pm 0.18$	$10.58 \pm 0.07$	$7.53 \pm 0.08$	$7.67 \pm 0.08$
PL	29.53 ± 0.10	26.61 ± 0.05	$27.73 \pm 0.07$	$28.58 \pm 0.14$	$28.40 \pm 0.11$	$28.37 \pm 0.07$
PBP	$11.40 \pm 0.05$	$10.00 \pm 0.05$	$10.07 \pm 0.03$	11.93 ± 0.08	$17.07 \pm 0.08$	$10.03 \pm 0.06$
SBP	$26.83 \pm 0.16$	$22.13 \pm 0.08$	$23.13 \pm 0.08$	$25.50 \pm 0.08$	$37.47 \pm 0.08$	$29.07 \pm 0.13$
FGP	$190.70 \pm 0.14$	132.90 ± 0.21	$142.67 \pm 0.18$	$147.37 \pm 0.17$	$142.63 \pm 0.09$	$123.27 \pm 0.08$
UFGP	82.00 ± 0.15	$32.03 \pm 0.17$	$30.13 \pm 0.12$	$33.90 \pm 0.16$	$21.40 \pm 0.05$	$47.17 \pm 0.09$
GP	$107.80 \pm 0.15$	$101.63 \pm 0.13$	$114.50 \pm 0.13$	$83.70 \pm 0.08$	121.18 ± 0.09	$75.97 \pm 0.16$
YH	$7.17 \pm 0.15$	$5.98 \pm 0.18$	$10.30 \pm 0.08$	$22.40 \pm 0.18$	$41.20 \pm 0.11$	$73.47 \pm 0.25$
YT	$1.17 \pm 0.03$	$1.02 \pm 0.04$	$1.06 \pm 0.06$	$2.06 \pm 0.04$	5.47 ± 0.05	9.59 ± 0.19
TGW	19.13 ± 0.08	$29.80 \pm 0.05$	$34.17 \pm 0.04$	$20.60 \pm 0.17$	$20.67 \pm 0.09$	$30.23 \pm 0.19$

DTH days to heading, DTM days to maturity, FGP no. of filled grain per panicle, GP no. of grain per panicle, INL internode length, P parents, BC backcross, PBP no. of primary branch per panicle, PH plant height, PL panicle length(cm), SBP no. of secondary branches per panicle, TGW thousand grain weight, TH no. of tiller per hill, UFGP no. of unfilled grain per panicle, YH yield per hill, YT yield per tiller

other non-allelic components were found to have non-significant interaction causing dispersion of the incomplete dominance. Days to heading showed significant but negative heterosis though the traits were significantly influenced by additive and additive  $\times$  dominance effect. Once again, it indicated that dominance  $\times$  dominance gene effects have predominant role for controlling the plant height. The results of heterosis are presented in Table 2.

Significant and positive heteroses were also observed in plant height, tiller hill<sup>-1</sup>, yield hill<sup>-1</sup>, and grain panicle<sup>-1</sup> but component h was non-significant, while additive  $\times$  dominance interactions were important for both the traits. These traits were significantly influenced by additive x additive as well as additive x dominance gene action. Dominance x dominance gene action was also influenced for days to maturity, while in both cases h was insignificant.

Regarding panicle length, additive gene effect and complementary epistasis have been recorded having reinforcing effect and can easily be exploited for developing fixed lines. Significant inbreeding depression was found for days to maturity, plant height, filled grain panicle<sup>-1</sup>, no. of unfilled grain panicle<sup>-1</sup>, no. of grain panicle<sup>-1</sup>, yield hill<sup>-1</sup>, and 1000 grain weight.

# The scaling test adequate to the additive-dominance model:

The days to heading and unfilled grain panicle<sup>-1</sup> were positively significant for scale B. However, A, B, and C were negative highly significant, but scale D were positively highly significant for days to maturity. Scales A, B, C, and D were positively for plant height. Scale A and C were positive and D was negatively significant for primary branches. Scale D was positively highly significant for inter-node length and grain panicle<sup>-1</sup>. Scales A, B,

**Table 2** Estimates of heterosis as deviation from mid-parent (MP) and better parent (BP) and inbreeding depression (%) for yield and contributing traits

Traits	Heterosis	(%)	Inbreeding depression (%)	Traits	Heterosis (%)		Inbreeding depression (%)
	BPH	MPH			BPH	MPH	
DTH	3.38	8.51	00.43	SBP	13.78	5.51	10.23
DTM	6.46	3.07	16.13	FGP	6.21	9.34	26.89
PH	13.82	11.85	08.06	UFGP	5.93	47.15	12.50
INL	3.59	3.33	04.22	GP	25.18	11.83	03.29
TH	48	52.58	07.26	YH	43.72	56.61	117.48
PL	6.16	1.28	03.14	YT	9.19	2.85	96.44
PBP	11.69	5.92	18.54	TGW	14.65	39.65	39.71

and C were positively significant in secondary branches panicle<sup>-1</sup>, yield hill<sup>-1</sup>, and yield tiller<sup>-1</sup>. Estimated significant deviation from zero indicated the presence of nonallelic interaction for the above traits. Table 3 shows results of scaling test.

### Gene action

Six-parameter model (i.e., additive, dominance and interactions) identified best-fit models with significant non-allelic interactions for all traits and the estimates of different genetic components. The mean effects were highly significant for all traits (Table 4).

The estimates d (additive component) were positively highly significant for plant height, primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, no. of unfilled grain panicle<sup>-1</sup>, and no. of grain panicle<sup>-1</sup> but days to heading was negatively highly significant.

The estimates h (dominance component) were significant in primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, no. of grains panicle<sup>-1</sup>, yield hill<sup>-1</sup>, yield tiller<sup>-1</sup>, and 1000 grain weight. The estimates i (additive  $\times$  additive) were positively highly significant for primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, no. of grains panicle<sup>-1</sup>, no. of unfilled grains panicle<sup>-1</sup>, yield hill<sup>-1</sup>, yield tiller<sup>-1</sup>, and 1000 grain weight. The estimates i were insignificant for rest of the studied traits.

The estimates j (additive × dominance) were positively highly significant for plant height, primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, and filled grains panicle<sup>-1</sup>. The j showed negatively highly significant for days to heading and days to maturity.

The estimates l (dominance  $\times$  dominance) showed positively significant for days to heading, days to maturity, plant height, inter-node length, tiller hill<sup>-1</sup>, primary branches panicle<sup>-1</sup>, no. of grains panicle<sup>-1</sup>, and no. of unfilled grains panicle<sup>-1</sup>. The estimates l were shown to be insignificant for rest of the traits.

The estimates of components of genetic variance indicated that duplicate epistatic (D; 15:1) interaction (h and l having opposite sign) was predominant for all the traits except panicle length which showed complementary epistasis (C; 9:7) (h and l having same sign).

# Heritability and genetic advance

Broad-sense heritability was relatively high for all traits and ranges from 63.90 to 93.52% (Table 5). Narrow-sense heritability 55.44%, 53.11%, and 43.66% for days to heading, yield per hill, and filled grain per panicle, respectively, and the lowest narrow sense heritability 17.54% was observed for panicle length. Considerable genetic advance was found 7.94%, 2.72%, 1.78%, 0.70%, 1.56%, and 1.18% for plant height, no. of tiller per hill, days to heading, panicle length, no. of grain panicle<sup>-1</sup>, and 1000 grain weight, respectively.

# Discussion

Analysis of heterosis revealed that most of the traits show duplicate type of epistasis. Duplicate epistasis is non-fixable and which cannot be exploited through the general breeding procedures of self-pollinated crops (Bhadra and Dey 1985). Even, some traits were not similar to the expected heterosis indicating the inadequacy of the model used by Mather and Jinks (1971). Positive

Table 3 Scale estimation of different traits in submergence tolerant rice

Character	Scale effects ± Standard error							
	A	В	С	D				
DTH	$-12.833 \pm 0.307$	2.000 ± 0.333***	$-15.500 \pm 0.414$	$-2.333 \pm 0.236$				
DTM	$-50.600 \pm 0.308^{**}$	$-42.767 \pm 0.427^{**}$	$-66.567 \pm 0.672^{**}$	13.400 ± 0.381**				
PH	17.430 ± 0.545***	$8.763 \pm 0.562^{**}$	$74.660 \pm 0.702^{**}$	24.233 ± 0.328**				
INL	$-9.733 \pm 0.482$	$-3.133 \pm 0.322$	$-2.799 \pm 0.394$	$5.033 \pm 0.317^{**}$				
TH	$-1.067 \pm 0.318$	$-1.200 \pm 0.268$	$9.667 \pm 0.517^{**}$	$5.967 \pm 0.182^{**}$				
PL	$-0.447 \pm 0.243$	$2.407 \pm 0.157^{**}$	$2.759 \pm 0.569^{**}$	$0.399 \pm 0.295$				
PBP	12.667 ± 0.168**	$0.000 \pm 0.143$	$6.200 \pm 0.329^{**}$	$-3.233 \pm 0.188^{**}$				
SBP	24.967 ± 0.211**	12.867 ± 0.282**	$6.767 \pm 0.375^{**}$	$-15.533 \pm 0.217$				
FGP	20.033 ± 0.264**	$-64.200 \pm 0.290$	$-103.633 \pm 0.408$	$-29.733 \pm 0.201$				
UFGP	$-69.333 \pm 0.221$	32.167 ± 0.279**	$-38.700 \pm 0.726$	$-0.767 \pm 0.338$				
GP	$-48.100 \pm 0.275$	$-29.033 \pm 0.303$	$-19.467 \pm 0.795$	28.833 ± 0.364**				
YH	64.933 ± 0.266**	$130.647 \pm 0.546^{**}$	55.847 ± 0.769**	$-69.867 \pm 0.451$				
YT	$8.748 \pm 0.097^{**}$	17.147 ± 0.283**	3.976 ± 0.161**	$-10.959 \pm 0.164$				
TGW	$0-11.967 \pm 0.214$	$-3.500 \pm 0.386$	$-34.867 \pm 0.689$	$-9.700 \pm 0.401$				

<sup>\*\*</sup> indicates significant at 1% level of significance

Table 4 Estimation of component of generation means for different traits in submergence tolerant rice

Traits	Gene effect ± standard error						
	[m]	[d]	[h]	[/]	[/]	[/]	
DTH	75.83 ± 0.075**	$-3.00 \pm 0.183^{**}$	$-2.47 \pm 0.493$	4.67 ± 0.471**	$-7.47 \pm 0.220^{**}$	6.17 ± 0.839**	D
DTM	95.33 ± 0.149**	$-0.40 \pm 0.238$	$-23.47 \pm 0.778$	$-26.80 \pm 0.762$	$-3.97 \pm 0.241$	120.17 ± 1.163**	
PH	$151.00 \pm 0.093^{**}$	$6.50 \pm 0.270^{**}$	$-33.66 \pm 0.721$	$-48.47 \pm 0.567$	4.33 ± 0.381**	22.27 ± 1.289**	
INL	25.73 ± 0.079**	$-3.23 \pm 0.274$	$-9.20 \pm 0.645$	$-10.07 \pm 0.634$	$-3.30 \pm 0.280$	22.93 ± 1.168**	
TH	10.58 ± 0.071**	$-0.13 \pm 0.114$	$-8.53 \pm 0.424$	$-11.93 \pm 0.365$	$0.07 \pm 0.164$	14.20 ± 0.691**	
PL	28.58 ± 0.134**	$0.03 \pm 0.122^*$	$-1.16 \pm 0.597$	$-0.79 \pm 0.590$	$-1.43 \pm 0.135$	$-1.16 \pm 0.750$	C
PBP	11.93 ± 0.079**	$7.03 \pm 0.102^{**}$	5.83 ± 0.379**	$6.47 \pm 0.376^{**}$	$6.33 \pm 0109^{**}$	$-19.13 \pm 0.525^{**}$	D
SBP	25.50 ± 0.077**	8.40 ± 0.152**	29.72 ± 0.447**	31.07 ± 0.434**	$6.05 \pm 0.167^{**}$	$-68.90 \pm 0.714$	
FGP	83.70 ± 0.068**	45.20 ± 0.148**	69.25 ± 0.429**	59.47 ± 0.402**	42.12 ± 0.179**	$-15.30 \pm 0.718$	
UFGP	33.90 ± .161**	$-25.77 \pm 0.104$	$-25.35 \pm 0.698$	1.53 ± 0.678*	$-50.75 \pm 0.157$	35.63 ± 0.837**	
GP	$147.37 \pm 0.172^{**}$	19.37 ± 0.120**	76.80 ± 0.756	$-57.67 \pm 0.728$	$-9.53 \pm 0.172^{**}$	134.80 ± 0.929	
YH	22.40 ± 0.179**	$-32.27 \pm 0.275$	143.46 ± 0.913**	139.73 ± 0.902**	$-32.86 \pm 0.299$	$-335.31 \pm 1.342$	
YT	2.06 ± 0.037**	$-4.14 \pm 0.146$	21.89 ± 0.329**	21.99 ± 0.327**	$-4.20 \pm 0.149$	$-47.81 \pm 0.607$	
TGW	20.60 ± 0.169**	$-9.57 \pm 0.213$	29.10 ± 0.803**	19.40 ± 0.801**	$-4.23 \pm 0.219$	$-3.93 \pm 1.098$	D

m mean, d additive effect, h dominant effect, i additive-additive interaction, j additive-dominant interaction, l dominant-dominant interaction, C complimentary epistasis. and D duplicate epistasis

better parent heterosis was observed by Swindell and Poehlman (1978) for plant height, 1000 grain weight, and no. of grains panicle<sup>-1</sup>. These results confirm the findings of Gawas et al. (2007).

On the other hand, the values of scales A, B, and C were non-significant for the traits, internode length, no. of grain hill<sup>-1</sup>, and 1000 grain weight. Non-significant values of A, B, and C indicated the adequacy of additive-dominance model for the inheritance of the above traits.

**Table 5** Estimates of broad (h<sup>2</sup>b) and narrow (h<sup>2</sup>n) sense heritability and genetic advance for yield-contributing traits

Traits	$h^2b$ (%)	h²n (%)	( <b>Δ</b> g%)
DTH	87.91	55.44	1.78
DTM	84.75	34.52	0.66
PH	82.6	43.59	7.94
INL	75.3	32.29	0.15
TH	72.03	29.34	2.72
PL	80.16	17.54	0.7
PBP	67.1	32.14	0.42
SBP	66.66	31.52	0.27
FGP	83.09	43.66	1.56
UFGP	87.09	32.12	0.14
GP	63.9	47.13	0.05
YH	75.22	53.11	0.52
YT	93.52	38.06	0.03
TGW	79.82	39.68	1.18

# Nature of gene action

Results shown in Table 5 revealed that the additive component d > h was significant for all the traits except for secondary branches, indicating the predominant role of additive type of gene action for regulating the traits. The interaction parameters (i, j, and 1) for panicle length was smaller than their standard errors and non-significant. Therefore, there was no evidence of non-allelic interaction for panicle length which agreed with the results from the scaling tests. Similar type of results for tiller plant<sup>-1</sup> was reported by Murty et al. (1976). A similar gene action for inter-node length, no. of grain panicle<sup>-1</sup>, and yield plant<sup>-1</sup> was reported by Sultan et al. (2014) and Patil et al. (2006). Singh and Singh (1972), Reddy and Sreeramulu (1982), and Wilson et al. (1985) have agreed with these findings.

For the remaining traits like, panicle length, plant height, days to heading, days to maturity, tiller hill<sup>-1</sup>, primary branches panicle<sup>-1</sup>, secondary branches panicle<sup>-1</sup>, no. of unfilled grains panicle<sup>-1</sup>, and no. of grains panicle<sup>-1</sup> at least one of the three (i, j, and l) interaction parameters were significantly different from zero. This was again complete in agreement with scaling tests.

The component j was significant and negative for days to heading and d > h. Such results indicated additive type of gene effects for the character and the presence of additive  $\times$  dominance for days to heading and dominance  $\times$  dominance as well as additive  $\times$  dominance interaction for inter-node length. Inheritance of days to heading was associated with both additive and non-additive effects mostly with additive effects in the studies

<sup>\*\*</sup> indicates significant at 1% level of significance

of Iftekharuddaula et al. (2008), Rao et al. (1984), and Wilson et al. (1985). They also noted significant additive × dominance interaction in one cross. Murty et al. (1976) reported that additive × dominance gene action was involved in the expression of internode elongation. Dominance effects and duplicate epistasis played an important role in expression of internode elongation as reported by Rao et al. (1984).

Estimates of d were negatively significant and greater than h for days to heading. The values for i and j were positively significant. These results indicate additive, additive  $\times$  additive, and additive  $\times$  dominance gene action for the trait. Dominance  $\times$  dominance interaction was also observed for days to maturity. These results are in agreement with Abd-Allah (2000) and Abd El-Aty et al. (2002) for days to heading.

The estimate d was positively significant, and the estimate j was negatively significant for grain panicle<sup>-1</sup>. The higher estimates of h over d for grain panicle<sup>-1</sup> indicated dominance effect of the character and presence of additive  $\times$  dominance interaction. Luthra et al. (1979) observed that partial dominance was responsible for grain panicle<sup>-1</sup>. These results also confirm the findings of Bhadra and Akhtar (1993).

From the overall results, it is clear that considerable amount of genetic variability was available for yield and its component traits in the cross. The magnitude of the different genetic component was unequal for different traits. However, the displaying significant additive effects can be used in future genetic improvement programs by capitalizing this variance. Significant additive effect along with complementary epistasis as recorded in primary branches panicle<sup>-1</sup> indicated the possibility of exploiting the combined variability through the evolution of the parents.

# Heritability and genetic advance (GA)

The broad-sense heritability is high for all the traits. Days to heading showed high (> 50%) narrow sense heritability. High narrow sense heritability with moderate GA observed in days to heading indicated the additive effects. The traits with usually high heritability particularly with narrow sense heritability would give high response to selection.

High narrow sense heritability with high genetic advance shows better selection in early segregating generations leading to substantial improvement of the character. In the present study, days to heading would give better response to selection. These results indicated the predominant role of additive effects and the prospect for improving short days to heading and higher yield plant<sup>-1</sup>. Similar results were previously reported by Panwar et al. (1997), Tripathi et al. (1999), Sarawgi et al. (2000), and Hammoud (2004).

Although the traits panicle length and days to maturity showed high broad-sense heritability, low narrow sense heritability, and genetic advance, suggesting that these traits were predominantly controlled by non-additive gene action and selection for these traits would give good response in early segregating generation. High broad-sense heritability but poor narrow sense heritability might be due to presence of non-allelic interaction and sampling error for these traits. Johnson et al. (1955) and Rita Bisne and Sarawji (2009) reported that heritability estimates along with genetic advance upon selection were more valuable than the former alone in predicting the effect of selection.

Furthermore, it could be recognized that heritability estimates in broad-sense were high for all studied traits, while in narrow sense were moderate to high. These estimates are in the same line with those for different types of genetic variance. This turn leads to conclusion that these traits could be improved by the traditional breeding methods and selection could be effective mostly in early segregating generation. This was proved by entire values of the predicted genetic advances were low in most cases. Similar findings were also reported by Shivani and Reddy (2000), Gannamani (2001) and Sao (2002).

High heritability with high genetic advance indicates the control of additive gene and selection may be effective for those traits.

# Conclusion

It may be concluded that days to heading is an additiveadditive as well as additive-dominant control character and selection is important as per emergence in submergence tolerant rice Beside days to maturity and panicle length also important and selection will be effective in early segregating generation.

# Abbreviations

A, B, C, and D: Different scales of scaling test; BC: Backcross; d: Additive component; GA: Genetic advance; GMA: Generation mean analysis; h: Dominant component; i: Additive-additive interaction; j: Additive-dominant interaction; l: Dominant-dominant interaction; P: Parents

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# Authors' contributions

Conceptualization, data curation, writing, original draft preparation was done by RKG. Writing the review and the editing were done by MGR, US, AS, and MF. Supervision was done by MGR. Data analysis and visualization was performed by RKG and MGR. All authors revised, read, and approved the final manuscript.

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# Availability of data and materials

The data sets generated and/or analyzed during the current study are included in this study.

# Ethics approval and consent to participate

Not applicable

# Consent for publication

Not applicable

### Competing interests

The authors declare that they have no competing interests.

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